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STRUCTURAL AND ECOFUNCTIONAL BIODIVERSITY OF THE AMPHIPOD CRUSTACEAN BENTHIC TAXOCOENOSES IN THE SOUTHERN OCEAN

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ABSTRACT

Within the Antarctic Coastal and Shelf Ecosystem (ACSE) the peracarid crustaceans constitute the most diverse animal group in terms of species richness, life styles, trophic types, habitats and size spectra.

Using as a model group the amphipod crustaceans –in turn the richest taxon among peracarids with more than 850 species in the Southern Ocean– this study aimed at describing and evaluating the role of the biodiversity of the vagile macrobenthos in the structure and functioning of the Antarctic Coastal and Shelf Ecosystem.

In the framework of the SCAR EASIZ programme some key structural and ecofunctional aspects of biodiversity were investigated.

Different structural biodiversity features were characterised, namely faunal composition, geographic and bathymetric distribution, habitats and microhabitats, bio-ecological traits. Comparative investigations were performed in two EASIZ benthic reference sites, the eastern Weddell Sea Shelf Community in the High Antarctic, and the Maritime Antarctic sublittoral community of Admiralty Bay, King George Island. In the latter site, species abundance was followed during a complete year cycle, allowing to evidence strong seasonal variations.

Gammaridean amphipods appeared ubiquitous in the shelf communities of the eastern Weddell Sea. Their specific habitats were investigated by comparing catches from different collecting gears and by ethological observations in aquaria. Six main habitats were distinguished: endobenthic, epibenthic, hyperbenthic, benthopelagic, pelagic and cryopelagic. Among epibenthic species, which form the bulk of the fauna, three different strata were detected, together with four symbiotic microhabitats.

The ecofunctional role of biodiversity was approached through the study of trophic diversity and trophodynamics and the significance of the unusually wide size spectra of the Antarctic amphipod crustaceans.

The trophic preferences of 40 dominant amphipod species of the eastern Weddell Sea benthos were deduced from both stomach content analyses and behaviour observations in aquaria. These combined 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. This feeding type diversity was corroborated by a preliminary analysis of the carbon and nitrogen stable isotopes. Among these eight types, no particular one was dominant. In the same way, types involving microphagy and macrophagy were equally represented. Predatory types (opportunistic or exclusive) accounted for 64% of the analyzed species, while scavenging types (facultative or obligate) accounted for 60%. The overlap suggests that many amphipod species have a wide dietary spectrum and are able to take advantage of different food resources.

The impact of the amphipod community on the eastern Weddell Sea shelf ecosystem was approached using feeding type results and biomass data. It appeared that sedimenting plankton particles, crustaceans and fish carrion were the 3 main items consumed by these crustaceans, accounting respectively for 10-27, 22-32, and 5-18% of the biomass. In addition, a extensive bibliographic investigation was performed in order to estimate the significance of amphipods in the diet of higher trophic levels: 33 species of invertebrates, 48 of birds, 101 of fish and 10 of mammals are regular consumers of amphipods, the share of this type of prey reaching up to 99%.

As the Antarctic amphipod size spectrum appeared to be the widest, after Baikal Lake, precise length data were gathered about more than 2,000 amphipod species from 15 sites world wide, from polar to tropical, and from marine to freshwater environments. It was shown that gigantism was not directly related to water temperature as often stated, but instead to oxygen availability. Maximum size increases dramatically with oxygen, modal size increases less, and minimum size does not increase at all.

To contribute to a more accurate assessment of the Southern Ocean biodiversity new synthetic tools for compiling, increasing, managing, and disseminating biodiversity information were developed, in particular a "Biodiversity Reference Centre", devoted to Antarctic amphipod crustaceans. It is comprised of comprehensive databases (organising the taxonomic, biogeographic and bio-ecological information), validated and operational reference collections, and a network of contributing specialists engaged in the taxonomic revision of the Antarctic amphipod fauna and the preparation of new conventional and electronic identification guides. These efforts will facilitate monitoring biodiversity in selected EASIZ reference sites.

Keywords: biodiversity, Crustacea, Amphipoda, benthos, habitats, trophodynamics, gigantism, Antarctic, Southern Ocean.

1. INTRODUCTION

Biodiversity, at its different integration levels –from genes to species and to ecosystems– is a critical element in the evaluation of the resilience of natural systems to environmental changes. In addition, understanding the patterns and processes of biodiversity in relation to production is of fundamental importance for the sustainable management of marine living resources.

Within the Southern Ocean, the Antarctic Coastal and Shelf Ecosystem (ACSE) is the most complex and productive, the richest in species, and likely the most sensitive to global environmental changes. In order to improve our understanding of the ACSE structure and dynamics within the perspective of the global environmental changes, the Scientific Committee on Antarctic Research (SCAR) recently elaborated the programme "*Ecology of the Antarctic Sea-Ice Zone*" (EASIZ). This programme pays a particular attention to these features that make the biology of this ice-dominated ecosystem so distinctive and to understand seasonal, inter-annual, and long-term changes. For a decade, EASIZ proposed an integrated study of the ice, water column and benthic sub-systems focussing on key processes and key organisms in key communities, in a network of study sites (SCAR, 1994).

In the ACSE, the Antarctic macrozoobenthos is characterized by a relatively high species diversity and richness. Several zoological groups, namely the sessile suspension-feeders such as Porifera and Bryozoa and the 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).

But the latitudinal and vertical patterns of the Antarctic macrobenthos biodiversity in a global perspective, its spatial and temporal variations and the causes of its particular traits remain poorly understood, as well as its roles in the structure and functioning of benthic systems, in particular their productivity and their resilience in the global warming and ozone depletion context.

In the Antarctic benthic communities, in the quasi-absence of decapods, the peracarid crustaceans (Amphipoda, Isopoda, Tanaidacea, Cumacea, Mysidacea,...) are by far the most species-rich group (De Broyer and Jazdzewski, 1996) and probably one of the most diversified in terms of trophic types, modes of life, habitats and size spectra, thus making a good model group for biodiversity studies. The most numerous, the amphipods, comprise more than 850 species in the whole Southern Ocean, 741 of which are benthic species. It was suggested that this high specific diversity could be related to a high heterogeneity of habitats and a variety of ecological roles which remain to be described and understood.

Amphipod habitats and distribution

Recent observations by still and video underwater cameras, coupled with analyses of benthos samples, have allowed a rather precise description of the variety of benthic assemblages from the eastern Weddell Sea shelf (e.g. Galéron et al. 1992; Gutt and Starmans 1998; Gutt and Schickan 1998). The continental shelf, to a depth of more than 600m, is colonised in many places by species-rich assemblages of abundant, diverse and multistratified suspension feeders, like sponges, bryozoans, cnidarians, hydrozoans, holothurians and crinoids. However, there is a gradient of species-rich assemblages of suspension feeders, mostly in the Kapp Norvegia region, to extremely poor detritus feeder’s assemblages, in the southernmost part of the Weddell Sea. The shelf bottom cover appears mostly patchy and ranges from a few percent to 100% of the bottom surface. The patchy, diverse and multistratified sessile benthos offers a high diversity of potential microhabitats to small vagile invertebrates.

Gammaridean amphipods, often collected in benthic samples, seem to be ubiquitous in the benthic communities of the eastern Weddell Sea where they constitute an often abundant and always diverse group (Voß, 1988; De Broyer and Klages, 1990; Klages, 1991; De Broyer et al., 1997, 1999; De Broyer et al., 2001). Some species also occur in the pelagic zone where they are usually outnumbered by hyperiid amphipods (*e.g.* Boysen-Ennen and Piatkowski, 1988). They have been so far exceptionally recorded in cryopelagic habitats, at the undersurface of the sea-ice (Günther and Dieckmann, pers. com.). The precise habitat has been described in details only for a few species (Klages, 1991; 1993; Kunzmann, 1992).

At King George Island (South Shetland Islands, Antarctic Peninsula), on the other hand, although the general distribution of the amphipod fauna has been investigated in Admiralty Bay by Jazdzewski et al.(1992), a detailed account of the species habitats and depth range is still lacking. Useful comparison can be made with the neighbouring sites of the Magellan region (De Broyer and Rauschert, 1999) or of Maxwell Bay and Fildes Strait where Rauschert (1991) studied the distribution of 103 amphipod species, not all of them occurring in Admiralty Bay.

Roles in trophic webs

Our knowledge of the ecofunctional, and specifically the trophodynamic role of the Antarctic amphipods is still very limited, despite the pioneering studies of Richardson (1977), Oliver and Slattery (1985), Slattery and Oliver (1986), Coleman ($1989_{a,b,c}$; $1990_{a,b}$), and Klages and Gutt ($1990_{a,b}$). 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 the feeding appendage morphology. Some necrophagous lysianassoids, however, show a particular mandibular structure, with a specialised molar process, which is a clear indication of their feeding mode (see *e.g.* De Broyer and Thurston, 1987).

The benthic crustaceans (comprising peracarids and natant decapods), despite their low biomass, are a dominant group in terms of energy fluxes in the Weddell Sea shelf ecosystem (Jarre-Teichmann et al.,1997). Amphipods, on the other hand, provide an important food resource to many Southern Ocean demersal and benthic fishes (*e.g.* Gon and Heemstra, 1990; Kock, 1992; Olaso et al., 2000), and to a number of benthic invertebrates (*e.g.* Dearborn, 1977; McClintock, 1994), seabirds (*e.g.* Jazdzewski, 1981; Rauschert, 1991; Cherel and Kooyman, 1998) and seals (*e.g.* Dearborn, 1965; Green and Burton, 1987).

Size spectrum and gigantism

Amphipods are known to have large sized representatives at high latitudes (Barnard, 1962; De Broyer, 1977), which makes the Antarctic amphipods size spectrum rather distinctive when compared to other marine areas. This higher frequency of big specimens, both at the species and the individual level has probably an impact on the ecofunctional role of the amphipod community as a whole.

Although well recognised, this polar gigantism is still poorly understood, due to a lack of thorough analyses. Suggested limiting factors are both physiological and ecological and include temperature, growth rate, resource availability, predation pressure and mortality (Atkinson,1996; Atkinson and Sibly,1997), with most of them tested only at the species level.

Biodiversity assessment tools

Comprehensive and easily accessible biodiversity information is crucial to an accurate assessment of the Southern Ocean biodiversity in the context of global change and of the requirements of the “Global Biodiversity Assessment” (UNEP, 1995). Although the high diversity of the Antarctic peracarid crustaceans and in particular the amphipods is well established, the level of knowledge of their taxonomy, distribution and ecology is insufficient to allow a accurate assessment of the Antarctic marine biodiversity (Barnard and Karaman, 1991; De Broyer and Jazdzewski, 1996). Synthetic biodiversity information tools and efficient identification tools are still totally lacking. In taxonomically difficult groups, these deficiencies handicap both the accurate studies of patterns, processes and role of biodiversity and the development of monitoring programmes linked to global changes. New technologies to describe, analyse and disseminate the biodiversity information allow today new developments (*e.g.* Pankhurst, 1991; Dallwitz et al., 1993; Schalk and Los, 1993; Olivieri et al. 1995).

The present paper reports the results of the research activities conducted in the framework of the Belgian Scientific Research Programme on the Antarctic (Phase IV) and focussing on the description and evaluation of the role of the biodiversity of the macrobenthic peracarid crustaceans in the structure and functioning of the Antarctic Coastal and Shelf Ecosystem (ACSE), in particular in two reference sites of the EASIZ programme (Admiralty Bay, King George Island, and the eastern Weddell Sea). Different structural aspects of the Antarctic peracarid biodiversity were investigated (faunal composition, spatial distribution, habitats…) as well as some ecofunctional features of this diversity (trophic diversity and trophodynamics, size spectra). In addition, the development of the "Biodiversity Reference Centre" for Antarctic Amphipoda including comprehensive databases is presented.

2. MATERIALS AND METHODS

2.1 Study sites

The reference benthic communities belong to two EASIZ Programme key-sites, for which a background knowledge already exists and from which important study material is available:

2.1.1 ***The Eastern Weddell Sea Shelf Community*** (Figure 1) in the High Antarctic (see e.g. Voß, 1988; Klages, 1991; Galéron et al., 1992; Gerdes et al., 1992), investigated with the collaboration of the Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI), Bremerhaven, Germany.

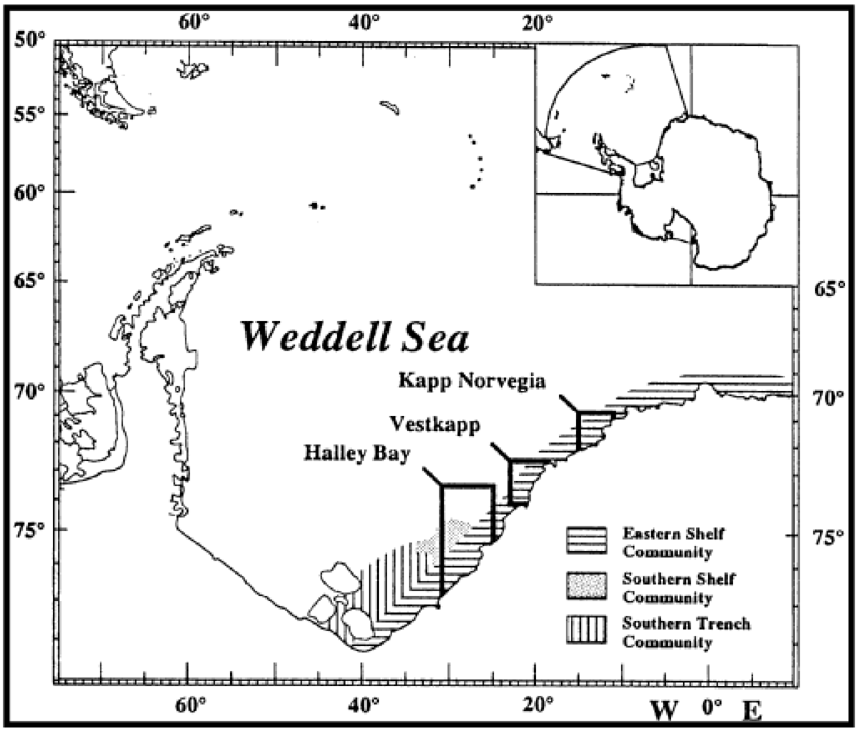


Figure 1: *Location of the sampling areas, Weddell Sea eastern shelf (from Voß, 1988).*

2.1.2. ***Admiralty Bay***, King George Island, West Antartic (Figure 2) (see *e.g*. Rakusa-Suszczewski, 1993, Jazdzewski and Sicinski, 1993), investigated in co-operation with University of Lodz, the Polish Academy of Sciences and the Brazilian Antarctic Programme.

