Claude De Broyer[1], Jean-Henri Hecq[2] and Sandra Vanhove[3]

Life under the ice: biodiversity of the Southern Ocean

Abstract

In the present global context of environmental changes and accelerating loss of biodiversity, the assessment of Antarctic biodiversity, the understanding of its role in ecosystem functioning as well as the requirements for its conservation appear of critical importance.

This contribution presents a brief overview of the current knowledge on Antarctic marine biodiversity and some aspects of its role in key ecological processes. It also shows how the Belgian research programme ANTAR-IV contributes to biodiversity research in Antarctica by means of three complementary approaches integrated in the international programmes SCAR EASIZ (Ecology of the Antarctic Sea Ice Zone) and SO-GLOBEC (Southern Ocean-Global Ocean Ecosystems Dynamic Research).

The EASIZ (Ecology of the Antarctic Sea Ice Zone) programme investigates the structure and dynamics of the marine Antarctic coastal and shelf ecosystem, the most complex and productive in Antarctica, the richest in species and likely the most sensitive to global environmental changes. Particular attention is given to the Antarctic benthic sub-system. At the macrobenthos level, the project conducted at IRScNB focuses on the description and evaluation of the ecofunctional role of biodiversity (in particular the species richness, trophodiversity and size spectra) using as target group, the peracarid crustaceans. In addition, it aims at developing new synthetic tools for the characterisation of the structural biodiversity of the Southern Ocean crustaceans and its spatial and temporal variability. The project of the Marine Biology Section of the University of Gent, also a part of EASIZ, focuses on the importance of structural and functional biodiversity of meiobenthos for the productivity of the coastal and deep shelf zones of the Southern Ocean ecosystem. Meiofauna communities contain a large number of species, usually an order of magnitude greater than for any other major benthic taxon. Emphasis is placed on the relation of the meiofauna (species, size and trophic aspects) with the micro-environment and macrobenthic structures and on the interactions between the biotic and abiotic parameters of the south polar marine environment. The meiobenthic resilience capacity to iceberg scouring is studied with particular reference to the Global Warming.

In the framework of the SO-GLOBEC (Southern Ocean-Global Ocean Ecosystems Dynamic Research) programme, the pelagic compartment of the Southern Ocean ecosystem is addressed by the Ecohydrodynamic unit of the University of Liège. The project's main objective is to develop a coupled physical/biological model capable of simulating multiparametric variability in biodiversity and productivity, specifically connected to climate and anthropogenic changes. Within this project, the importance of picophytoplankton at the basis of the food web will be assessed by using molecular tools for the characterisation of algal biodiversity.

The three approaches contribute to the objective of the ANTAR-IV programme to develop a better understanding of the role of biodiversity in the production and resilience of the Southern Ocean.

[1] Institut royal des Sciences naturelles de Belgique, Département des Invertébrés (Laboratoire de Carcinologie), Rue Vautier 29, B-1000 Bruxelles, Belgium - claude.debroyer@naturalsciences.be

[2] Université de Liège, Ecohydrodynamique, Sart Tilman - Physique B5, B-4000 Liège, Belgium, jhhecq@ulg.ac.be

[3] Universiteit Gent (RUG), Instituut voor Dierkunde, Mariene Biologie, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium, sandra.vanhove@rug.ac.be

The *Belgica* Expedition Centennial: perspectives on Antarctic science and history. Proceedings of the Belgica Centennial Symposium, 14-16 May 1998, Brussels. Decleir H. and C. De Broyer (Eds). VUB Brussels University Press. Brussels, Belgium.

Introduction

The richness of life on Earth, the Planet's biodiversity, is under threat even in the most remote places of the globe.

Changes in the global environment, in particular the global warming and the increased UVB radiation due to the seasonal ozone hole, effects of global pollution, non sustainable exploitation of living resources and increasing local tourism have or may have negative impacts on the biodiversity of the Antarctic continent and the Southern Ocean.

The high patrimonial and scientific value of the Antarctic biodiversity and environment and the threats to their conservation prompted the signature of the "Protocol on Environmental Protection to the Antarctic Treaty" in Madrid in 1991. Signatory parties agreed on "the comprehensive protection of the Antarctic environment and dependent and associated ecosystems" and to designate Antarctica "a natural reserve devoted to peace and science".

In the present global context of environmental changes and accelerating loss of biodiversity, the assessment of Antarctic biodiversity, the understanding of its role in ecosystem functioning as well as the requirements for its conservation appear of critical importance. Today, in many places all over the world, biodiversity research focuses on fauna and flora inventories, taxonomy and classification or on the processes driving the origin, maintenance and change of biodiversity. The roles of biodiversity in ecosystem functioning as well as conservation, restoration, sustainable use and monitoring of biodiversity are other very active research fields. World wide research efforts are tentatively catalysed and promoted under the umbrella of the international DIVERSITAS programme (Diversitas, 1996).

For the Southern Ocean, the rationale (and concern) behind the biodiversity research can be summarised in a few fundamental questions challenging Antarctic biologists today:

- What is living there and what do we know about it? What is the origin of the Antarctic biodiversity?
- How and to what extent is (or will be) the Southern Ocean biodiversity affected by enhanced UV levels due to the seasonal ozone hole, or by direct or indirect effects of the global warming or by global or local pollution?
- How and to what extent will loss or changes in biodiversity affect the structure and functioning of the Southern Ocean ecosystems? Are these changes and their responses predictable? How can we discern natural changes from man-induced changes?
- What is biodiversity's role in the resilience of ecosystems facing striking climatic changes or unusual biotic events?

So far, few of these crucial questions have received even partial answers.

The present paper intends to briefly overview the current knowledge on Antarctic marine biodiversity and some aspects of its role in key ecological processes. It will also show how the Belgian Research Programme on the Antarctic (ANTAR-IV) contributed to biodiversity research in Antarctica by means of three complementary approaches integrated in the international programmes SCAR EASIZ (Ecology of the Antarctic Sea Ice Zone) and SO-GLOBEC (Southern Ocean-Global Ocean Ecosystems Dynamic Research).

Composition and patterns of biodiversity

The depth of our ignorance

Biological diversity was defined by the Rio Convention as: "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". Biodiversity can thus be approached at the level of its three major hierarchical and complementary components: the genetic level (genes and genetic variability), the organismal or taxonomic level (species and populations) and the ecological level (ecosystems, landscapes). In structural biodiversity studies dealing with the description of the biodiversity components (composition) and the way they are organised (e.g. patterns of distribution), the organismal or species level is central as species are the basic units of classification, constitute the ecological groupings and also are the most practical and commonly used currencies when referring to biodiversity.

The complexity of the world's ecosystems is immense, and the knowledge currently available on global biodiversity is very fragmentary. According to the Global Biodiversity Assessment, less than 1.8 million species of all types of living organisms (animals, plants, fungi, bacteria, viruses,...) have been described so far world-wide, whereas estimates of the real number of species range from 5 to 30 million (UNEP, 1995). Even in the best-known phyla new species are still being discovered at a significant rate. Systematic biologists are being asked to accelerate their exploration of life on Earth to provide science and society with essential background knowledge, to

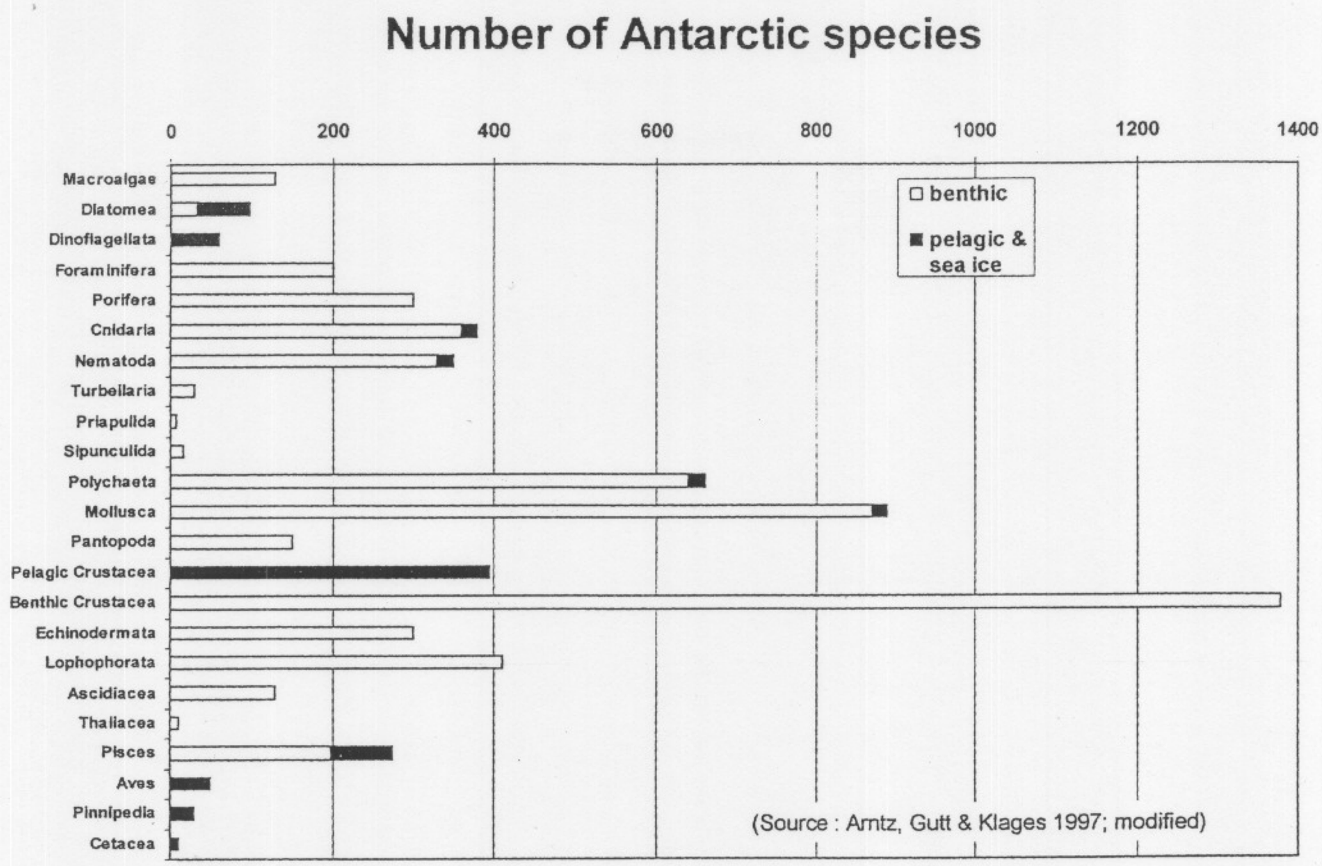


Fig. 1. Species richness in Antarctica. The bars give the number of species occuring in the benthic sub-system (grey area) and in the pelagic and sea-ice sub-systems (black area).

discover and utilise new biological resources and make informed decisions that will ensure preservation of the earth's biological diversity.

The gaps in our knowledge of marine biodiversity are obviously deeper than in terrestrial biodiversity: only about 250 000 marine species have been described to date (Winston, 1992). This ignorance is well illustrated by the recent controversial discussion about the potential number of deep-sea bottom species: numbers of several tens of millions (Grassle & Maciolek, 1992), half a million (May, 1992) or 5 million (Poore & Wilson, 1993) of undescribed species have been suggested for the very poorly known bathyal (continental slope) and abyssal fauna of the world's oceans.

The general lack of knowledge of the world marine species clearly stresses the need for taking significant actions to discover, describe, and understand marine biodiversity, for consolidating the existing knowledge and the often vanishing taxonomic expertise and for efficiently organising and distributing the biodiversity information.

Biodiversity of the Southern Ocean

The species richness of the Antarctic seas appears much higher than can be expected *a priori* from this extreme environment that is characterised by permanent low temperatures, a long polar night, a wide ice cover and a marked seasonality of primary production strongly limited to a short summer period.

Since the pioneering studies of the Antarctic marine fauna – in particular the bottom fauna, by the *Belgica* expedition one hundred years ago – a substantial number of taxonomic and ecological works have contributed piece by piece to the assessment of the Southern Ocean biodiversity. The last two decades have seen a new phase of discovery mainly due to technological progresses. They included the use of well equipped research icebreakers, sophisticated remotely operated vehicles (ROV) and more efficient collecting methods and gears such as epibenthic sledges, Rectangular Midwater Trawls, Autonomous Trap Systems, video-controlled Multiboxcorers or the generalization of SCUBA diving.

The present state of knowledge of the nature of the Southern Ocean biodiversity is unevenly developed according to the different ecosystems (oceanic, coastal, shelf or deep sea), the various components of these ecosystems (sea-ice, water column or bottom sub-systems) and, finally, the different taxonomic groups. The overall species richness for most marine animals and plants taxa that occur in the Southern Ocean south of the Polar Front was recently compiled by Arntz *et al.* (1997) (Fig. 1). The graph shows the relative importance of polychaetes and molluscs and the predominance of crustaceans.

The faunistic inventory can be considered close to completion for the Antarctic vertebrates, but for invertebrate taxa the inventory is obviously far from complete. Estimates of unknown species are inevitably speculative and varied according to the groups and the specialists. For example, only a small number of about 350 on presumably 2000 or more meiobenthic nematode species are effectively described. Most of these descriptions dated back to Antarctic expeditions in the first half of previous century.

The patchy nature of coverage of biodiversity and ecological surveys in the Southern Ocean must be stressed: there is still a number of geographical regions and bathymetric zones which are largely undersampled or unknown. The Antarctic deep sea in particular (i.e. the bottoms along the continental slope and the abyssal plains) are virtually unknown. In this context it is interesting to note that studies of deep sea macrofauna in the north western Atlantic by Grassle and Maciolek (1992) and studies of isopods in south-east Australia by Poore *et al.* (1994) pointed to unexpectedly high species diversity at slope depths. In the former case, 64% of peracarid crustaceans were undescribed species, while in the latter the proportion amounts to 90% of unknown isopod species.

Meiobenthic species diversity studies in the deep-sea are few in general: Dinet and Vivier (1979) reported for the first time a peak in meiofaunal nematode diversity at 4000m in the Bay of Biscay, and recent work on nematode diversity in the western Indian Ocean (Muthumbi, 1998) similarly elucidated high deep-sea diversity. Nothing at all is known from the Antarctic deep sea.

Large areas of the Antarctic continental shelf remain to be explored. Some particular habitats (e.g. the benthic boundary layer, the benthic symbiotic habitats, the under ice habitats,...) have not received enough attention. A number of taxonomic groups (e.g. polychaetes, nematodes,...) remain understudied. In general, pelagic species – usually less numerous, widely distributed and easier to collect – are better known than the less accessible and highly endemic bottom fauna and flora. There is, however, in both pelagic and benthic systems, a larger ignorance of small-sized (e.g. meio- and microbenthos) or very small-sized species (e.g. picoplankton).

The belief that Antarctic bottom communities are so rich and diverse that they can compare, for example, with tropical seagrass or coral communities, received some support from recent studies but remains under debate (Arntz *et al.* 1997). Species number compilations clearly indicated that there is a variety of species-rich and species-poor taxa: sponges, bryozoans, molluscs, polychaetes, amphipods and isopods indeed have a high absolute number of species, but this does not hold true for instance for stomatopods (which are totally absent), reptant decapods (which are almost absent), and natant decapods, which are few.

Moreover, there seems to be no common pattern for species richness in the various subsystems (e.g. pelagic versus benthic, shallow versus deep). On the other hand, any sound comparison of Antarctic marine biodiversity with other regions remains strongly hampered by differences in area, environment, sampling and processing, and level of taxonomical knowledge. Whether macrobenthic diversity is actually higher in the Antarctic than in other marine ecosystems remains therefore to be demonstrated.

For meiofauna it is even worse. Although sampling and processing is quite comparable in many meiofaunal studies, diversity measures are often constricted to the community level and, in most cases, absent on species level, especially in the deep sea and obviously in Antarctica. Yet, our current knowledge on meiofaunal species diversity does not allow any decent comparison between Antarctica and other parts of the world.

Belgian contributions to structural biodiversity research in the Southern Ocean

The water column

As a part of the ANTAR-IV programme, and in the framework of a more comprehensive study of the picophytoplankton (the plankton size fraction of 0.2-2 μm) in the Southern Ocean, the Department of Botany of the University of Liège has undertaken by using molecular techniques the assessment of the genotypic diversity of the different types of organisms present in the picoplankton (picocyanobacteria and plastids of picoeukaryotic algae), at the basis of the pelagic food web of the Southern Ocean (Wilmotte *et al.*, in press).

The macrobenthos

Marine benthic animals (or zoobenthos) are often present in large numbers on Antarctic bottoms (Plate 34). They can be divided into different groups according to habitat or to size category: macrobenthos (above 0.5 or 1mm), meiobenthos (defined as interstitial organisms within the size range of 38 μm and 1mm) and the very small microbenthos (below 0.1 mm: mainly bacteria and unicellular organisms).