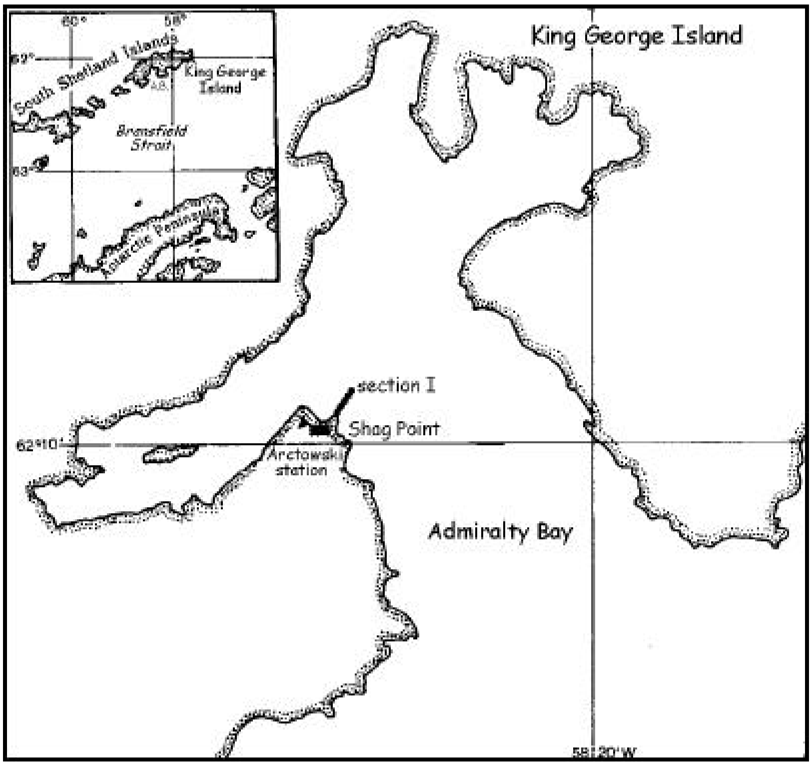


Figure 2: *Location of the main sampling area (section I), Admiralty Bay, King George Island (South Shetland Islands)*

2.2. Field sampling

2.2.1. ***Admiralty Bay:*** A large amount of peracarid samples were collected between 0 and 500 m by the Polish-Belgian and Brazilian-Belgian missions 1987-1994, by trawls, dredges, grabs, traps or by SCUBA diving. Two series of year-round monthly samples (1988 and 1993) simultaneously collected by traps and trawls at 4 different depths (15 to 300 m) as well as another series of quantitative upper sublittoral samples (1997) were used for studies on life history and seasonal and inter-annual variations of abundance and distribution.

One reference transect, from 0 to 300 m (corresponding to the section I in Figure 2), has been chosen to follow both qualitatively and quantitatively the temporal variations of spatial distribution but also the taxonomic composition, the relative abundance of species, and the population structure. An annual series of monthly samples taken simultaneously by trawl and trap at 15, 30, 50, 90 and 150 m was collected with the co-operation of University of Łódź. An additional series was taken at 0m at the sublittoral fringe of a stony beach which habitat consisted of cobbles lying on sand and gravel

2.2.2. ***Eastern Weddell Sea***: Amphipods were collected from benthic and suprabenthic samples taken 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). In total 130 catches provided about 80.000 specimens of amphipods from water depths of 60 to 2554 m. Collecting gears included Agassiz, benthopelagic and bottom trawls, dredges, epibenthic sledges, TV grabs, giant and multi– boxcorers, and baited traps (±48 h deployments). Most of the specimens were caught by trawls, the mesh size of which (15 mm) did not retain very small species.

2.3. Habitat characterisation

General information on Weddell Sea bottom habitats came from an interpretation of bottom pictures and ROV videos taken by J. Gutt (AWI) during *Polarstern* cruises and from published habitat descriptions (e.g. Ekau and Gutt, 1991; Gutt and Starmans, 1998; Farhbach et al., 1992; Galéron et al., 1992; Bathmann et al., 1991)

Characterisation of the amphipod habitats in the eastern Weddell Sea was based on a comparative analysis of catches taken by different gears: grabs and corers for the endobenthos (and in smaller extent epibenthos), trawls, dredges, sledges and traps for the epibenthos (and partly endobenthos), epibenthic sledges for the hyperbenthos and RMT (Rectangular Midwater Trawl) for the water column. Identification of microhabitats was based on aquarium and incidental catches observations during the cruises as well as on published records (Kunzmann, 1992).

Ethological observations (habitat choice, food detection and capture, mobility patterns) were performed on living specimens of more than 40 species kept in a cool container on board and afterwards in a cool laboratory at IRScNB, Brussels. Amphipods were maintained at –1°C (±1°C) in aquaria with volumes of 2 to 30 l. Aquaria were provided with different kinds of substrates, according to the known or suspected life style of studied species. A large aquarium with a “reconstituted natural bottom” (30 cm high) was used to study the species behaviour. This “reconstituted” bottom was composed of a mosaic of mixed (fine/coarse) sediment, of sponge spicule mat, of stones and of different common sessile organisms like sponges, cnidarians, hemichordates and bryozoans. Observations were qualitative and movements and position of amphipods in aquaria were checked at least twice a day for periods ranging from 10 to 56 days. Typical behaviours were video-recorded.

2.4. Trophic type determination and impact on the ecosystem

Feeding experiments were performed in the same aquaria as described above, 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 (the "amphipod juice").

Amphipod gut content analyses were performed 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 then 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 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: 75 to 100% of the volume is filled; 3: 50 to 75%; 2: 25 to 50%; 1: 0 to 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:

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

where *I(i)*, dimensionless, is the importance of item i in the diet of a given species, and *x* the number of specimens dissected;

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

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

Beside gut content analyses, a tentative approach was performed based on lipid class analyses (Graeve et al., 2001) and on natural stable isotope abundances (carbon and nitrogen) as tracers of amphipod position in the Weddell Sea food web (Nyssen et al., 2000). This abundance was measured by isotope-ratio mass spectrometry (IRMS) on muscle tissue of eight species representative of different trophic types. Isotopic ratios were expressed in δ notation as the proportional deviation (in parts per thousand, ‰) of the sample isotope ratio from that of an international standard according to the following formula:

$$\delta X = [(Rsample/Rstandard) - 1] * 1000 \qquad (3)$$

where X is ^{13}C or ^{15}N, R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The appropriate standards were Vienna-Peedee-Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.5 and 0.4‰ for carbon and nitrogen, respectively.

The trophic impact of these amphipod species on the eastern Weddell Sea ecosystem was approached by coupling feeding preferences and relative species abundance with the basic formula:

$$T(i) = \sum_{sp=1}^{x} \frac{\overline{N}_{sp}}{\overline{N}_{tot}} * R(i)_{sp} \qquad (4)$$

where $T(i)$ is the trophic impact on food item i (in %), x the number of analysed species, and $\overline{N}$ the mean number of individuals of a defined species (sp) and of all the x analysed species (tot) for all the samples of a cruise. Only classical benthic sampling devices (trawls and box-corers) were taken into account for evaluating $\overline{N}$, as baited traps for instance do not reflect the actual instantaneous abundance of a species in a defined sampling area.

In order to evaluate the feeding rates of Antarctic amphipods, some experiments were performed at King George Island with 4 different species. After sampling and identification, animals were placed in aquaria and starved out for periods of 9 to 15 days. During this fast, faeces and exuvia were removed daily. Despite animals did not receive any food, the lack of filter on the water circuit might allow suspended particulate matter to be provided in aquariums and this organic matter could eventually be used by amphipods. After starvation, a calibrated food item (piece of squid or alga) was introduced every day (during periods of 7 to 28 days) in the aquarium. Uneaten food was removed after 24 hours, rinsed with freshwater, drained on filter and dried at 60°C during 24 to 48 hours. Results are expressed as $g_{food\text{-}DW}.animal^{-1}.day^{-1}$ or $g_{food\text{-}DW}.g_{animal\text{-}DW}{}^{-1}.day^{-1}$. The latter expression, if better, does not allow to compare precisely the ingestion rates between species as they can differ in their skeleton calcification rate.

Egestion rates were also estimated after some feeding experiments. After the 24 hours nutrition period, animals were placed in nylon gauze baskets hung a few mm over the bottom of 25 ml jars. The basket mesh size (2 mm) allowed the faecal pellets to pass through, so avoiding coprophagy. Faeces collection was performed twice a day. Dissection of some individuals, after experiment, gave information about the emptiness of digestive system. As for food remains, faeces were dried at 60°C during 48 hours and weighed.

Finally, an attempt was made to evaluate the importance of amphipods as food source for the higher trophic levels in the Southern Ocean (invertebrates, fishes, birds and mammals). This approach was done by collecting information from an exhaustive survey of existing literature (>300 scientific papers).

2.5. Analyses of size spectra

Adult length from 1853 amphipod species were collected in the literature and from sampled material. These data produced detailed size spectra for 15 sites, including 5 from the Southern Ocean, from polar to tropical and marine to freshwater environments. Only benthic species were included and analyses were restricted to 250 m depth (mean continental shelf depth) except for Antarctic data, which include species to 500 m, as the continental shelf is depressed by the Antarctic icecap. Sites with less than 50 described species were not analysed.

Southern Ocean data (Magellanic region, Subantarctic Islands, South Georgia, West and East Antarctica) were compiled from several hundred references quoted in a check-list (De Broyer and Jazdzewski, 1993). Other data came from regional fauna lists: Madagascar (Ledoyer,1982), Mediterranean Sea (Ruffo, 1982-1998), Black Sea (Mordukhai-Boltovskoi et al., 1969), Caspian Sea (Birstein and Romanova, 1968), British Islands (Lincoln, 1979), Barents Sea (Bryagzin, 1997) and Lake Baikal (Bazikalova, 1945). This important data set also allowed the comparison of maximum size within species, thanks to the presence of many species in more than 1 of the 15 sites.

To approach gigantism, a focus on the right hand extreme of the size distribution of the regional taxocoenosis is needed. However, maximum size itself was not used because of potential sampling bias at some sites. Instead, the threshold size separating the 95% smallest species from the 5% largest (TS 95/5) has been used (allowing the use of the Titicaca Lake value, for which there is no available size spectrum).

2.6. Biodiversity database development

A comprehensive database on taxonomy, distribution and bio-ecology of the Southern Ocean amphipods was developed as a part of the “Biodiversity Reference Centre” for Antarctic amphipoda. The conception of the relational database was a four-steps’ operation. In the first step, the database objectives were defined *i.e.* to integrate all relevant information on the biodiversity of the Southern Ocean amphipods useful for an accurate assessment and monitoring of the Antarctic marine biodiversity, the management of specimen collections, the taxonomic revision of the fauna and the preparation of identification tools. Analysis of the logical database structure was the second step and aimed at identifying the different kinds of data and at building a model, a logical scheme that reflects, as close as possible, the actual investigations, including their inter-connections. The third step consisted in designing the forms, the queries and the reports that help the database users to encode, visualise and treat the data. Behind the design of these three main objects, the point was to identify precisely all the programming processes and procedures that answer to the flows of actions the application could encounter. The final step consisted in the technical and practical construction of the database according to the previous steps' requirements.

To perform the analyses and relational schemes two case tools were used: the software DBMain developed by the Computer Science Institute of the University of Namur (Anon., 1998) and the software Visio 5® (Microsoft®). The conceptual framework for this application relied on several sources: Fortuner (1993); the comprehensive model of biodiversity database named "Recorder 2000" (Copp, 1998); the study of the Committee on Computerization and Networking from the Association of Systematics Collections (ASC, 1992); the project “Data Faune Flore” from the University of Mons (Barbier, 1998); the Global Biodiversity Assessment recommendations (Olivieri et al., 1995); the Systematics Agenda 2000 recommendations (SA2000, 1994); the BIOTA program (Colwell, 1996); the Platypus program (http://www.ento.csiro.au/platypus/platypus.html); and the “Information Model for Biological Collections” (Berendsohn et al., 1996).

Developed in Microsoft® Access® 97, the database should move in a near future to an Oracle® data server and should be made accessible through the WWW.

3. RESULTS AND DISCUSSION

3.1. STRUCTURAL BIODIVERSITY

3.1.1. Composition of the peracarid taxocoenoses

3.1.1.1. Admiralty Bay. The detailed faunistic investigations on the Malacostraca allowed to identify so far 127 spp of amphipods, 59 spp of isopods, 14 spp of mysids, 13 spp of cumaceans and 12 spp of tanaids (Table I). Despite an important material still under analysis, the crustacean fauna of Admiralty Bay appears one of the best known in Antarctica. Several new species with ecological importance (Amphipoda: *Orchomenella n.sp., Eusirus n.sp., Oradarea n.sp., Schisturella n.sp.,…)* have been discovered and are under description. This rich material also allowed undertaking taxonomic revision of poorly known species.

***Table I**: Number of malacostracan taxa collected in Admiralty Bay*

	Species	Genera	Families	References
Leptostraca	2	2	1	De Broyer, unpubl.
Mysidacea	14	5	3	Konopko, unpubl.
Cumacea	13	7	4	Blazewicz and Jazdzewski, 1995
Tanaidacea	12	8	3	Blazewicz and Jazdzewski, 1996
Isopoda	59	29	19	Arnaud et al., 1986; Teodorczyk, unpubl.
Amphipoda	127	75	30	Jazdzewski et al., 1992; De Broyer and Jazdzewski, 1993; Munn, unpubl.
Euphausiacea	5	2	1	Stepnik, 1982
Decapoda	2	2	2	Arnaud et al., 1986

3.1.1.2. Eastern Weddell Sea. The EPOS, EASIZ I and EASIZ II *Polarstern* campaigns allowed to collect more than 80.000 specimens of amphipods which were identified to the genus or the species level. Due to this efforts, the gammaridean and caprellidean amphipod fauna from the Weddell Sea amounts today more than 237 spp among which about 50 species are considered new to science (before the *Polarstern* investigations only 26 amphipod spp were known from the Weddell Sea).

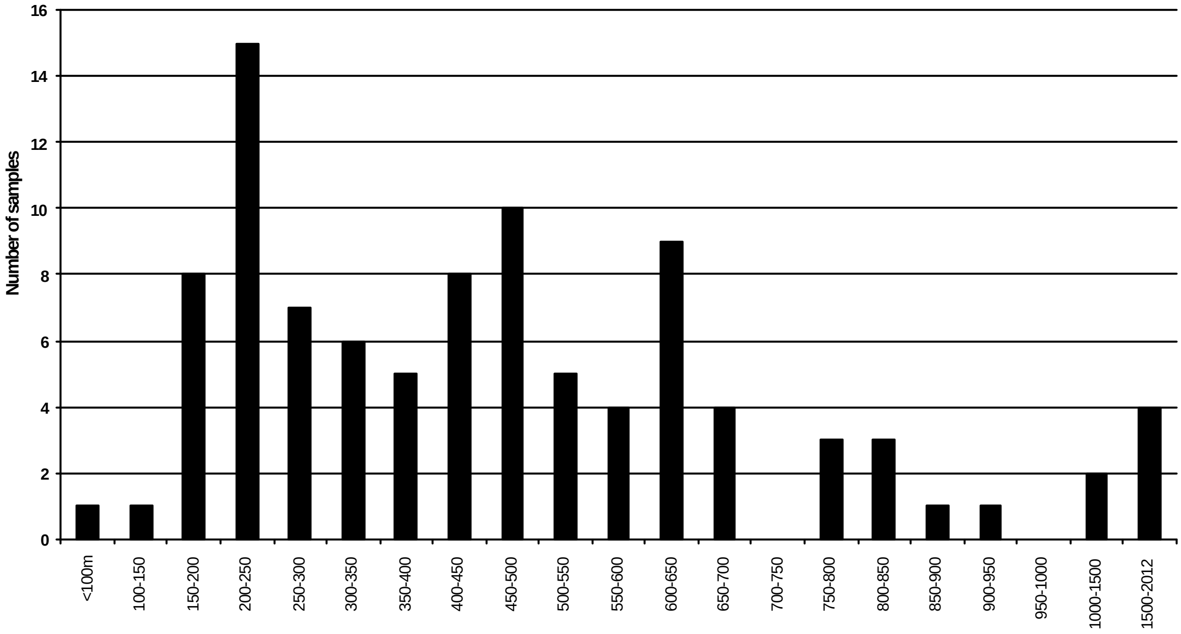


Figure 3*: Benthos sampling effort in relation with depth for the three EPOS, EASIZ I and EASIZ II cruises in the eastern Weddell Sea. Gears used were bottom- or Agassiz trawls, dredges, baited traps, TV- grabs and epibenthic sledges.*

In a attempt to evaluate the present state of faunal survey of the eastern Weddell Sea and its geographic, bathymetric and ecological coverage, a compilation was made of benthos sampling operations in the eastern Weddell Sea during the benthos-dedicated EPOS and EASIZ I (Gutt et al., 2000) and II campaigns. This compilation indicated the more intensively prospected sectors (Kapp Norvegia) and bathymetric zones: for instance, 80% of the benthos sampling effort was made on the shelf between 150 and 700m (Figure 3). It also revealed the under-sampling of some habitats like the under-surface of the sea ice in the neritic zone where bentho-pelagic, pelagic and cryopelagic species can be found.

3.1.2. Bathymetric distribution and seasonal variations in Admiralty Bay

Spatial and bathymetric distribution of the amphipod fauna was recorded in Admiralty Bay and the temporal variations of the spatial distribution, taxonomic composition, relative abundance of species and population structure were followed quantitatively along the reference transect, from 0 to 150m (section I in Figure 2).

At 0 m, on a stony beach, the macrozoobenthos samples taken during a complete annual cycle appeared to be very rich in vagile fauna settled between and under stones. Macrobenthos consisted mainly of amphipods (ca. 85% of total number), gastropods (11%) and nemerteans (3%). Abundance of the whole macrofauna ranged up to over 50,000 ind.m^{-2} and its biomass over 600 gm^{-2} (FW). Seven species of Amphipoda and four species of Gastropoda were found. Amphipoda were dominated by *Gondogeneia antarctica* (over 70% of all amphipods) and *Paramoera edouardi* (over 20%), whereas among gastropods *Laevilitorina antarctica* prevailed (over 70%). Unexpectedly high abundance and biomass of Amphipoda were observed in the first half of winter (May - July), surpassing otherwise important summer amphipod abundance (Figure 4). This phenomenon could be due to the high autumn abundance of decaying algae on the beach in the tidal zone providing detritus that are probably the main food source for Amphipoda (Jazdzewski et al., 2001)

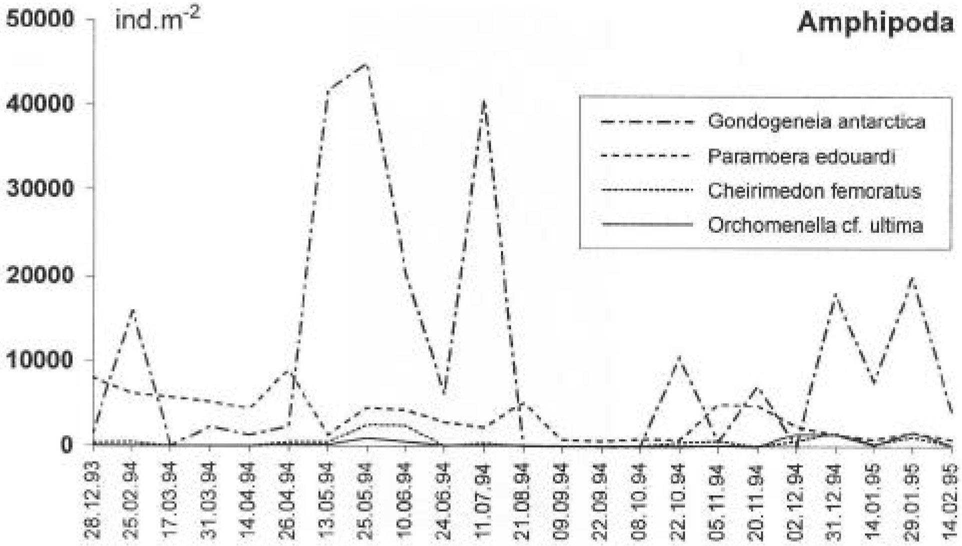


***Figure 4**: Year-round abundance fluctuations of the most common amphipod species in the upper sublittoral fringe of Admiralty Bay.*

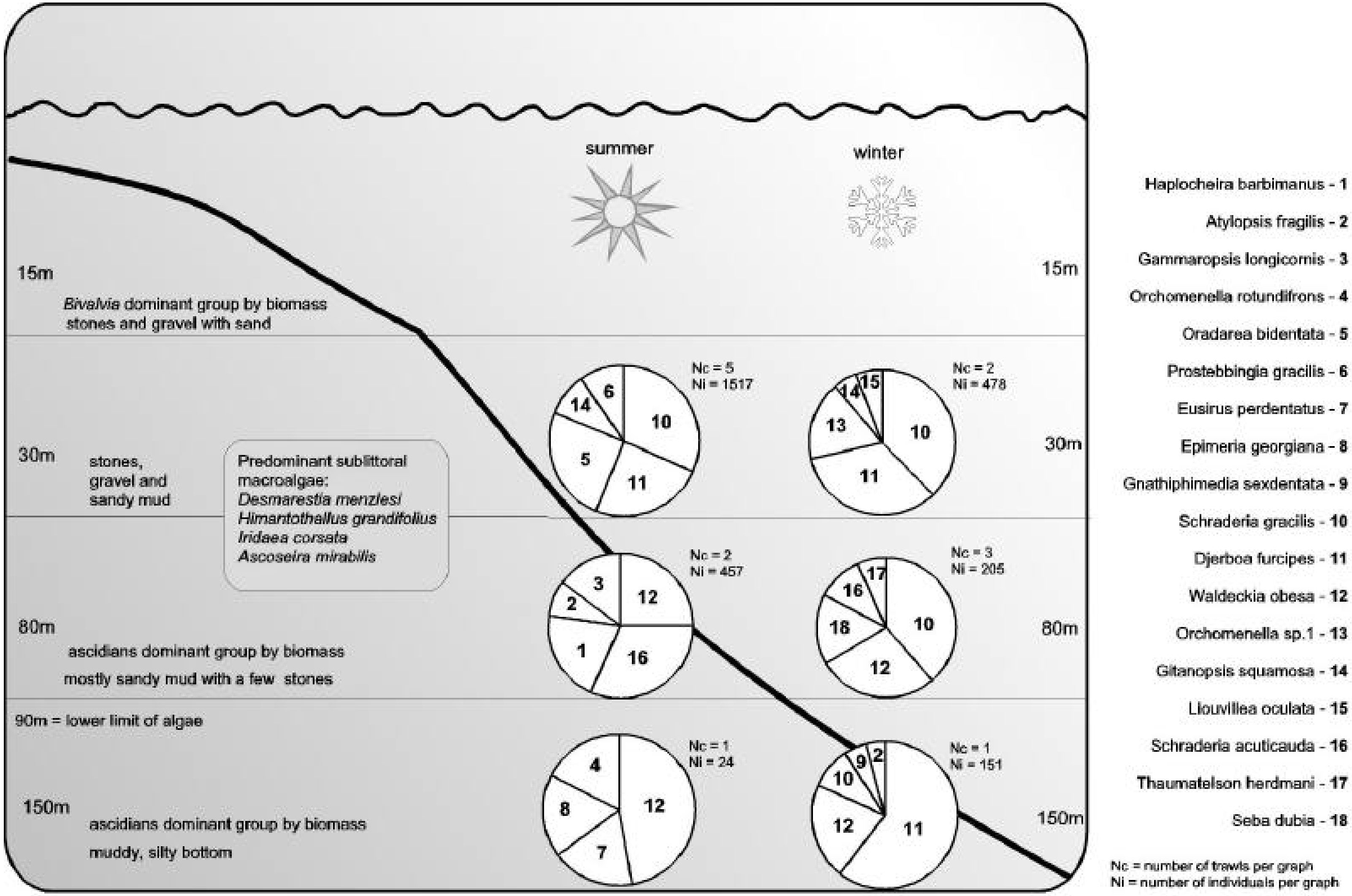


***Figure 5**: Seasonal bathymetric variations of benthic amphipods assemblages along section I, Admiralty Bay.*

The material of the monthly time series from the deeper part of the reference transect (15-150m) amounted more than 24.000 specimens in total and 76 spp were identified. The relative abundance in trawls of the top five species from each depth per season is represented on Figure 5. Although the number of samples and individuals was low, it is nevertheless possible to note some patterns. For example, the herbivorous *Schraderia gracilis* and *Djerboa furcipes* were among the five most abundant species for both seasons at 30m. At other depths they were among the top five but only in the winter. This was the first time that *Djerboa furcipes* was collected at 150m, well below the phytal zone, and this relatively deep occurrence may be due to the attraction to the drifted decaying algae found at these depths as indicated by the preliminary examination of stomach contents. Some species are common to more than one assemblage and have high relative abundance at more than one depth. Overall, there are clearly different assemblages corresponding to different depths (Munn et al. 1999).

3.1.3. Vertical distribution in the Weddell Sea

The EASIZ I and II campaigns allowed to add substantial data on the depth distribution range and preferendums between 65 and 2500 m. This is partly due to the extensive and systematic utilisation for the first time of an autonomous trap system which also allowed to detect a probable faunal limit – at least for the scavengers - on the upper slope between 800 and 1000m (De Broyer et al., 1999_a) (Figure 6).

3.1.4. Habitats and microhabitats in the Weddell Sea

Comparative analysis of catches allowed to distinguish six major amphipod habitats in the neritic zone (Figure 7). The *endobenthic habitat* is constituted of the first centimetres of the sediment and occupied by sedentary tube- or “cell”-dwellers of the family Ampeliscidae and by permanent burrowers belonging to the Oedicerotidae and Phoxocephalidae and temporary burrowers of the Lysianassoidea. The *epibenthic habitats* with three strata described in more details hereafter, is colonised by numerous free-living species, the most abundant being the Epimeriidae, Eusiridae *s.l.*, Iphimediidae and Lysianassoidea. Among the epibenthos, several *symbiotic* and *inquilinous microhabitats* are occupied mainly by some Colomastigidae, Dexaminidae, Leucothoidae, Lysianassoidea, Sebidae, Stenothoidae and Stilipedidae.

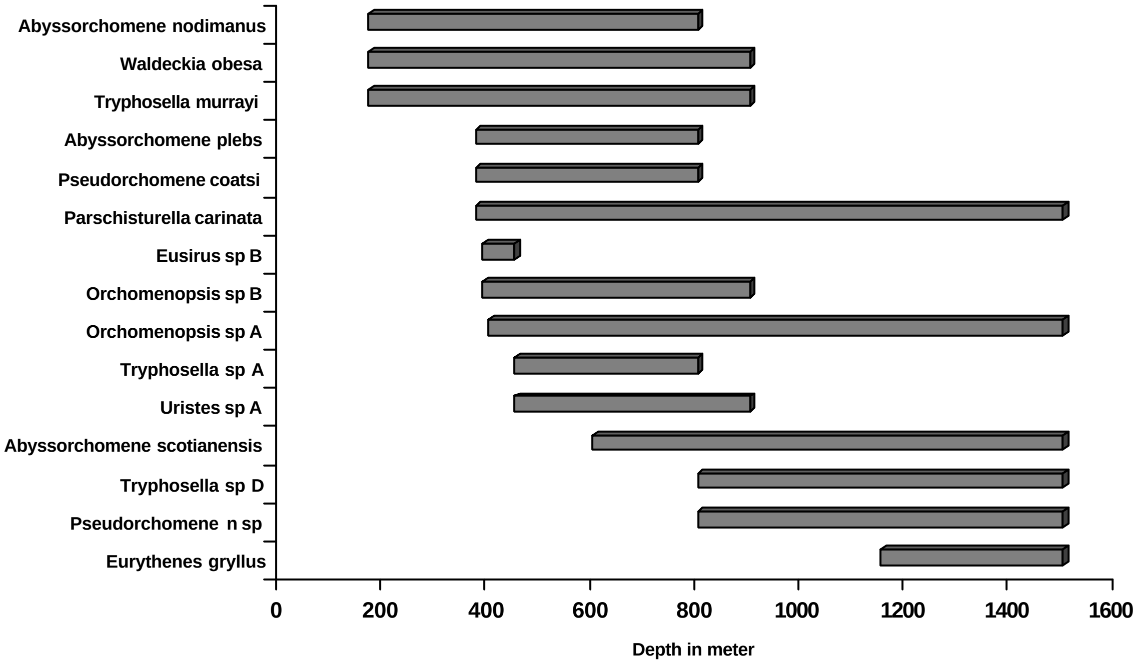


Figure 6: *Vertical distribution of the main amphipod scavenging species in the eastern Weddell Sea shelf and upper slope.*

The Benthic Boundary Layer forms the *hyperbenthic* (or suprabenthic) habitat of some swimming Eusiridae *s.l.* and Lysianassoidea. Along the upper slope off Vestkapp and Halley Bay between 1054 and 1983 m, 32 species (one quarter new to science) from 15 families have been collected at about 1.0 m above the bottom by an epibenthic sledge (Andres, pers. comm.).