To contribute to the assessment of the biodiversity of the benthic communities of the South-

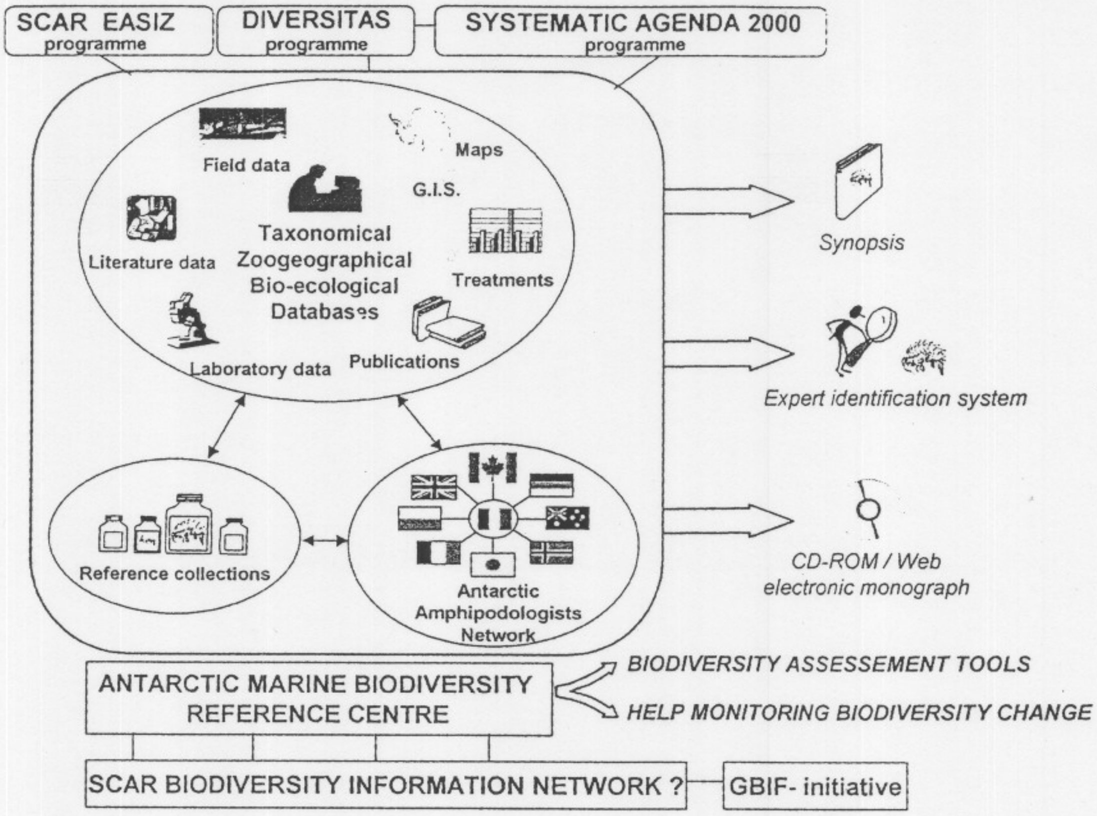


Fig. 2. Scheme of the stucture of the "Biodiversity Reference Centre" for Antarctic Amphipoda (ANT'PHIPODA).

ern Ocean, the ANTAR-IV project conducted at the Department of Invertebrates of the Belgian Royal Institute of Natural Sciences investigates the peracarid crustaceans, as a target group representative of the vagile macrobenthos. According to our present knowledge, these crustaceans (Amphipoda, Isopoda, Tanaidacea, Cumacea, Mysidacea) form the most species-rich animal group in the Southern Ocean (De Broyer & Jazdzewski, 1996). They also constitute one of the most diverse marine groups, in terms of modes of life, trophic types and habitats.

Their diversity and the limited knowledge of their taxonomy, distribution and ecology prompted the project to conduct detailed investigations of the peracarid fauna in different regions of the Southern Ocean and to elaborate new synthetic IT tools to describe, analyse, and disseminate the biodiversity information on this important group of Antarctic marine animals.

In particular, the project aims at developing a "Biodiversity Reference Centre" devoted to amphipod crustaceans (Fig. 2). The reference centre will be comprised, on one hand, of a comprehensive database designed to compile the widely scattered published data and new information on taxonomy, distribution, ecology and biology of the Southern Ocean amphipod crustaceans, and, on the other hand, of extensive reference collections of specimens and specialised documentation. It will operate with the collaboration of a network of contributing specialists grouped in the "Antarctic Amphipodologist Network". The Network is engaged in a revision of the whole Antarctic amphipod fauna in order to develop new conventional identification tools and computer interactive keys. It will also synthesise the taxonomical distribution and ecological knowledge of this important group of crustaceans. In addition, with the development of related local biodiversity databases (such as the Belgian-Polish project of "Admiralty Bay Benthos Biodiversity Database" at King George Island), it should contribute to the monitoring of local changes in biodiversity in selected (EASIZ) reference sites.

The meiobenthos

The meiofauna are the most important metazoan group in marine sediments, in terms of abundance. With their high productivity, grazing and respiratory activity they form a potentially important step in the detrital food web (Giere, 1993). They harbour many different habitats in which they constitute a variety of life forms. Despite the very high meiobenthic standing stocks in the Southern Ocean (reaching almost 20 million individuals per m^2, Vanhove *et al.*, 2000) meiobenthos research remains a big white spot in Antarctic benthic diversity studies. Therefore meiobenthos is studied at the Marine Biology (Ghent University) within the framework of the

ANTAR project (phase III and IV). As about 80 to 90% of the Southern Ocean meiofauna are composed of nematode communities, this faunal group was chosen as a target group representative of the Antarctic interstitial meiobenthos.

The nematode communities in the Southern Ocean are highly diversified along the ice-shelf up to the upper slope (Plate 28). Although primarily influenced by food and grain size, underlying mechanisms include productivity, hydrodynamics, and iceberg-related processes. But also macrofaunal structures such as sponge spicule mats and bryozoan debris are important environmental forces behind this high diversity (Vanhove *et al.*, 1999).

However, two remarks should be made:

(i) our current knowledge on meiobenthic diversity is limited to one region only (i.e. the Weddell Sea). Obviously, the degree of variability in meiobenthic diversity remains to be established among a multitude of different Antarctic habitats.

(ii) Although sampling and processing is quite comparable in many meiofaunal studies, diversity measures are often constricted to the community level and, in most cases, absent on species level, especially in the deep sea and obviously in Antarctica. This is due to the high percentages of juveniles (40-70%) and inadequate descriptions of deep-sea and Antarctic nematodes superimposed on the high proportion of undescribed Antarctic species.

Many questions that have been answered partly for macrobenthos have not been touched at all for meiobenthos: How many meiobenthic species (described and undescribed) are there in the Southern Ocean? How many are endemic? Are Antarctic deep-sea nematode communities diverse? Does meiobenthic diversity in the Antarctic agree with the often observed high species richness for macrobenthos?

If progress in the field of diversity studies is to be achieved, an increased distribution of available knowledge on nematode taxonomy is needed. Therefore a methodological tool for improving identification, classification and description of specimens has been developed at the Marine Biology of Ghent University. The approach, "NEMASLAN: Biodiversity of Antarctic nematodes", is an Access database application available on CD-ROM. It provides all necessary information to identify the animals and allows synthesis of the taxonomical knowledge, together with distribution and ecological information of the 350 species of free-living marine nematodes from the Southern Ocean.

Ecofunctional biodiversity

More than counting species: the role of biodiversity in ecosystem functioning

The concept of biodiversity is not only reflected by the number of species or taxonomic entities present in a given area and in the distribution of individuals among species, but also by the variety of ecological roles of species and functional groups of species. Functional biodiversity addresses in particular the variety of species interactions with ecological processes (Martinez, 1996).

Human pressure on the marine environment has never been so intense. Many human-induced physical, chemical and biological changes are adversely affecting biological diversity, and a range of activities are currently resulting in widespread degradation or even complete destruction of different marine habitats. There is growing evidence that biological diversity plays a role in the resilience of ecosystems. Based on the latest evidence, the capacity of ecosystems to resist changing environmental conditions, and to rebound from unusual climatic or biotic events, is related positively to species numbers. The presence of many species would generally increase the chance that, if rapid change exterminated some species, there would be an ecological equivalent present, that is more tolerant to the particular change and able to take over the roles of the absent species (UNEP, 1995).

Ecofunctional biodiversity of the Southern Ocean

A first but unavoidable step in understanding the role of biodiversity in the functioning of the Southern Ocean ecosystem – a topic that remains poorly studied – is the investigation of the variety of ecological roles of species or functional groups of species in the various marine subsystems. Among the different ecosystems that can be distinguished in the Southern Ocean, the Antarctic Coastal and Shelf Ecosystem (ACSE) in the seasonal sea-ice zone appears to be the most complex and species-rich ecosystem. It has not only a long evolutionary history and a limited human impact, but, compared to other marine ecosystems, it reveals relatively constant conditions of temperature and salinity in contrast to the highly fluctuating seasonal light regime and sea ice cover. Furthermore, compared to other oceanic regions, the pelagial of the Southern Ocean, in the seasonal sea-ice zone, exhibits the unique feature of a very short, but intense summer phytoplankton bloom, followed by a very poor production period during the rest of the year (e.g. Clarke, 1988; Arntz *et al.*, 1994). This high pro-