Rather few Epimeriidae, Eusiridae *s.l.*, Lysianassoidea and Stegocephalidae occupy the neritic water column showing either a *benthopelagic* or a purely *pelagic* life-style. With the exception of *Eusirus propeperdentatus*, which appeared mostly in the deepest layer of the surface water, the amphipods showed no clear preference for one of the strata (300-200 m, 200-50 m, 50-0 m) (Boysen-Ennen and Piatkowski, 1988). Part of the species found in the water column at several tens or hundreds of meters above the bottom were also found on the bottom, in particular in baited traps. These species are considered *benthopelagic* spending part of their time or part of their life close to or on the bottom in particular for feeding purposes.

The *cryopelagic* habitat -*i.e*. the under-surface of the sea ice- constitutes an habitat for a specialized cryopelagic flora, the sea-ice algae, and a cryopelagic fauna of krill, harpacticoid and calanoid copepods, and nematodes. Only three species of cryopelagic amphipods have been incidentally recorded so far in the eastern Weddell Sea at Drescher Inlet: one lysianassoid, one eusiroid and surprisingly one stenothoid (Rauschert, pers. comm.).

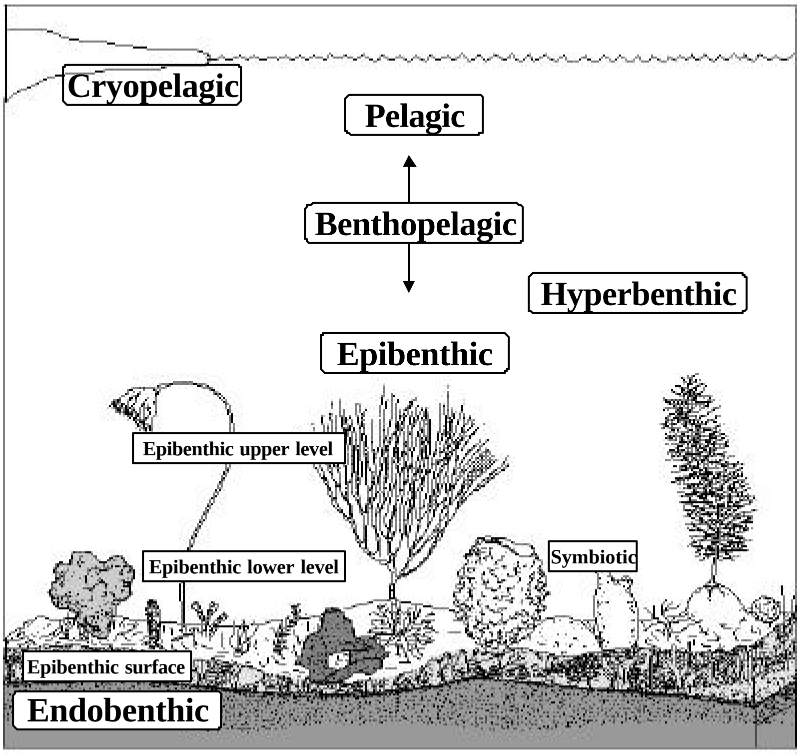


Figure 7*: Scheme of the amphipod macrohabitats in the eastern Weddell Sea neritic zone.*

3.1.4.1. Epibenthic habitats:

The epibenthic layer of the eastern Weddell Sea shelf includes all habitats from the sediment surface level up to the top of sessile organisms which offer secondary substrates to colonisers. Its thickness can reach about 1m as shown by bottom pictures and the size of the biggest sessile invertebrates collected. Amphipods appear distributed on the bottom in three different strata: the sediment surface and the lower and upper strata of the sessile epibenthos.

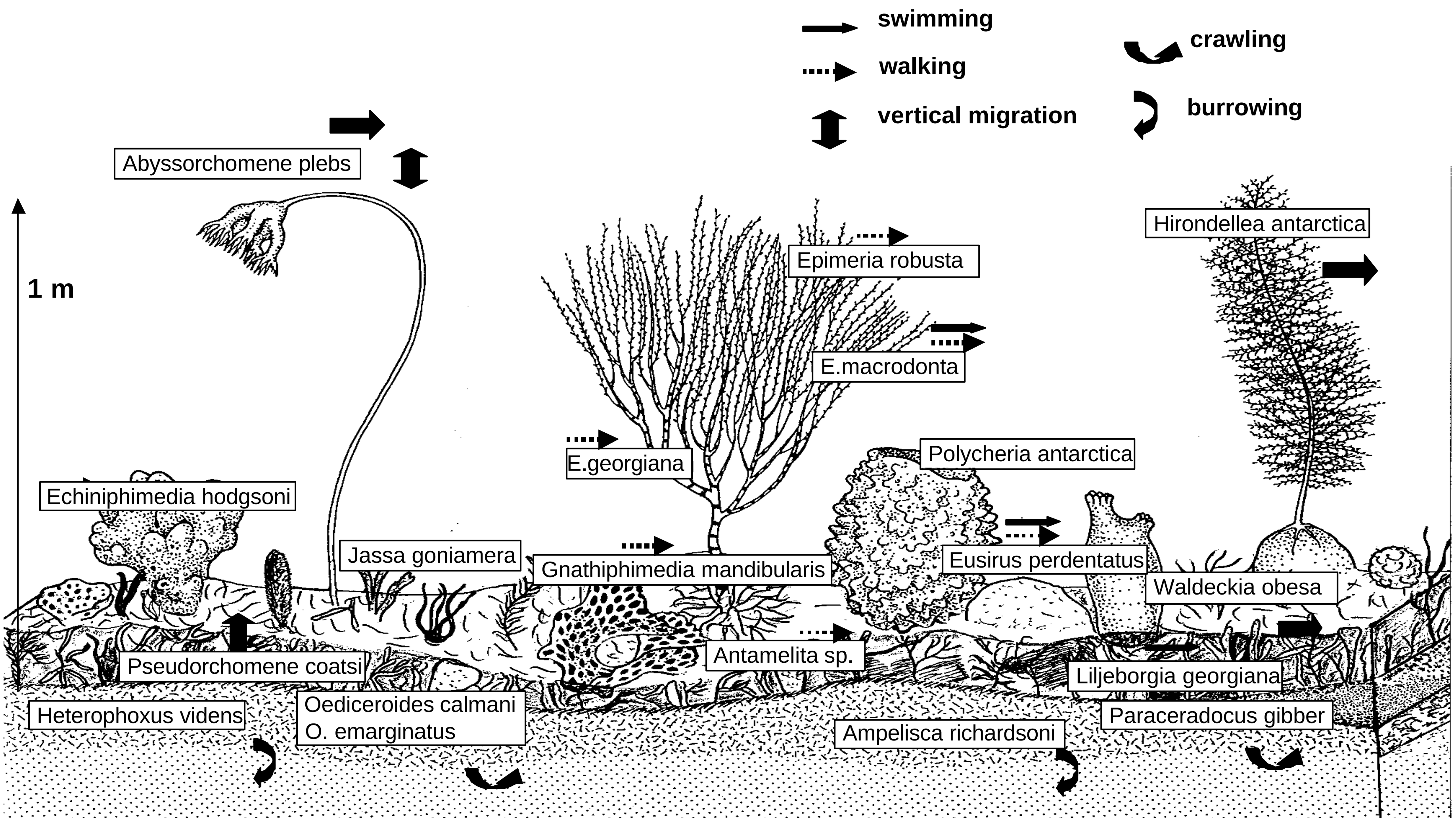


***Figure 8**: Scheme of habitats occupied by representative amphipod species on the eastern Weddell Sea shelf.*

3.1.4.1.1. The sediment surface

Heterogeneous in its composition, structure and thickness, the sediment surface varies from the soft type like sand and mud to the detritic type like coarse bryozoan debris or sponge spicule mats. Dropstones from icebergs can be mixed with this soft or coarse sediment. This very heterogeneous sediment surface often with cracks, interstices and holes offers a great variety of microhabitats to a number of small vagile invertebrates like amphipods (Figure 8). Some amphipod species live only temporarily in this biotope, looking for transitory substrate and protection. Representative species include: Lysianassidae: *Waldeckia obesa*, *Uristes gigas* and *U. adarei*, *Abyssorchomene scotianensis*, *Lepidecreella sp A*, *Orchomenella acanthura*, *Orchomenella pinguides*, *Parschisturella carinata*, *Tryphosella murrayi*.

Other amphipods appear sedentary finding there shelter and food. Representative species from the soft sediment surface include: Melitidae n. sp., *Melphidippa antarctica* and *Epimeria georgiana*; from coarse or mixed sediment surface: *Liljeborgia georgiana* and *Paraceradocus gibber*.

3.1.4.1.2. The lower level of sessile epibenthos

Covering the bottom by patches or in continuous layers, the diverse assemblages of hexactinellids and demosponges (Barthel and Gutt 1992), the various bryozoans and the multiple cnidarians and hydrozoans form highly heterogeneous structures including multiple cavities. This sessile epibenthos provides numerous substrates for amphipods. According to their feeding type, many amphipods also find there food in abundance (Coleman 1989$_{b,c}$, 1990; Klages and Gutt 1990$_{b}$; Dauby et al., 2001$_{a}$). Aquarium observations indicated that some species occupied preferably the lower part of the erected substrates, whereas others occurred on the upper part or showed no apparent preference and occurred in both levels and sometimes also on the sediment surface. Representative species typically found in this substrate include several Iphimediidae e.g. *Echiniphimedia hodgsoni*, *E. scotti*, *Gnathiphimedia mandibularis*, *Iphimediella cyclogena* and *Maxilliphimedia longipes*; Epimeriidae: *Epimeria rubrieques*; Eusiridae: *Eusirus perdentatus*; Ischyroceridae: *Jassa goniamera*.

3.1.4.1.3. The upper level of sessile benthos

ROV video records of the sessile suspension-feeder community showed a succession of ball-like, urn- or finger- shaped sponges, tree-like hydrozoans or flower-shaped gorgonians or bryozoans. The canopy of these assemblages, composed of a mixture of delicate and strong organisms, constitutes a secondary bottom colonised by other invertebrates, the most obvious being echinoderms (e.g. the crinoid *Promachocrinus kerguelensis,* several *Ophiurolepis*), and by fish (*Artedidraco skottsbergi*, *Trematomus scotti*) (Gutt and Schickan, 1998). Amphipods are suspected to be also present in this layer, but, due to their size, are usually not visible on pictures. The family Epimeriidae comprises typical representatives of this habitat with at least four common species: *Epimeria macrodonta, E. robusta, E. similis* and *Epimeriella walkeri*. Additional representative species are: *Hirondellea antarctica* (Lysianassoidea), a good swimmer also found in the water column, and *Alexandrella mixta* (Stilipedidae).

3.1.4.2. The symbiotic and inquilinous habitats

Among amphipods living on sessile invertebrates, some species, usually sedentary, have established different symbiotic relationships with their hosts which remain to be described.

Species associated with ***sponges***: no less than 16 spp of amphipods were recorded on common hexactinellids and demosponges by Kunzmann (1996), who did not established any host-specific relationships. Among her material, four species appear frequently and in relatively high numbers in some sponges: *Seba antarcica, Polycheria antarctica s.l., Colomastix simplicicauda* and *Andaniotes linearis.* They can be considered preferential spongicolous species, but not exclusive as *S. antarctica and P. antarctica s.l.* have also been recorded on ascidians. According to Kunzmann (1996), *S. antarctica* and *P. antarctica* are ectoparasites eating the host tissues and using the sponge as a shelter from predators. In our material, *P. antarctica* was found in holes in the surface tissues of the demosponge *Crella crassa*. Stomach content analysis revealed no sponge spicules but only small particles (less than 100 µm) of unidentifiable organic matter, diatoms fragments and mineral grains (Dauby et al., 2001) which do not confirm Kunzmann’s observation of ectoparasitism. In addition, a new species of *Scaphodactylus* (Stenothoidae) was found on an unidentified demosponge.

Species associated with ***ascidians***: species of the families Leucothoidae, Lysianassoidea, Stegocephalidae or Stenothoidae have been found in the branchial cavity of different ascidians. *Leucothoe sp.* was found in *Corella eumyota*. The lysianassoid *Orchomenyx sp.* was found in *Ascidia challengeri* and an unidentified species in a “large red ascidian”. Stegocephalids have been found in *Ascidia challengeri* and in *Eugyrioides polyducta*. *Metopoides* sp.nov.2 (Stenothoidae) was recorded in *Ascidia challengeri* at depths of 600 and 710 m. Preliminary examination indicated no apparent host specificity.

Species associated to **hydrozoans**: two new stenothoid species of the genus *Torometopa* were found on *Oswaldella billardi*. *Thaumatelson* sp. (Stenothoidae) was found on a unidentified hydrozoan. The stolons produced by *Tubularia ralphii* and *Oswaldella antarctica* on several stones from the underwater hilltop of Four Seasons Inlet (NE of Kapp Norwegia) host a few hundreds of stenothoids from 2 spp, which could however not be associated with the hydrozoans but simply shelter in this tri-dimensional substrate (Gili et al., 1999; De Broyer et al., 1999_a).

Species associated to **gorgonarians**: one stenothoid species of the genus *Torometopa* was found on *Primnoella* sp. at 400 m while *Polycheria* sp. (Dexaminidae) occurred on a unidentified gorgonarian host.

Precise habitat determination at shelf depths has strong methodological limitations. Bottom pictures and video records have been particularly useful for characterising the habitats of fishes (Ekau and Gutt, 1991) or conspicuous macrobenthos (*e.g.* holothurians: Gutt, 1991; shrimps: Gutt et al., 1991; sponges: Barthel and Gutt, 1992) but are of little help for the small and often hidden amphipods. Analysis of trawl catch contents is of limited or no value to indicate the potential habitat of collected amphipods because of the usually disturbed state of the catch (often a mixture of sediments, stones and diverse fauna) and also the usual high patchiness of sampled assemblages (see e.g. Gutt and Koltun, 1995). They can however be informative in case of homogeneous bottom catches or symbiosis on well-preserved hosts for instance. On the contrary, undisturbed bottom samples from corers and large grabs (which should be more systematically checked) can provide useful epibenthic habitat indications. Aquarium observations can provide information on the general behaviour (see *e.g*. Enequist, 1949; Klages and Gutt, $1990_{a,b}$) and on the species ability to select a particular habitat (*e.g*. Coleman, 1989_a). On the other hand, extrapolations on the basis of similar morphologies to infer similar habitats can be hazardous, as shown for instance by the *Eusirus* case: *Eusirus perdentatus* is a typically epibenthic animal, walker and poor swimmer (Klages, 1993) although its sister species *Eusirus propeperdentatus* is a purely pelagic animal (Andres, 1979; De Broyer & Jazdzewski, 1993).

From a preliminary comparison with the other amphipod macrohabitats in the eastern Weddell Sea, the epibenthic zone, here subdivided in three different levels, appears the most heterogeneous and the richest in species. The presumed habitats of some representative epibenthic species are presented schematically on Figure 8. Each epibenthic strata from the heterogeneous sediment surface to the top of the erected sessile benthos offers to amphipods different habitats characterised by some physical parameters and by nature and availability of food. Some species find there a temporary substrate or a shelter, others forage in this habitat, in some cases at the expense of the living substrate itself. The comparatively high number of “walker-climber” species (mainly belonging to the Iphimedioidea, with more than 50 spp), mostly found on the different levels of the rich suspension feeder assemblages, seems unique to the eastern Weddell Sea. It is most probably linked to the diversity of microhabitats and the abundance of food offered by the rich epibenthos to these specialised micropredatory grazers or unspecialised predators (feeding types according to Coleman, 1989$_{b,c}$; Klages and Gutt, 1990$_{b}$; Dauby et al., 2001$_{a}$).

Aquarium observations have indicated two possible levels of amphipod distribution on the sessile epibenthos substrates, which require confirmation. It seems nevertheless possible to differentiate the environmental conditions of the two levels. At the top of the epibenthic substrates, the upper level strata can be more exposed to strong currents (a current of 40 cm/sec was recorded in Kapp Norvegia at 5m above the bottom at a depth of 676m; Fahrbach et al., 1992). This seems *a priori* a favourable position for the free-living suspension-feeders (Ischyroceriidae…) to collect the organic rain from the above water column and from lateral advection. Currents can also carry carrion smell and this place could be advantageous for scavengers like Lysianassoidea (see Ingram and Hessler, 1983). These trophic advantages are balanced, however, by a greater exposure to predators. Benthic fish stomachs contents (*Trematomus spp., Pogonophryne spp., Artedidraco orianae*…) for instance frequently revealed *Epimeria* species supposed to stay at this level (Olaso, 1999; Olaso et al., 2000).

The selected species undoubtedly represent the most conspicuous and the most common ones in the epibenthic catches so far analysed. But most specimens have been caught by trawls with a 15 mm mesh size which do not always allow adequately collecting small species, which can be numerous judging from the preliminary analysis of material from small mesh-sized dredge (Rauschert, unpubl.). The diversity of symbiotic and inquilinous habitats is probably highly underestimated. Only sponge habitats have been systematically investigated (Kunzmann, 1996) so far. Ascidians remain to be more systematically checked for their inquilinous fauna. Potential associations with cnidarians and hydrozoans should draw more attention. A number of small species, among which the numerous Stenothoidae, might have developed preferential relationships with some hosts. They could represent an important part of the specific diversity of the eastern Weddell Sea amphipods.

3.2. ECOFUNCTIONAL BIODIVERSITY

3.2.1. Trophic diversity in the Weddell Sea

Almost all known feeding types can be encountered in the amphipod benthic communities of the eastern Weddell Sea shelf. A notable exception is the macroherbivory which is apparently lacking, probably due to the apparently complete absence of macroalgae in that ice-covered deep shelf area. On the basis of both diet analyses (*i.e. R(i)*'s distribution in species' digestive tract contents, see M&M) and ethological observations in aquarium, the following eight feeding types can be distinguished (Figure 9) (Dauby et al., 2001_a).

A. *Suspension–feeding type*. Amphipods of this group are typically epibenthic and feed on particulate organic matter (plant or animal, dead or alive) from the water column, such as plankton or micronekton organisms or by-products (*e.g.* faecal pellets), and advected material. The main amphipod families of that type are Ampeliscidae, Melphidippidae, Dexaminidae and Ischyroceridae. These animals are always weakly motile, or sedentary. Depending upon the strategy used for taking food, different behavioural categories can be distinguished:

* *active suspension-feeders*, which either improve the collection of food by moving part of their body or by creating a water current (*e.g. Ampelisca richardsoni*), or which seize or trap sinking material by the way of their antennae (*e.g. Jassa goniamera*).

* *passive suspension-feeders*, which stay motionless upside-down on the bottom, feeding on sinking particles (*e.g. Melphidippa antarctica*);

Analyses of the stomach and gut content of these organisms revealed the prevalence of plankton-originating items and of miscellaneous detrital bodies.

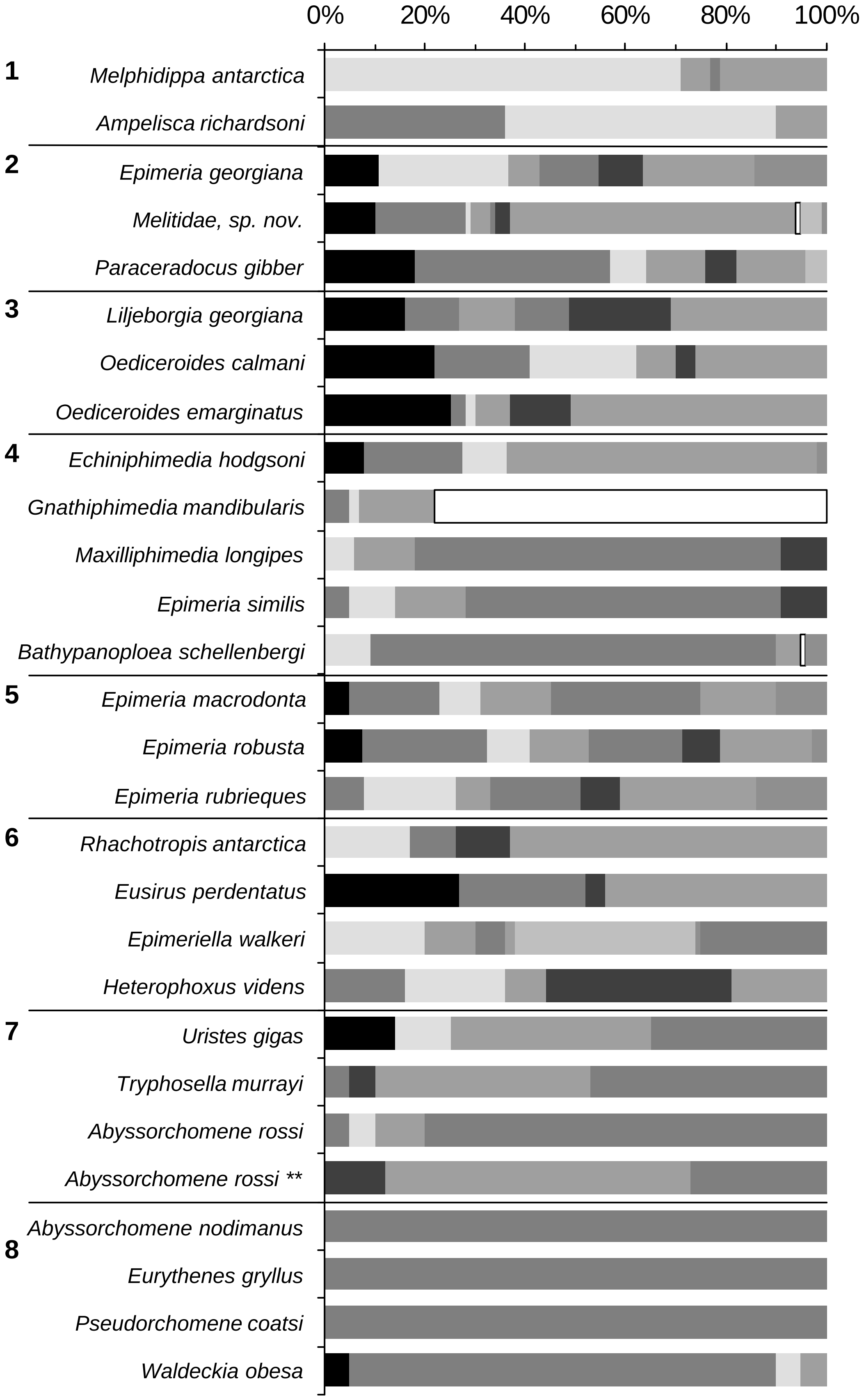
B. *Deposit–feeding type.* Also typically epibenthic, these amphipods feed on relatively large particles collected on the seafloor, originating either from the water column or from the breakdown of benthic biota. Families Epimeriidae, Melitidae or Gammaridae (*Ceradocus* group) have representatives of that type, with common Antarctic species *Epimeria georgiana, Antamelita sp., Paraceradocus gibber.* Gut contents of these amphipods usually show a wide variety of organic debris: sponge spicules, worm setae, echinoderm ossicles, crustacean appendages, or plankters, associated with mineral particles.

C. *Deposit–feeding / predatory type*. Amphipods of this trophic type, mainly belonging to Liljeborgiidae and Oedicerotidae, 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 preys such as polychaetes and tiny amphipods. Crustacean fragments represent a significant share of the gut content. Common representative species: *Oediceroides emarginatus, O. calmani, Liljeborgia georgiana.*

D. ***Opportunistic predatory type.*** Amphipods of this trophic type are epibenthic and belong mainly to Epimeriidae (*Epimeria macrodonta, E. robusta, E. rubrieques*). They feed on miscellaneous small material that they detect with antennae and capture with gnathopods. They are weakly motile but can walk on the seafloor in search of food. Analyses of gut contents reveal a wide diversity of animal food items (hydrozoan, gorgonian, sponge, polychaete, holothuroid and crustacean parts) and some plankton-originated stuffs.

E. ***Micropredatory browsing type.*** Animals of this feeding type collect small food elements from sedentary organisms which are unable to flee. Browsers (or "grazers") use to eat only part of each prey item without killing it. Eastern Weddell Sea browsing amphipods specialized in grazing on colonies of different benthic invertebrates. Organisms of this type are also known as "surface microphagous browsers", "carnivorous browsers", or "micropredatory grazers". Grazers on periphyton ("microherbivorous browsers"), albeit existing, are not selective and can conveniently be classed in deposit-feeders. Micropredatory browsing behaviour has been developed in different families of Antarctic amphipods (Epimeriidae, Iphimediidae or Lysianassidae *s.l.*). These are typically epibenthic, and are moreover usually feeding preferentially on one kind of prey: *Epimeria similis* and *Hirondellea antarctica* graze on cnidarian colonies, *Echiniphimedia hodgsoni* on sponges, *Gnathiphimedia mandibularis* on bryozoans, *Bathypanoploea schellenbergi* on gorgons.

F. ***Macropredatory / opportunistic scavenging type.*** This trophic type, mainly predatory, embraces a large number of species belonging to various families: Epimeriidae (*Epimeriella walkeri*), Eusiridae (*Eusirus perdentatus, E. antarcticus, Rhachotropis antarctica*), Phoxocephalidae (*Heterophoxus videns*) or Stilipedidae (*Alexandrella mixta*). 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, ambushing) are also encountered in this group.


0%
20%
40%
60%
80%
100%
1
Melphidippa antarctica
Ampelisca richardsoni
2
Epimeria georgiana
Melitidae, sp. nov.
Paraceradocus gibber
3
Liljeborgia georgiana
Oediceroides calmani
Oediceroides emarginatus
4
Echiniphimedia hodgsoni
Gnathiphimedia mandibularis
Maxilliphimedia longipes
Epimeria similis
Bathypanoploea schellenbergi
5
Epimeria macrodonta
Epimeria robusta
Epimeria rubrieques
6
Rhachotropis antarctica
Eusirus perdentatus
Epimeriella walkeri
Heterophoxus videns
7
Uristes gigas
Tryphosella murrayi
Abyssorchomene rossi
Abyssorchomene rossi **
8
Abyssorchomene nodimanus
Eurythenes gryllus
Pseudorchomene coatsi
Waldeckia obesa

■ inorganic M. ■ unidentified O.M. ■ plankton
■ Porifera ■ Cnidaria ■ Polychaeta
■ Crustacea □ Bryozoa ■ Ophiuroidea
■ Holothuroidea ■ fish muscles

***Figure 9**: Mean proportions [R(i)'s] of the different food items in the digestive tract of different Weddell Sea amphipods. Numbers refer to trophic types (see text).*

G. *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 constitutes only a fraction of the diet. These species are able to kill preys, 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 is spatially and seasonally dependent. Common representative species (all belonging to the Lysianassidae family) are: *Tryphosella murrayi, Uristes gigas, Abyssorchomene rossi, A. plebs.*

H. *Necrophagy type.* This vast group of epibenthic, benthonectonic or benthopelagic amphipods frames most of its diet with pieces of muscle or other tissues from dead animals, either vertebrates or invertebrates. Representatives of this trophic type all belong to the Lysianassoidea superfamily: *Abyssorchomene nodimanus, Pseudorchomene coatsi, Parschisturella carinata, Eurythenes gryllus, Waldeckia obesa*. These forms are ubiquitous, highly motile, and always abundant. Experiments carried out in aquarium show that olfaction is the main process involved in the detection of carrion.

3.2.2. Stable isotope approach

Specific $\delta^{13}C$ and $\delta^{15}N$ values in amphipods are presented in Figure 10. *Ampelisca richardsoni* is completely isolated from other amphipods with the lowest δ for the carbon and for the nitrogen ($\delta^{13}C$ = -27.1 ± 0.9‰; $\delta^{15}N$ = 6.6 ± 0.6‰). These values are the closest to those displayed for SPOM and are significantly different from values of all the other species (ANOVA $p < 0.01$) except for the $\delta^{13}C$ of *Epimeria similis* and *Iphimediella cyclogena*. *Eusirus perdentatus* and *I. cyclogena* present similar $\delta^{13}C$ but their nitrogen ratios are significantly different from each other (ANOVA $p = 0.0005$). *E. perdentatus* $\delta^{15}N$ values differ significantly from all other species nitrogen ratios except from *E. similis* single 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 the four latter species stable isotope ratios are not significantly different from each other, neither for the carbon nor for the nitrogen (Nyssen et al., 2000).