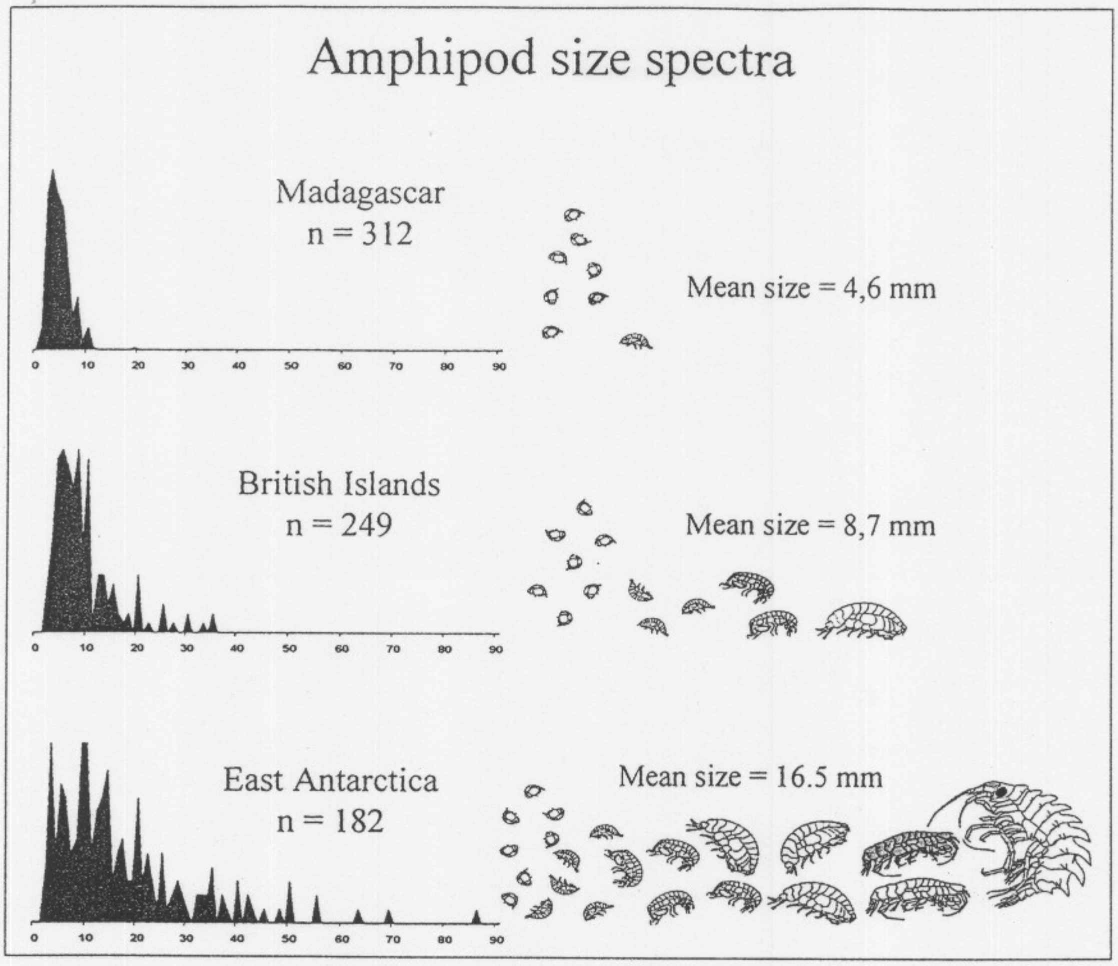


Fig. 3. Marine amphipod crustacean size spectra from the tropics to the pole, showing the increase in mean size (colored amphipod). (Chapelle, in press).

duction is particularly obvious in some coastal and neritic areas of the Antarctic ocean and is often associated with the melting of sea ice. As benthic communities depend heavily on the supply of resources from the water column above (Graf, 1992), the seasonality, intensity and spatial heterogeneity of the vertical fluxes resulting from the pelagic production significantly affect its size and structure. Finally, the Antarctic benthic environment is exposed to high physical variability and disturbance due to the current regime and ice-related factors (anchor ice, iceberg scours, ice shelves).

To improve our understanding of the structure and functioning of the ACSE, the "Ecology of the Antarctic Sea Ice Zone" (EASIZ) programme was launched by SCAR. EASIZ proposed an integrated study of the sea ice, the water column, and the benthic subsystems principally organized around the investigation of key-processes (and key-species) in a network of reference sites (SCAR, 1994).

The macrobenthic communities in the ACSE show in many places high species richness, abundant populations, and high biomasses. The continental shelf, (in particular in the well investigated Weddell Sea), to a depth of more than 600m, is often dominated by species-rich and multi-stratified assemblages of abundant and diverse suspension feeders, such as sponges, bryozoans, cnidarians, hydrozoans, holothurians and crinoids. Abundance, structure and composition of this mega-epibenthos appear however quite variable from one region to another, depending on different biological parameters and environmental factors, such as shelf area, depth, current, or sedimentation (Gutt & Starmans, 1998). Shelf bottom cover appears mostly patchy and ranges from a few percent to 100% of the bottom surface. This patchy, diverse and multi-stratified sessile benthos offers a high diversity of potential microhabitats to small vagile invertebrates, like peracarid crustaceans and interstitial meiofauna.

Size diversity and gigantism in macrobenthos

Many benthic species, especially in the High Antarctic, exhibit particular life history features ("K-strategists"): delayed maturity, incubation of large yolky eggs, absence of larval stages, slow growth and high longevity. It is also well known to benthologists that the largest representatives of several marine groups' are found on the Antarctic bottoms. This gigantism is particularly conspicuous for the arthropods, with among others, the 8

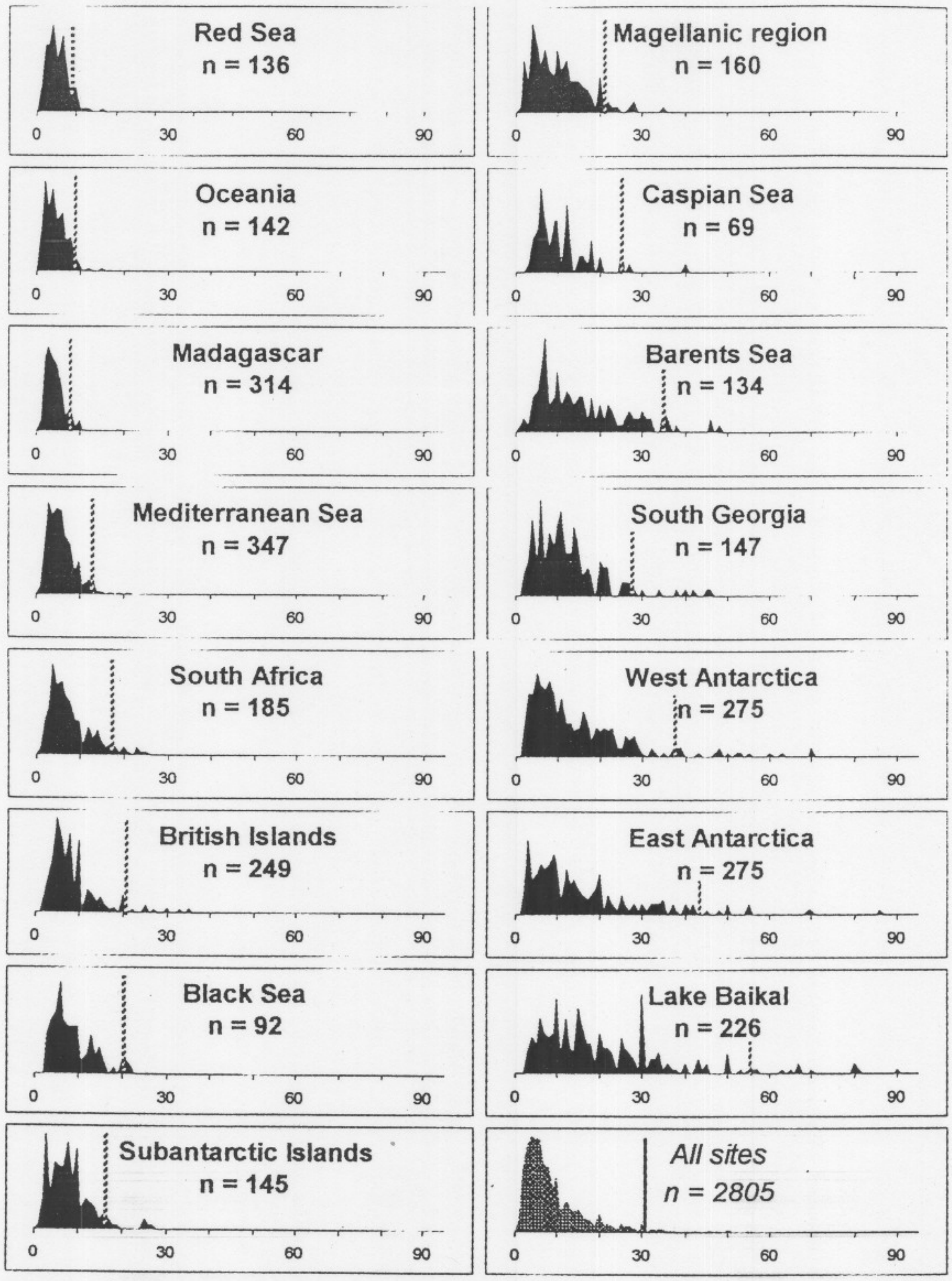


Fig. 4. Amphipod crustacean size spectra for the 15 selected sites (12 marine and 3 brackish or freshwater). The order follows the absolute oxygen concentration gradient. The last graph pools all the other ones. For each spectrum, n = number of species. The bar indicates the TS95/5, which corresponds to the Threshold Size separating the 95% smallest species from the 5% largest for each area. (Chapelle, in press).

to 12-legged giant pycnogonids or the 12cm long *Glyptonotus* among the isopods.

Among the highly diverse amphipod crustaceans, there is a remarkable number of Antarctic species with an adult size bigger than 30mm, which can be considered giants in the group. Although spectacular, this size diversity remained to be characterised in details as well as its underlying factors (Fig. 3).