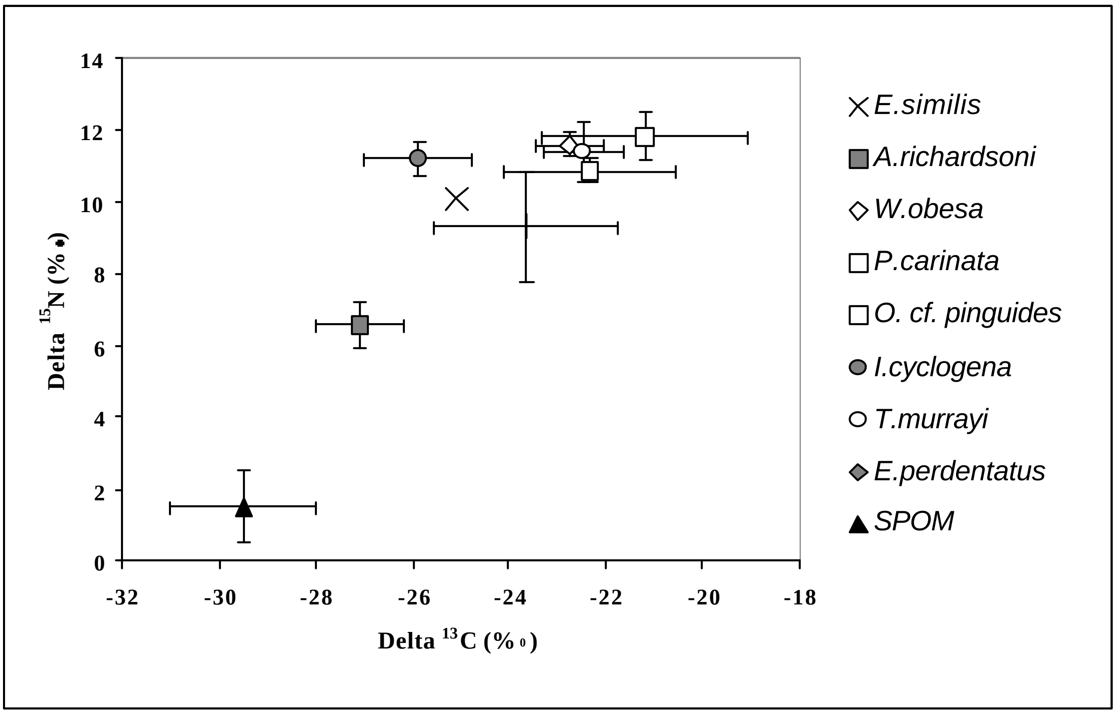


Figure 10: *d^{13}C versus d^{15}N values of SPOM and of 8 amphipod species from the eastern Weddell Sea.*

3.2.3. Impact of amphipods on the benthic ecosystem

The mean relative abundance (*R(i)*, in %) of the different food items in the digestive tract of the most important Weddell Sea amphipod species was presented in Figure 9. The analysed species were chosen on the basis of their relative abundance, each one representing at least 0.4%, on the average, of the total amphipod population collected during each cruise. For the EPOS cruise (1989), these species represent 52.8% of total amphipods (58% of all the samples have been analysed), while, for the EASIZ I cruise (1996), they represent 70.9% of total amphipods (82% of the samples have been investigated) (Dauby et al., 2001_b).

The amphipod trophic impact on the different available food items [*T(i)*, see M&M] of the Weddell sea is presented in Figure 11, for the EPOS and the EASIZ I cruises, respectively.

For the EPOS samples, crustaceans appear to be the most frequently consumed items (32%), followed by fish carcasses (18%). If we do not take into account the unidentified organic matter (unrecognizable organic bodies without any specific features like cnidocysts, or without any hard structures like chitinous plates or spicules), particles of planktonic origin represents the third most common item. Sponges, cnidarians and worms (polychaetes and nematodes) are about equally consumed (5 to 7%), while bryozoans and echinoderms represent only a tiny fraction of the amphipod diet.

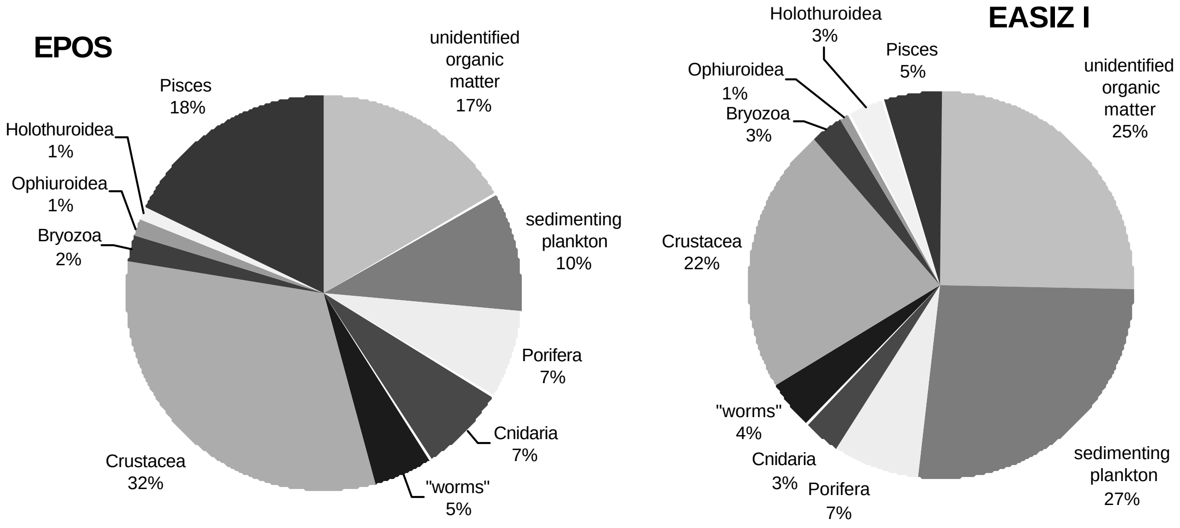


***Figure 11**: Mean relative trophic impacts [T(i)] (in %) of the eastern Weddell Sea benthic amphipod community on the different potential food sources, during the EPOS (1989) and EASIZ I (1996) cruises. Inorganic material (sediment grains) were omitted for calculation.*

Results from the EASIZ I cruise are rather different. Plankton-originating cells (together with the unidentified matter) are the main dietary component (27%), before crustaceans (22%). Fish flesh constitute only a small fraction (5%), of the same order of occurrence as worms, bryozoans or holothuroids. Sponges, with 7%, are the third item in importance in the amphipod diet.

3.2.4. Amphipod feeding rates

Eight species, representative of different trophic types (herbivory, omnivory, necrophagy), were used to try to evaluate the Antarctic amphipod feeding (FR), egestion (ER) and thus assimilation (AR) rates. These specific mean rates are presented in Table II.

***Table II**: Mean feeding rates ($g_{food\text{-}DW}.g_{animal\text{-}DW}{}^{-1}.day^{-1}$), egestion and assimilation rates (% of ingested food) for the different analysed amphipod species.*

species	**given food**	**FR (%.day^{-1})**	**ER (% food)**	**AR (% food)**
Djerboa furcipes	algae	6.2	54	46
Eurymera monticulosa	squid	3.0	13	87
	algae	2.4	n.d.	n.d.
Gondogeneia redfearni	squid	15.7	10	90
Prostebbingia brevicornis	squid	9.5	44	56
Abyssorchomene nodimanus	squid	3.8	n.d.	n.d.
Parschisturella carinata	squid	2.2	n.d.	n.d.
Tryphosella murrayi	fish	2.1	n.d.	n.d.
	squid	1.4	n.d.	n.d.
Waldeckia obesa	fish	3.1	33	67
	squid	2.2	n.d.	n.d.

It clearly appears that feeding rates present large variations (one order of magnitude) with respect to amphipod species. But, for a given species, these rates, albeit slightly different, are not strongly influenced by the kind of offered food.

It must be pointed out that the data presented in Table II are average values over several feeding experiments, and that results from each experiment are average values over several days (cfr. M&M). An example of the day-to-day variations in the feeding rate during an experiment with *A. nodimanus* is shown in Figure 12. Feeding

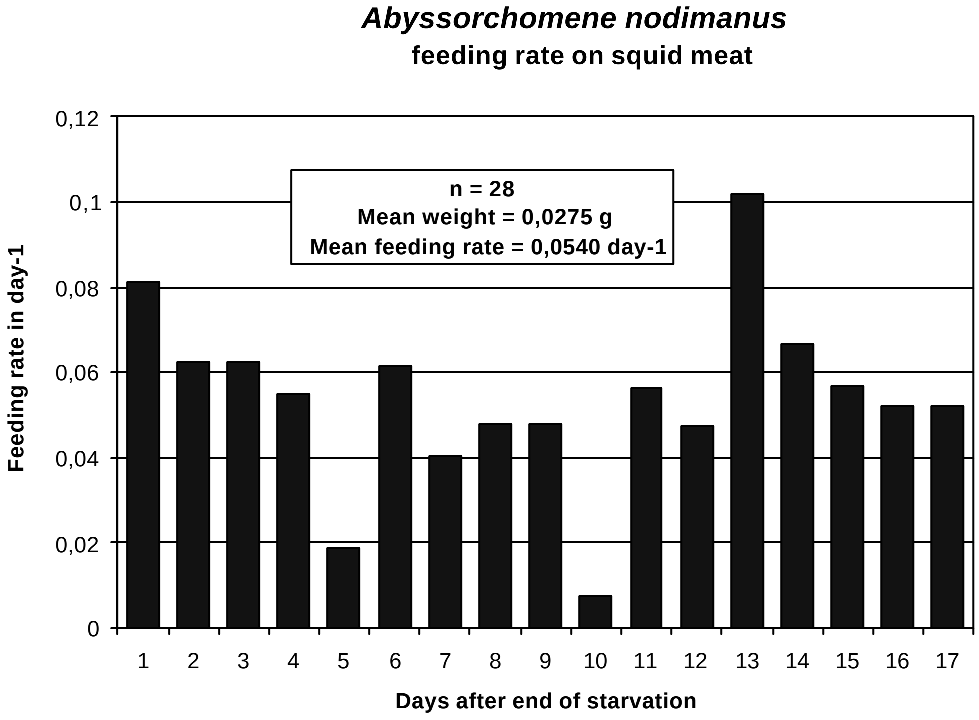


Figure 12*: Example of the day-to-day variation of the feeding rate of* Abyssorchomene nodimanus *fed on squid.*

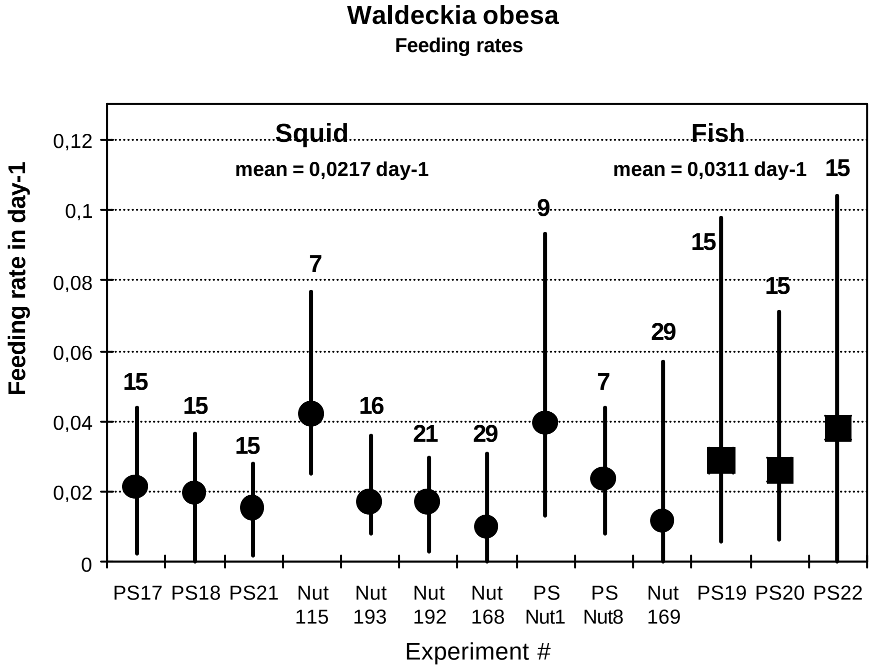


Figure 13*: Feeding rates (mean + day-to-day variations) of* Waldeckia obesa *fed with squid (circles) or fish (squares) during different experiments. Numbers above bars indicate numbers of specimens used for each experiment.*

is obviously not constant, and a kind of cycle (rhythm?) is observed with periods of intense activity and periods of quasi fasting, maybe corresponding to the digestion time. A high feeding rate is always noticed at the beginning of experiment, after the starvation phase. In the same way, rather important differences can be seen when comparing the rates estimated for distinct experiments (example of *W. obesa* in Figure 13), as results may vary by a factor of 4 to 5.

3.2.5. Amphipod as food source for higher trophic levels

An exhaustive survey of the Antarctic literature allowed to record 192 different known predators on pelagic and benthic amphipods in the Southern Ocean. A summary of these records is given in Table III.

***Table III**: Overview of the amphipod predators in the Southern Ocean (bibliographic data). "Groups" refers to the number of different predator families (fishes and birds) or orders (invertebrates and mammals), species to the predator species number, and citations to the total number of recorded pairs [amphipod-predator].*

	"groups"	**species**	**citations**
Invertebrates	12	33	69
Fishes	19	101	798
Birds	11	48	529
Mammals	2	10	39

The exploitation of this dataset is, however, rather difficult. In the early Antarctic literature, most of the data about amphipods in predators' digestive tracts were in the presence/absence form. From the mid 20th century, some quantitative information became available, mainly as "frequency of occurrence". But it is only since the 1980's that were published valid data in the form of preyed amphipod mass and/or volume percentages in predator diets. Moreover, even in recent papers, most authors have not tried to determine amphipod species, making the information less useful.