In the framework of the ANTAR-IV programme at IRScNB, this characterization has been approached so far by establishing and analyzing the size spectra of the Antarctic fauna compared to 14 other geographical areas.

Combining temperature as well as salinity variations, this wide scale comparison of more than 2000 species over the world has yielded an unexpected result: the size spectrum width of a given site is directly related to the oxygen availability. In other words, for an amphipod crustacean, it means the more oxygen is present, the bigger it can get. (Fig 4).

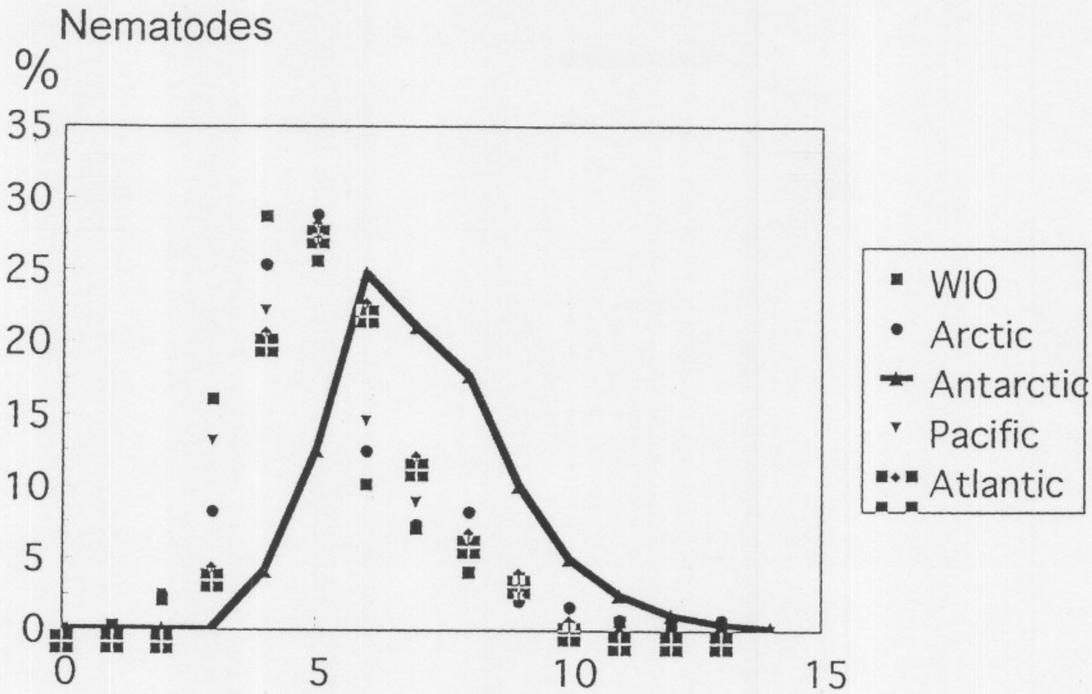


Fig 5. Relative frequency distribution of total nematode numbers over different weight classes on a geometric scale. It shows a clear shift in Antarctic nematodes towards the higher size classes. Biomass spectra are constructed using X2 geometric size classes in which size class 0 = 0.00465-0.0093 µg dwt, class 1 = 0.0093-0.0186 µg dwt and so on.

Beyond its physiological implications, this very clear trend also might allowed to focus the existing debate about the relationship between size and temperature for ectotherms. Before this study, it was widely believed that the Antarctic amphipods simply were bigger than their low latitude relatives. This assumption was logically followed by the hypothesis that cold temperatures should lead to bigger sizes. But our results point to a different conclusion: the bigger size are dictated by oxygen availability. The oxygen availability does not act as a selective pressure towards a bigger size, but, on the contrary, sets an upper limit to the size. And it is this upper limit (defined as the Maximum Potential Size) that increases with oxygen availability, while the lower limit of the spectrum is stable throughout the different sites.

The following physiological mechanism was proposed to explain this phenomenon (Chapelle & Peck, 1999). As respiration at rest in amphipods is mainly passive, it can be speculated that the amount of oxygen diffusing inside the circulatory system is directly proportional to the absolute concentration of oxygen in the water. Consequently, a greater mass of oxygen can be passed into the blood in Antarctic conditions, although the difference between the external and internal partial pressures remains constant throughout all sites. As there is more oxygen in a given volume of haemolymph, it can circulate through a longer path length before complete depletion of its oxygen by the mitochondria. Hence, a bigger size of the whole organism is possible (but not obligatory). Whatever the explanation, once applied to the Antarctic bottoms, this principle opens potentially one of the widest of the studied size spectra, as the reduced temperature (0°C around the year) increases oxygen solubility. Furthermore, as the Antarctic climate has been sufficiently stable for the last few million years, the amphipods have had the time to exploit the whole size spectrum (ranging from the 2mm-stenothoid to the 100mm-*Paraceradocus gibber*). This has been done by developing a number of species with a size never reached in warmer environments, opening and occupying in the process a whole variety of new "niches".

Size diversity and biomass spectra in meiobenthos

For the meiobenthic nematodes biomass figures clearly differ from other deep-water communities (Fig 5). Although the combination of high but seasonal oscillating food input and low ambient temperatures may be the key to the understanding of this phenomenon, real evidence is lacking. Until now it is not clear whether this characteristic (observed at 2000m) is a general rule for Antarctic nematodes or whether only a set of species fulfill a specific functional role by enlarged biomasses.

Biodiversity and trophic webs in the Southern Ocean: macrobenthos

The trophodynamic role of the peracarid crustaceans at the level of Antarctic benthic communities was investigated at the Royal Belgian Institute of Natural Sciences within ANTAR IV. These crustaceans, and in particular the amphipods, can show high abundance in littoral,

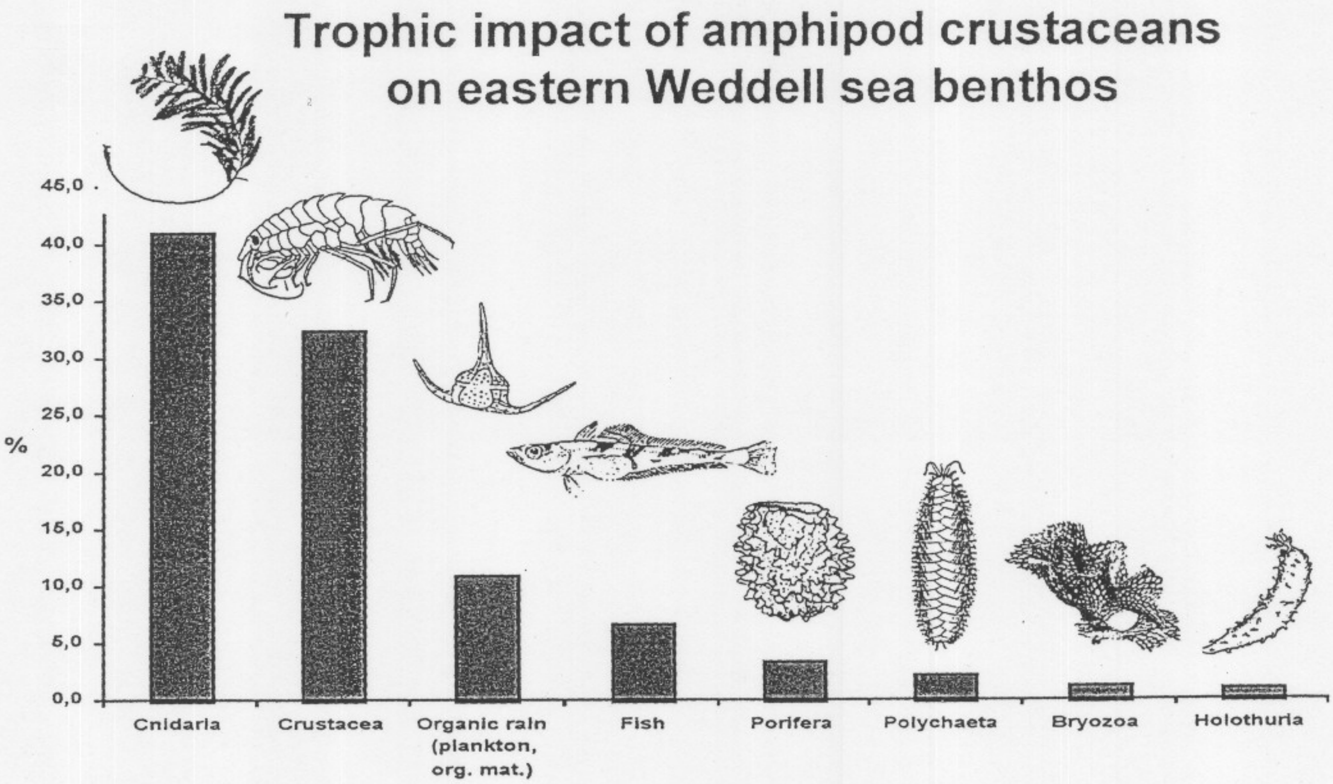


Fig 6. Mean relative trophic impacts (in %) of the Eastern Weddell Sea benthic amphipod community on the different potential food sources, as calculated by Dauby et al. (2001b).

sublittoral and shelf communities (Jazdzewski *et al.*, 1991), and, despite their low biomass, they constitute one dominant group in terms of energy fluxes in the High Antarctic shelf ecosystem (Jarre-Teichmann *et al.*, 1997).