Notwithstanding, a tentative inventory of predators for which amphipods represent a significant share in the bulk of their diet was established; some of these are listed in Table IV. For most of the other recorded predators, amphipods constitute a smaller dietary fraction (in the order of few percents). As shown in Table IV, hyperiid species (mainly *Themisto gaudichaudii*) are largely consumed by predators feeding in the water column (myctophid fish, petrels, penguins and

group		**species**	**habitat**	**%**	**amphipods**
Annelida	Polychaeta	*Harmothoe spinosa*	B	→ 99	GAM
Crustacea	Amphipoda	*Bovallia gigantea*	B	→ 99	GAM
Pisces	Artetidraconidae	*Artetidraco orianae*	B	→ 80	GAM
		Pogonophryne permitini	B	→ 73	GAM
	Channichthyidae	*Champsocephalus gunnari*	P	→ 86	HYP
	Harpagiferidae	*Harpagifer bispinis*	B	→ 98	GAM
	Myctophidae	*Electrona carlsbergi*	P	→ 27	HYP
	Nototheniidae	*Gobionotothen gibberifrons*	B	→ 38	GAM
		Lepidonotothen larseni	B-P	→ 40	GAM-HYP
		Notothenia coriiceps	B	→ 88	GAM
	Rajidae	*Bathyraja maccaini*	B	→ 58	GAM
Aves	Oceanitidae	*Oceanites oceanicus*	P	→ 45	HYP
	Procellariidae	*Pachyptila belcheri*	P	→ 70	HYP
		Pachyptila turtur	P	→ 60	HYP
	Sphenicidae	*Eudyptes chrysolophus*	P	→ 37	HYP
		Pygoscelis adeliae	P (B)	→ 58	HYP-GAM
Mammalia	Cetacea	*Balaenoptera borealis*	P	→ 45	HYP

***Table IV**: Mass percentages of amphipods in the diet of some Antarctic predators (from various sources).*
B: benthic species; P: pelagic species; GAM: gammarids; HYP: hyperiids.

whales), while gammarids abound in the diet of benthic predators (invertebrates and notothenioid fish).

3.2.6. Size diversity and polar gigantism

To determine the significance of big Antarctic species, size spectra have been established in various sites, from polar to tropical latitudes, and from freshwater to marine sites. At all 15 sites, these size spectra are right skewed; however, skewness increases as temperature decreases (Figure 14). Thus, mode, mean and maximum size all increase with decreasing temperature whereas minimum size does not change.

Gigantism itself is addressed by the TS95/5: when plotted against mean water temperature for marine sites, this parameter increases curvilinearly as temperature decreases (Figure 15 A).

However, non marine sites do not fit this pattern. Lake Baikal (salinity: 0‰), and less conspicuously, the Caspian (13‰) and Black Sea (17‰), lie above the relationship for marine sites, and the discrepancy increases as salinity decreases. The Lake Baikal TS95/5 is x1.8 the marine value for the same temperature. On the other hand, the high altitude Lake Titicaca value lies under the relationship.

Re-plotting the TS95/5 values against water dissolved oxygen content removes the discrepancy between marine and other environments (Figure 15 B). The produced relationship covers all sites, is linear and accounts for >97% of the variance in the data:

$$\text{TS95/5} = -43.4 + 0.244\ \text{AE2} \quad (N = 13;\ r2=0.97) \qquad (4)$$

Thus the factor controlling TS95/5 is oxygen availability. When data (not shown) for TS90/10, TS80/20, TS50/50 and TS20/80 are regressed against mean environmental oxygen the fit of the relationships improves as TS value increases, indicating that oxygen becomes more important and other ecological factors reduce in effect as size increases. Furthermore the relationship between TS95/5 and temperature for marine sites in Figure 15 A is curvilinear, reflecting the non-linear relationship between seawater oxygen content and temperature (Chapelle and Peck, 1999; Peck and Chapelle, 1999; Chapelle, 2001).

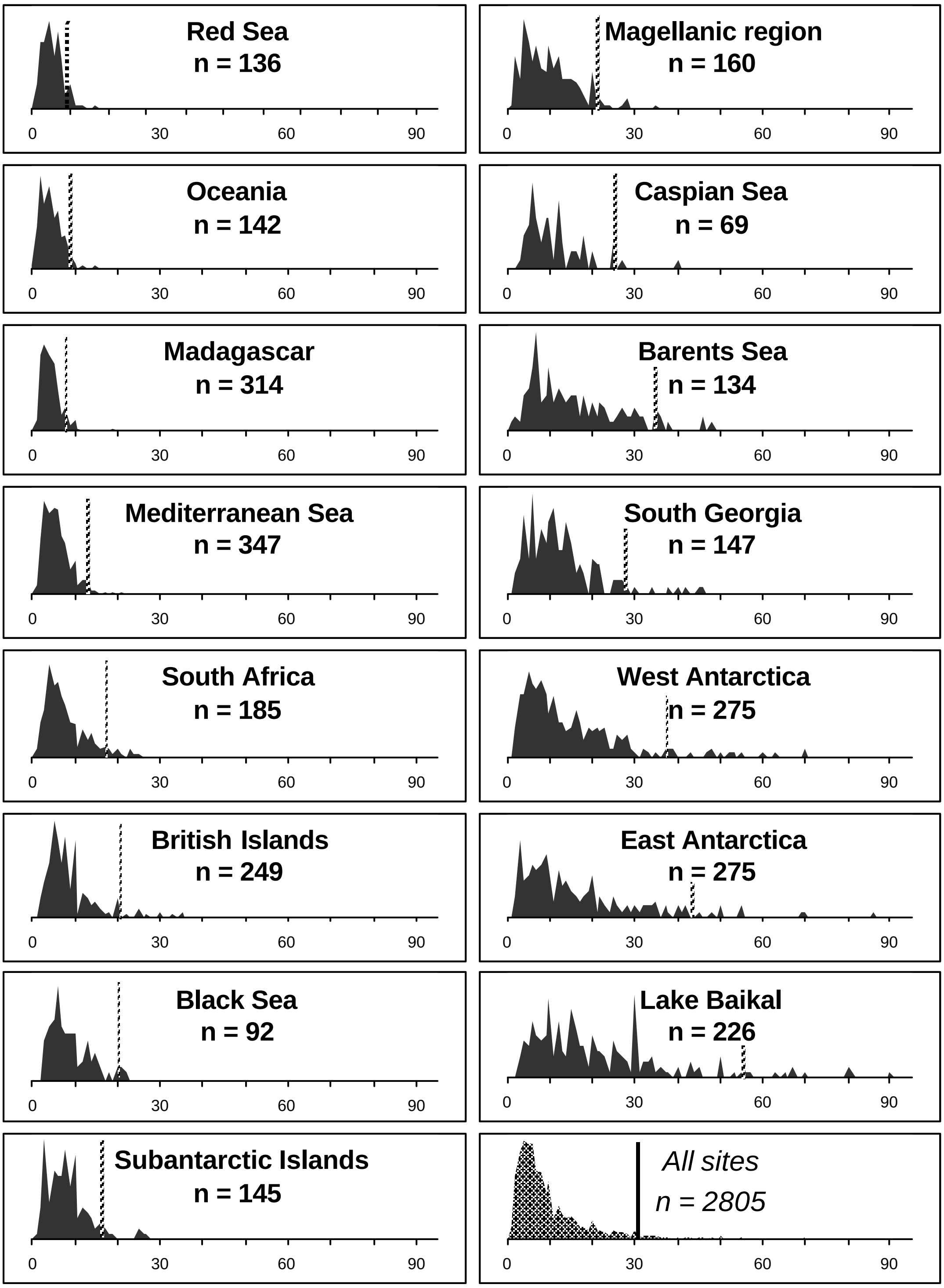


Figure 14: *Amphipod crustacean size spectra for the 15 selected sites (12 marine and 3 brackish or freshwater). The order follows the absolute oxygen concentration gradient. The last graph pools all the other ones. For each spectrum, n= number of species and the bar indicates the TS95/5 value.*

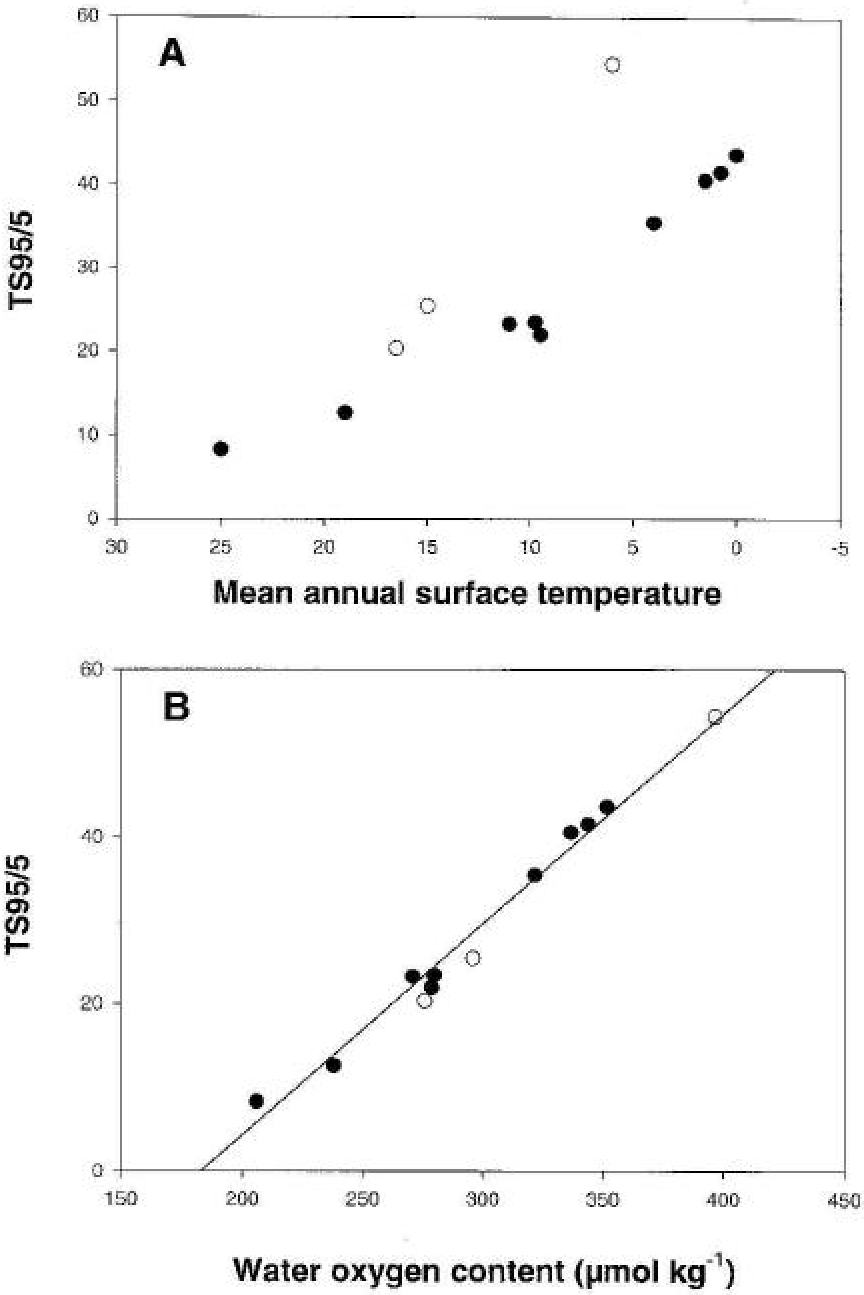


Figure 15: *Effects of (A) temperature and (B) oxygen availability on the biggest amphipod crustacean sizes for 9 marine (filled circles) and 3 reduced salinity sites (open circles). (A) 95%/5% threshold size (TS95/5) vs mean annual water temperature (inverted scale). (B) TS95/5 vs calculated dissolved oxygen content at saturation (µmol kg*$^{-1}$*), based on the surface water mean temperatures and salinity. Although not every habitat in the considered sites will experience permanent high oxygen saturation, this 100% value represents the optimal conditions for species to attain large size.*

TS95/5 in the equation *(4)* reaches zero when mean environmental oxygen is 183 µmol.kg^{-1}. This could indicate an environmental limit for amphipods. A variety of hot and/or highly saline conditions could produce 183 µmol.kg^{-1} of oxygen. No amphipods are found in such hot brine areas which are inhabited by organisms including brine shrimp and ostracods.

Surprisingly, minimum size does not vary significantly, either with temperature (Pearson correlation coefficient (PCC)=-0.019, P=0.952), or environmental oxygen (PCC=0.402, P=0.195). Clearly oxygen availability is not an overall selective pressure towards increased size for all species, but sets upper limits to maximum attainable size for the largest species (MPS).

Our data also show this increase of maximum size with oxygen to exist at the superfamily, family and genus level. Furthermore, comparing the size of the species present in more than one ecosystem revealed a similar trend within species (569 pairs analyzed).

If modal size corresponds to optimal size for a given body design, then optimal amphipod size increases with oxygen availability. However, minimum size is independent of environmental oxygen, temperature or salinity within the range of the investigated sites. Thus MPS increases dramatically with oxygen, modal size increases less and minimum size not at all, and the overall effect widens the size spectrum.

Having established that MPS in amphipods is tightly linked to environmental oxygen we now examine underlying mechanisms potentially underpinning this limitation: 1) the metabolic rate relationship with temperature. 2) haemolymph oxygen carrying capacity and 3) external oxygen availability,

1. Ectothermal basal metabolic rate rises with temperature, increasing tissue maintenance costs (Clarke, 1991; Ivleva, 1980). Although body size tends to decrease with increased temperature at marine sites, the largest amphipods were not found in our coldest sites (high Antarctic, 0°C), but in Lake Baikal (+6°C). Temperature-dependent trade-offs between tissue synthesis and catabolism apparently do not limit MPS, as the observed increase in MPS at freshwater sites despite the enhanced osmoregulatory costs would require an unlikely increase in resource acquisition.

2. Oxygen enters amphipod blood through a low-efficiency gill (Wolvekamp and Waterman, 1960), and is transported both by passive diffusion and bound to haemocyanin. Marine amphipod haemolymph contains 10-20 mg.cm3 haemocyanin (Spicer, 1993), which is low for crustaceans. Data from the Antarctic

giant isopod *Glyptonotus antarcticus* (Whiteley et al., 1997), also showing a relatively low haemocyanin level, suggest that Antarctic amphipods carry about 60-70% of their circulating oxygen in solution, whereas tropical species carry about 30-40% and Lake Baikal amphipods carry about 60-70% (as they have haemolymph osmotic concentrations around 340-360 mOsm, although being freshwater species). This reduces the haemolymph dissolved oxygen content of Baikal amphipods at 6°C to similar levels to marine species at 0°C. Thus Lake Baikal and Antarctic species should be similar sizes, instead of which TS95/5 is 54.4 mm for Baikal amphipods and 43.6 mm for Antarctic. This suggests saturation levels of haemolymph dissolved oxygen must increase from tropical to polar, and marine to freshwater environments, and the critical factor dictating MPS is gill efficiency.