They provide an important food resource for bottom and demersal fishes and contribute to the diet of a number of bottom invertebrates (such as isopods, amphipods, shrimps, cephalopods, echinoderms,...) and also of many birds and seals (Dauby *et al.*, 2001a).

Previous work on the rich bottom communities of the Weddell Sea in the High Antarctic and at King George Island in the West Antarctic have indicated a rather great variety of feeding types and modes of life among the usually abundant amphipod crustaceans (De Broyer *et al.*, 1999; 2001; Dauby *et al.*, 2001a).

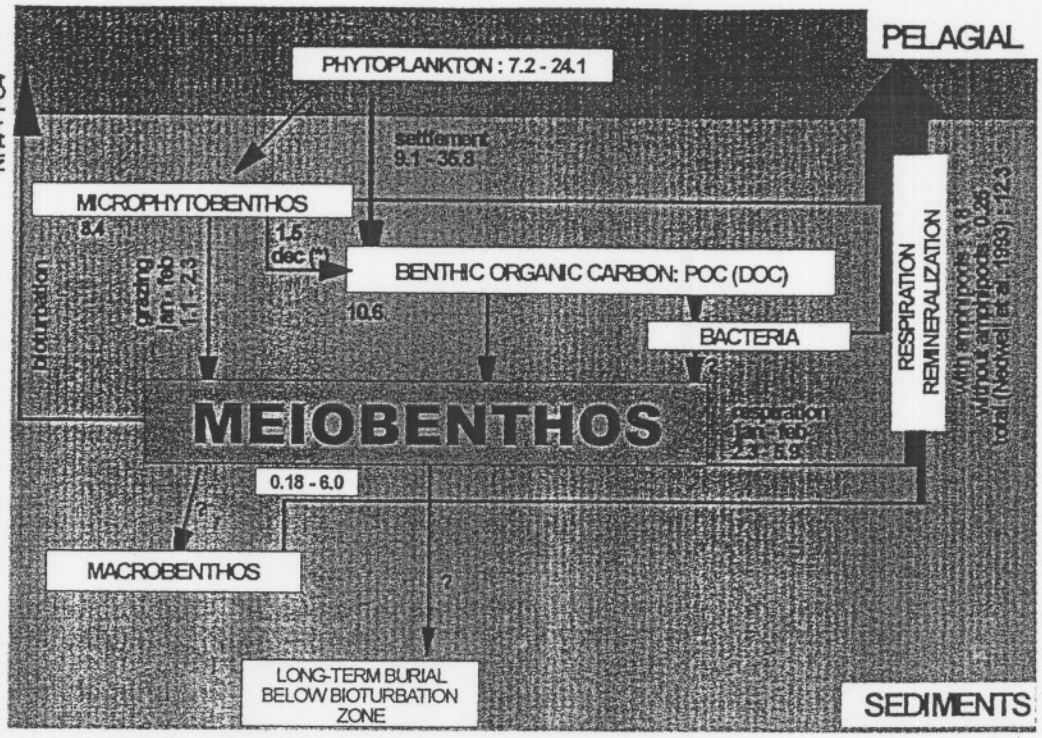
The trophic structure of the amphipod taxocoenoses in two EASIZ reference benthic communities was established by defining the diverse trophic guilds, or functional groups of species that exploit same or similar food and space resources and thus play a similar role in the food web. This guild concept integrates the trophic type, the mode of life, the habitat, and the potential foraging range (Plate 29).

To evaluate the relative importance of the different species in the trophodynamics of the ACSE system, and to try to detect potential key species, a quantitative estimation of the trophic impact of amphipods on the benthic system was made (Dauby *et al.*, 2001b) as well as an estimation of their importance as food for other trophic levels (Fig 6).

Biodiversity and trophic webs in the Southern Ocean: meiobenthos

Meiobenthos harbour many different habitats in which they constitute a variety of life forms and feeding mechanisms, including herbivory, bacterivory, detritivory, predatory, scavenging, absorption and suspension-feeding. Yet, an important aspect of meiobenthic studies is their energetic role. How much energy do they produce? What percentage of the total energy do they use? And what is their ultimate fate and function? are questions of striking interest in understanding the role of meiobenthos in a particular ecosystem.

Generally, close links between micro-organisms, detritus and meiofauna integrate meiofauna into a "detrital trophic complex" (Giere, 1993). Meiofauna preys on bacteria, but due to the immense bacterial productivity, the result is only rarely a reduction of bacterial biomass. On the contrary, gardening effects of meiofauna enhance bacterial stocks. By this grazing and by bioturbation meiofauna stimulate detrital breakdown in the bacterial food loop. Meiofauna also consume diatoms, flagellates, ciliates, etc... Alternatively, through their bioturbation activity the meiobenthos mix the sediment and change its physicochemical properties. Thus, they are important



note: * : recalculated from Gilbert 1991b

Fig. 7. Role and position of the meiobenthos in the Antarctic ecosystem carbon budget. Details are given in Vanhove *et al.* 1997.

organisms transferring phytodetritus through the sediment-water interface during the few days after particle deposition. As sediments are important sites of degradation of organic matter, leading to the transfer of nutrients (oxygen, nitrogen, phosphore, silicate and carbon) through the sediment-water interface, this burial of sedimented plankton enhances the initial decomposition processes, hence making more detritus available to macro-consumers.

The summation of all meiobenthic activity must be of high importance in the Southern Ocean, as an immense primary production settles down, though only a minor fraction of organic food remains in the sediments.

Experimental assays (grazing, respiration, nutrient fluxes) (Fig 7) show that meiofauna form, indeed, a potentially important step in the energy web in the Southern Ocean ecosystem (Vanhove *et al.*, 1997). Meiofauna respond efficiently to the seasonal varying Antarctic environment, which is a key characteristic for Antarctic ecosystems (Clarke, 1988). Based on annual P:B values for temperate nematodes, annual meiobenthic secondary production in the low subtidal zone of Signy Island (South Orkneys Islands) is estimated to be between 2.2 and 38.4 $gC.m^{-2}.y^{-1}$ for P:B values between 4 and 69. These values greatly exceed those calculated for nematodes in other regions in the northern hemisphere. When using the lowest value meiobenthic secondary production amounts to about 2% of the primary production for this region and 11% of the downward organic flux rates. Yet, a high percentage of the export flux is channelled into the meiobenthic communities of the Weddell Sea.

Flux measurements of organic matter, nutrients and oxygen suggest also that the meiofauna in Antarctic sediments may provide an important pathway by which deposited and *in situ* produced organic matter is channelled through the differing benthic components and from the sediment back into the water column. As Southern Ocean sediments are the major repository for biogenic silica and other nutrients, reintroduction (mediated by meiofaunal activity) may have a major effect on global nutrient cycling, and hence, the productivity of the Southern Ocean.

The project at the Marine Biology Section of the University of Gent, partly in the frame of EASIZ, will continue to focus on the importance of functional biodiversity of the meiofauna for the productivity of coastal as well as deep shelf zones of the ACS Ecosystem. Specific questions dealing with the relation of production and biodiversity of the Southern Ocean are: How does the meiofaunal component of the benthic system respond to these numerous abiotic and biotic peculiarities? How do changes in the environment result in ecosystem species composition?

In the ANTAR-IV programme emphasis is made on the relation of the meiofauna characteristics to the micro-environment and macrobenthic structures and to the study of the interactions between the biotic and abiotic parameters of the south-polar marine environment.

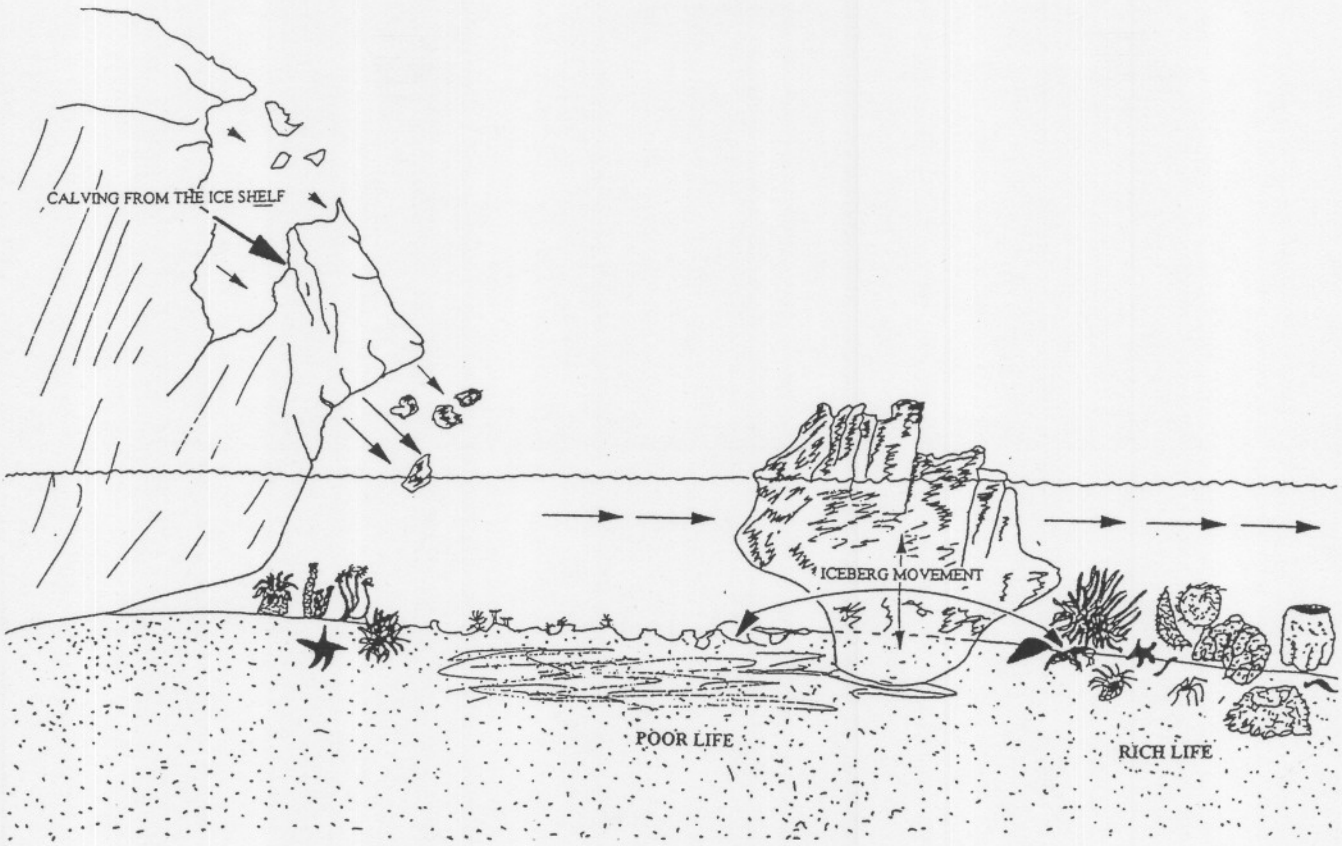


Fig. 8. Biodiversity and resilience in the Southern Ocean communities: recovery of the benthos after iceberg scouring.

Biodiversity and resilience in the Southern benthic communities

There are two opposing views about the importance of species diversity for ecosystem functioning. The first view holds that species in areas of high diversity are highly specialised and often co-evolved and that each species is of importance for ecosystem functioning. Every loss of a species is thought to affect ecosystem functioning, making it in some way less effective. According to the second view, many of the species present in high-diversity ecosystems may be redundant, as they carry out the same function, and the loss of some species is unimportant for ecosystem processes.

The Antarctic ecosystem is of particular interest for resilience studies as the species diversity among many small-bodied invertebrates inhabiting the Antarctic benthos is often very high. This surprisingly high species diversity is thought to be maintained by biologically generated habitat heterogeneity and patchy food resources acting in concert with biological disturbance at various scales (Arntz *et al.*, 1994).

Iceberg scouring is one such disturbance event that has a fundamental influence on the polar benthic ecosystems. It happens over wide areas in the Southern Ocean and a more frequent abrasion of the Antarctic sea floor habitats may be induced by global warming (Gammie, 1995). The resulting scouring activity of the grounded icebergs is a catastrophic event that physically disturbs benthic polar ecosystems. The process is considered as an ecologically important structuring factor for organisms living on the sea bed in the Southern Ocean. But what is the resilience of the Antarctic benthic communities?

The slow rates of population growth in macrobenthos suggest that, in areas disturbed by iceberg scouring, recovery of macrobenthic communities may take years, or even decades or centuries (Arntz *et al.*, 1994).

To contribute to the understanding of the resilience capacity of the supposedly sensitive Antarctic benthic systems, the recovery potential of meiobenthic organisms after ice-berg scouring of the bottom has been investigated. In contrast to the high longevity and slow growth in many macrobenthic species, meiobenthos have short life cycles, which make their response to environmental change, such as iceberg grounding, rapid, and hence easy to study. The investigations carried out by the Marine Biology Section at Ghent University (ANTAR 4) (Fig. 8) resulted in the observation that although communities from the low subtidal and the deeper shelf zones differ significantly when undisturbed, they do show high similar adaptive characteristics to iceberg scouring (Peck *et al.*, 1999; Lee *et al.*, in press1; in press2). Initially, most meiobiotic members suddenly disappear. But after some period of recolonisation a typical assemblage is re-established by immigration and reproduction of species found in the immediate area. Finally, the meiobenthos consists of sustainable populations that have favoured opportunistic r-strategies, and that appear to have a broad adaptation to natural disturbance conditions such as iceberg scouring.

Both from meiobenthic and macrobenthic observations (Gutt *et al.*, 1996; Peck *et al.*, 1999) it can be concluded that a slight increase in the frequency of iceberg grounding in the Antarctic due to global warming could probably be buffered by the benthic system due to its adaptation to natural catastrophic events. However, above a certain threshold, the benthic resilience will not suffice to prevent serious damage or collapse of the entire community.

The local extinction due to iceberg calving and the subsequent recolonisation can be regarded as a large *in situ* experiment. It serves as one example of how to define the resilience of biotic assemblages to natural disturbance in Antarctica. Indirectly, it gives an indication of the possible effects of anthropogenic impacts.

The Southern Ocean pelagic ecosystem

The study of ecosystem resilience through a modelling approach was a specific objective to contribute by the project co-ordinated by the Ecohydrodynamic Unit of University of Liège. This project concentrated on the pelagic ecosystem and aimed at developing a coupled physical/biological model able to simulate multiparametric variability in biodiversity and productivity, specifically connected to climate and anthropogenic changes.

The productivity and biodiversity of the Southern Ocean pelagic ecosystem is to a large extent determined by the specific environmental features of the Seasonal Ice Zone which extends over 20 millions km². Temperature never exceeds values higher than 3 to 4°C in summer and approaches -2°C near the ice shelves in winter. The input of fresh water and the stratification or vertical stabilisation of the upper layers of the water column are only due to ice retreat. As shown by satellite images, the highest plankton biomass is associated with the marginal ice zone where ice-algae are released by ice melting and where the stabilisation of the water column enhances productivity. The period of the maximum phytoplankton bloom and-ice algae release occurs during the ice-melting period when radiation and photoperiod are important. The mixing layer depth influences the time spent by phytoplankton in deeper waters where light and production are reduced. Because of losses by respiration or grazing, the net growth of the population is slow when the mixing layer is deep. On the contrary, shallow mixing layer maintains the phytoplankton in the upper layer until all nutrients of the mixing layer are consumed. In the seasonal ice zone, the ice melting implies a release of less saline water, salinity of Antarctic sea ice being about 7. This melting process releases a variable quantity of ice algae, induces a stabilising surface buoyancy flux, a subsequent decrease of the mixing layer depth and an increase of plankton production. Melting is essential for biological processes by inducing persistent shallow mixing layer and thus favorable conditions for phytoplankton.

Nutrients concentrations are high and do not limit the primary production. They are high enough to support a very high, quite unlimited productivity especially in the Ross Sea where the extreme southern latitude (75-78°S) and climatic anticyclonic forcing (low cloud coverage) impose a quite permanent solar radiation during spring and summer periods. But, it is a rare occurrence in the Southern Ocean and phytoplankton biomass rarely exceeds 10 μg . l^{-1}. A lot of hypotheses have been proposed to explain that "paradox of the Antarctic" like the very low growth rate due to low temperature, the mixed layer depth, the high grazing pressure, or the absence of elements like iron.

The Antarctic pelagic food web is unique among ocean ecosystems in that it is characterised by its large dependence on a single key species, the Antarctic krill (*Euphausia superba*). This species strongly limits the diatom standing stock. The krill itself depends on sea ice for some parts or all of its life cycle and on hydrodynamic processes on a larger scale.

The ring shaped ocean around the polar continent, its isolation by circumpolar fronts, the zonal transport by strong circumpolar currents coupled with seasonal changes in the light regime and sea ice cover have imposed common patterns of bioproductivity, species composition, distribution of biological resources. Therefore , the concept of a seasonal ice zone ecosystem in the Southern Ocean has been proposed.

However, limitations and spatial and temporal variability of this ecosystem are observed in relation to local characteristics of depth, climate, hydrodynamics, wind and ice coverage at the scale of single seas like the Ross Sea, the Bellingshausen Sea or the Weddell Sea. For example, the phytoplankton distribution in the Ross Sea shows that the bloom occurred one month later in the Terra Nova Bay area than in the central Ross Sea. It can be suggested that the delay is due to the strong winds occurring in the Terra Nova Polynya in December in turn delaying the stabilisation of the water column. A strong variability of the vertical distribution of phytoplankton in the Ross Sea Polynya exists in relation to diverse states of the melting ice edge and the vertical stability of the water column.