3. According to Fick's law a key parameter determining oxygen uptake across a gill is the partial pressure difference between the external medium and the circulating haemolymph. For similar external partial pressure and gill efficiency, more oxygen will enter the blood at sites with low temperature and salinity, and thus higher absolute oxygen concentrations. Thus the saturation levels and absolute concentrations of oxygen in the blood will be higher at low temperature and salinity sites and amphipod MPS will reflect this in the way observed.

The above arguments indicate MPS is limited by oxygen concentration in the external water, mediated by a less than 100% efficient gill. Thus large size will occur at high concentrations, because a greater mass of oxygen will pass across the gills, increasing the possible path length for oxygen in the circulatory system.

The strong relationships we obtained were between external oxygen concentration and length, not body mass. However amphipods, like other groups showing large size at low temperatures and especially in Antarctica (e.g. pycnogonids and nemerteans) have a restricted circulatory system with few lateral branches. In other groups a stronger relationship with body mass would be expected. Whether MPS is reached will depend on several factors. In any environment with many species selection pressures will drive them into as many niches as possible and both large and small size will be exploited.

Oxygen supply has been suggested as the reason for Carboniferous insect gigantism, because during this period atmospheric oxygen was 30-35% (Graham et al., 1995). Their demise when oxygen content fell could indicate that large species are susceptible to such change and the giant amphipods described here would disappear first following elevated temperatures or other global oxygen reducing events. Being close to the critical limit for MPS in a given oxygen environment may be a specialisation making giant species more prone to extinction over geological time.

If the increasing skewness shown by the spectra on Figure 14 reflects the adult size distribution, it is not very relevant to evaluate the amphipod trophic impact as a whole for a given time and surface. A size histogram with all cohorts would reveal for all ecosystems, including Antarctica, an even bigger predominance of the small specimens (for example smaller than 20 mm), as the juveniles and immatures for big species would also be part of that fraction. On the other side, it is precisely the higher part of this histogram (thus bigger than 20 mm), which would distinguish the Antarctic amphipod taxocoenosis from the other marine ones, as the size range of their prey is expected to match this large size. Although no accurate data exist, the density of at least some of the biggest Antarctic species seems to be important (e.g. *Ampelisca richardsoni, Eusirus perdentatus, Abyssorchomene plebs* or *Tryphosella murrayi,* see Klages 1993, Vo 1988). This might explain the small number of benthic shrimp species in general, and the very low density of the smaller species in particular : from the 5 Weddell Sea species, *Chorismus antarcticus, Nematocarcinus longirostris* and *Notocrangon antarcticus* are abundant, but with an adult size of about 100 mm not overlapping amphipod size range while a potential competition with the commonest giant amphipods might explain the scarcity of *Lebbeus antarcticus* and *Eualus kinzeri*, both with a size comprised between 100 and 25 mm (Sieg & Wagele, 1990; Gorny, 1999).

3.3. DEVELOPMENT OF A BIODIVERSITY REFERENCE CENTRE FOR THE SOUTHERN OCEAN AMPHIPOD CRUSTACEA

The development of some new tools for the assessment and the identification of the whole Southern Ocean amphipod biodiversity has been undertaken.

A « Biodiversity Reference Centre » for Antarctic Amphipoda (ANT'PHIPODA) was set up at IRScNB. (Figure 16). It comprises on one hand a comprehensive database on taxonomy, geographic and bathymetric distribution, ecology (habitats, trophic type,…) and biology (size, reproduction,…) of the 850 Southern Ocean species. In addition, it assembles a specialised documentation referenced in a searchable bibliographic database and a large iconographic file for species identification purposes (De Broyer et al., 1999_{b}, 2000).

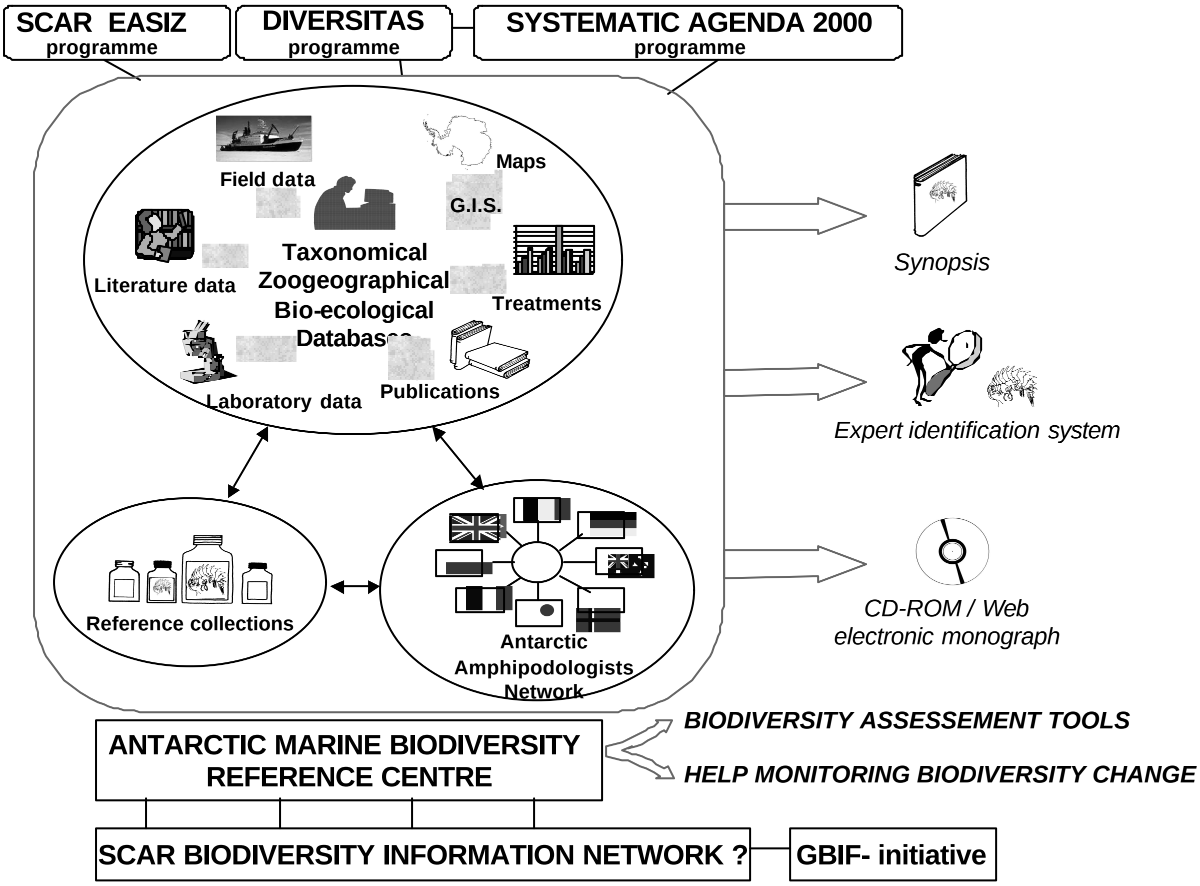


***Figure 16**: Scheme of the stucture of the "Biodiversity Reference Centre" for Antarctic Amphipoda (ANT'PHIPODA).*

On the other hand, the reference centre also includes extensive reference collection (400 000 specimens) of the Southern Ocean amphipod fauna provided by the Belgian Antarctic Expeditions and the Belgian participation in other Antarctic campaigns in the Weddell Sea, Queen Maud Land, Antarctic Peninsula region, Kerguelen Islands, Tierra del Fuego, or contributed by the « Antarctic Amphipodologist Network » or the Antarctic programmes of Argentina, Brazil, Chile, France, Germany, The Netherlands, New Zealand, Poland, Russia, U.K. and U.S.

A network of 13 specialists from 9 countries (the « Antarctic Amphipodologist Network ») was established to undertake the coordinated revision of the Antarctic amphipod fauna (see *e.g.* Berge et al., 2000; Berge, 2001$_{a,b}$) and the preparation of identification guides and an expert system for identification. The network includes : H.G. Andres (Hamburg); D. Bellan-Santini (Marseille); J. Berge (Tromsø); C.O. Coleman (Berlin); K. Conlan (Ottawa); C. De Broyer (Brussels, coordinator); M. Hendrycks (Ottawa), T. Krapp-Schickel (Bonn), K. Jażdżewski (Łódź); J.K. Lowry

(Sydney); M. Rauschert (Berlin); I. Takeuchi (Matsumaya) and M.H. Thurston (Southampton).

In paralell with the development of the reference centre « ANT'PHIPODA », a database (the « ABBED » database) on the benthos biodiversity of Admiralty Bay, King George Island, was set up in collaboration with the University of Łódź, Poland. Focussing on some representative groups (Crustacea, Echinodermata and Polychaeta), the ABBED database will integrate the abundant data collected during 25 years of study on the taxonomy, distribution and ecology of the Admiralty Bay benthos by Polish, Brazilian, German, Dutch and Belgian teams. It would contribute to manage and disseminate the biodiversity information and to monitor the benthic biodiversity change in this reference site of the SCAR EASIZ programme.

Finally, a web site devoted to « ANT'PHIPODA » has been created, at the URL:
http://www.naturalsciences.be/amphi

4. CONCLUSIONS

This study attempted to contribute to a better knowledge of the biodiversity of a nearly pristine area of the world, the Southern Ocean, and to a better understanding of the role of biodiversity in the Antarctic Coastal and Shelf Ecosystem.

In the present study, several key aspects of the structural and ecofunctional biodiversity of the peracarid crustaceans were investigated : composition of the taxocoenoses, spatial and quantitative distribution, specialisation with respect to ecological niches, roles in ecosystem trophodynamics and size distribution.

They were approached by field studies at the level of two reference sites of the SCAR EASIZ programme (Eastern Weddell Sea and Admiralty Bay, King George Island) and by a general study of the whole Southern ocean amphipod fauna.

The project first allowed some substantial additions to the inventory of the Antarctic benthic amphipods and to the knowledge of their precise habitats. New extensive data on their geographic and bathymetric distribution were collected, as well as detailed information on their ecological characteristics. New abundance and biomass data, which were still sparse at the amphipod group level and extremely limited at the species level in both reference sites, were gathered. Much effort has been devoted so far to the study of the eastern Weddell Sea reference community where particularly intensive and innovative sampling over several seasons provided a wealth of material. This effort also enhanced the crucial need for an intensification of comparable collection sets obtained with reliable quantitative samplers such as box-corers, in order to get accurate estimations of benthos biomasses and distribution over the whole Antarctic.

Rarely performed so far in the Antarctic, systematic observations of living animals in cool labs allowed new insights on the ecology and biology of a number of individual species. In particular, the behavioural observations and the gut contents analyses conducted on several hundreds of specimens of the most common amphipod species from the eastern Weddell Sea shelf clearly showed that these crustaceans have developed a wide range of trophic types, from suspension-feeding to carnivory, and feed on a large variety of food, from plankton to carrion. The only trophic type apparently lacking is macroherbivory, which can be explained by the absence of benthic macroalgae on shelf bottoms. Such a trophic diversity could probably be compared, and in some cases related to the diversity of benthic microhabitats. This large habitat diversity was demonstrated through the analysis of pictures got by still and video cameras, by observations in aquaria, and by sampling. Diverse symbiotic associations of amphipods with various invertebrates were also documented and appeared to be more common than expected.

Among the different feeding types noticed for the studied species, almost 50% deal with particulate organic matter (sinking or resuspended), the remainder being focussed on animal tissue consumption, either living (micro- and macropredatory) or dead (necrophagy). These trophic types, however, do not seem to be well defined for several species, some amphipods being likely able to shift from a diet to another (in a limited range of food size) with respect to environmental conditions and food availability. Taking into account the direct importance of particulate organic matter for detritivore and suspensivore amphipods, and its indirect importance as food source for the benthic invertebrates preyed by predator amphipods, it appears that the Weddell Sea benthic amphipod community is more closely dependent on primary production than previously thought. Many species are likely to suffer the seasonal variations of the latter, and could develop wintering strategies, such as diet change, reserve constitution or starvation. Necrophagy, for instance, could be a more exploited trophic way.

The role of the amphipod community in the global Antarctic food web, and in particular as prey for higher trophic levels, was approached through an extensive bibliographical survey. Amphipods are consumed by more than 190 different species of invertebrates, fishes, seabirds and marine mammals. They can represent almost 100% of the diet of some predators, either benthic or pelagic.

Another topic investigated in this project was the significance of the Antarctic amphipod size spectrum, gigantism and species richness. The arguments exposed in the results section indicate that Maximum Potential Size (MPS) is limited by oxygen concentration in the external water, mediated by a less than 100% efficient gill. Thus large size will occur at high concentrations, because a greater mass of oxygen will pass across the gills, increasing the possible path length for oxygen in the circulatory system. Whether MPS is reached will depend on several factors. In any environment, selection pressures will drive species into as many niches as possible and both large and small size will be exploited. It is clearly the case in Antarctica, where the minimum size for amphipod species is the same as in the tropics. If the number of such small species is still relatively low, taxonomic description of new small species is now increasing quickly (notably in the highly diversified family Stenothoidae) and this would allow a more accurate assessment of the size spectra.

Regarding this trend to use as many niches as possible, it is worth mentioning that the Antarctic species larger than 20mm show a wide trophic type diversity; macro-herbivores, detritivores, suspension-feeders, scavengers, micro- and macro-predators are all represented by giant species (Dauby et al., 2001_a). The selective pressures having driven these species to their large size are complex and related to many factors such as life style, fecundity, foraging range, competition and predation pressure to name a few. As such, they remain to be identified through careful case studies.

To contribute to a more accurate assessment of the Antarctic marine biodiversity, the “Biodiversity Reference Centre for Antarctic Amphipoda” has been initiated at the Royal Belgian Institute of Natural Sciences in Brussels with comprehensive databases, specimen collections and specialised documentation. In relation with the reference centre, an international group of specialists, the “Antarctic Amphipodologist Network” has been established and has started to revise the whole Antarctic amphipod fauna and to prepare new conventional identification tools and a expert system for identification.

In connection with the reference centre, the “Admiralty Bay Benthos Biodiversity Database” was designed through Belgian-Polish co-operation to compile and manage the pertinent data on benthos biodiversity, benthic environment and benthos-related biological and physical data. It remains to be implemented to contribute to assess and monitor the benthos biodiversity in a long studied reference site of the EASIZ programme, in the context of the global environmental changes.

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