To illustrate the concept of a Ross Sea Seasonal Ice Zone ecosystem (standard state) and to test the influence of physical constraints on the variability of the plankton ecosystem, a mechanistic modelling approach was undertaken. To balance between an excessive holistic view and a too complex realistic approach, a brief discussion of the principal physical and ecological sources of variability is presented as a conceptual scheme of the hypothetical standard system.

The physical variability in the Ross Sea

The principal physical cause of the variability in the Southern Ocean pelagic ecosystem is the existence of polynyas generated by strong winds which carry the ice cover and by heath coming from the ocean depths (Plate 30). In the Ross Sea, during winter and at the beginning of spring, the ice-free surface propagates from the south to the north as shown by the analysis of the weekly remote sensing pictures. The mode of formation of the polynya imposes local variability, induces a spatial heterogeneity of ice coverage and thus the initial timing of seasonal plankton cycle varies at the same scale. Moreover, the progression to the north of the ice-edge of the polynya is not a continuous process in relation to different ice thickness between the south and the north. This discontinuity in the progress of the polynya ice front causes a strong variability in the light, the stability of the water column, the algal release in the water column and influences the pattern of the whole ecosystem.

The phytoplankton variability in the Ross Sea

High phytoplankton concentrations and massive blooms from 10 to 40 $\mu g.l^{-1}$ of chlorophyll *a* were observed in the Ross Sea polynya, directly or by remote sensing in November when other southern regions were still ice covered. These high chl a concentrations were among the highest observed in the Southern Ocean and may justify a depletion in nutrients. A successive decrease of primary production was observed.

The early opening of the polynya and the early spring production period in the polynya could be an attractive factor for krill and predators like penguins, seals and whales.

The vertical distribution of phytoplankton in the water column and its variability was investigated during the ROSSMIZE cruise in November 1994. The diversity of phytoplankton populations was identified on the basis of pigments assemblages determined by HPLC. *Phaeocystis* dominated in the major part of the southern Ross Sea. High diatoms concentrations dominated in coastal area and in marginal ice zone even if those concentration are virtual (and replaced by phaeophorbids) in case of high grazing activity (controlled overall by krill) especially in the central part of the Ross Sea at the northern limit of the polynya. Microphytoplankton consisted in large size diatoms and dominated the periantarctic marginal ice zone. Nano- and pico-phytoplankton were more abundant in periantarctic ice free-zone.

On the other hand results have confirmed the idea of the temporal succession of various nanophytoplankton groups like chryptophytes and prasinophytes and the apparition of picoplankton cells later in the season.

The variability of biotic assemblages.
The Ross Sea example.

Variations in ecosystem patterns characterised by specific biota assemblages were identified on the basis of plankton composition in diverse areas of the Ross Sea.

The "*Phaeocystis*" assemblage in the southern Ross Sea is found along the permanent ice shelf and is dominated by the algae for which it is named. Zooplankton is scarce and no predation by higher trophic levels occurs. The "full trophic chain" assemblage is found in the deep Ross Sea which includes the northern part of the polynya where important ice melting determines a vertical stability favourable to phytoplankton productivity. All groups are present (diatoms - *Phaeocystis*, copepods - krill) including birds and whales. The "diatom-krill" assemblage in the northern Ross Sea along the periantarctic marginal ice edge exists where the depth exceeds 500 m in the south and 1000 m in the north. The "coastal diatom" assemblage is encountered in Terra Nova Bay Polynya where *Limacina helicina* is the dominant herbivorous plankter. In that coastal area, an herbivorous mesozooplankton food chain (diatoms, copepods, ostracods) exists, but the plankton ecosystem is dominated overall by a macrozooplankton food chain (diatoms- mollusks, amphipods, fish larvae stadium of *Pleuragramma* represent the carnivorous level).

These different biotic assemblages correspond to local particularities and seasonal succession of different phases of the whole Southern Ocean seasonal ice zone ecosystem, which is also controlled by specific physical conditions. They are not to be taken as different ecosystems, but more realistically as different states of a typical ecosystem locally controlled by specific constraints or progressing from pack ice to ice free waters. The retreat and melting of the marginal ice zone do not occur simultaneously in the whole Ross Sea, the central and southern part being open earlier than lateral parts. Some areas (generally shallower than 500 m) seem to be inaccessible to large krill swarms and grazing pressure is modified. For unknown reasons, ice algae content (as an initial condition for spring bloom) seems to be more important in the western part of the Ross Sea.

As a conclusion, it appears that diverse ecological and hydrodynamic processes control simultaneously the variability of the Ross Sea Seasonal Ice Zone ecosystem. All the trophic levels depend on sea ice at least during a part of their life. For all these reasons, this ecosystem is essentially sensitive to environmental changes such as climate.

The numerical model of the Ross Sea pelagic ecosystem

The interdisciplinary modeling approach has been followed to understand how the biological and physical processes, interlinked at various scales, govern the ecosystem.

The major vertical interactions between physical and biological processes have been simulated. The bloom dynamics and the water structure compare realistically with the rare data available from such type of environment. An explicit ice model was introduced. The impact of melting on the water column, which is essential to understand the bloom dynamics, is obtained from the model and not as initial condition or artificial parameterisation. Moreover, the evolution of biomass can be studied since the beginning of the bloom (under ice cover) until its decrease and not only after complete melting.

Ice acts mainly as a switch: if ice melting ice occurs, production is intense and massive blooms are possible even with high losses (grazing). In absence of ice melting, blooms are nearly impossible even with moderate losses. Phytoplankton biomass is also influenced by modification of biological parameters. Zooplankton is a potential powerful control factor of phytoplankton biomass but its stock and metabolism are poorly known. Primary production is better known but results are very sensitive to parameters included in its parameterisation. Precise values would be essential. Initial concentration in water and the presence of ice-algae seems to be of lesser importance.

This model seems to be convenient to understand key interactions between ice, upper ocean and biological populations and their implications for melting, structuring of the water column and productivity. However, we have neglected 3-D phenomena as ice dynamics or water advection, quantitatively important but less directly involved in vertical biological/physical coupling. In the present step, complex relations between upper biological groups have been also neglected.

The ECOHYDRO MVG model in its actual state is only seasonal and is used for simulating the microscale physical processes of vertical stabilisation of the water column at the level of the Marginal Ice Zone of the Ross Sea. It will need more developments for ice formation and biological processes within the ice (photo-adaptation, UV, etc).

Conclusions

There is obviously insufficient knowledge of marine biodiversity in the Southern Ocean. Three main objectives in terms of biodiversity research are challenging Antarctic biologists today:

- to continue to discover and to describe what is living there, by undertaking new surveys and taking all opportunities to complete the inventory of what is an important part of the marine fauna of the world.
- to understand biodiversity patterns at different spatial scales of pertinence and in this respect the Antarctic seems to be a key place for elucidating some world scale biodiversity patterns.
- to understand the connection between biodiversity and the functioning of ecosystems – in particular their productivity, stability and resilience.

Acknowledgments

The present research was performed under the auspices of the Scientific Research Programme on the Antarctic (Phase IV) from the Belgian Federal Office for Scientific, Technical and Cultural Affairs.

References

Arntz W.E., Brey T. & Gallardo V.A., 1994. Antarctic zoobenthos. *Oceanography and Marine Biology: an Annual Review*, 32: 241-304.

Arntz W., Gutt J. & Klages M., 1997. Antarctic marine biodiversity: an overview. In: Battaglia B., Valencia J. & Walton D.W.H. (eds.), Antarctic Communities: Species, Structure and Survival. Cambridge University Press: 3-14.

Brey T. & Clarke A., 1993. Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? *Antarctic Science*, 5(3): 253-266.

Clarke, A., 1988. Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology*, 90B (3): 461-473.

Chapelle G. & Peck L., 1999. Polar gigantism dictated by oxygen availability. *Nature*, 399: 114-115.

Dauby P., Scailteur Y., Chapelle G. & De Broyer C., 2001b. Potential impact of the main benthic amphipods on the eastern Weddell Sea shelf ecosystem (Antarctica). *Polar Biology*, 24: in press.

Dauby P., Scailteur Y. & De Broyer C., 2001a. Trophic type diversity within the eastern Weddell Sea amphipod community. *Hydrobiologia*, 443: 69-86.

De Broyer C., Rauschert M. & Scailteur Y., 1999. Structural and ecofunctional biodiversity of the benthic amphipod taxocoenoses. In: Arntz W. & Gutt J., The Expedition ANTARKTIS XV/3 (EASIZ II) of "Polarstern" to the Eastern Weddell Sea and the Antarctic Peninsula 1998. *Berichte zur Polarforschung*, 301: 163-174.

De Broyer C., Scailteur Y., Chapelle G. & Rauschert M., 2001. Diversity of epibenthic habitats of gammaridean amphipods in the eastern Weddell Sea. *Polar Biology*, 24: in press.

De Broyer C. & Jazdzewski K., 1996. Biodiversity of the Southern Ocean: towards a new synthesis for the Amphipoda (Crustacea). *Boll. Mus. civ. St. nat. Verona*, 20: 547-568.

Dinet, A. & Vivier, M.H., 1979. Le méiobenthos abyssal du Golfe de Gascogne. II. Les peuplements de nématodes et leur diversité spécifique. *Cahier de Biologie Marine*, 20: 109-123.

Diversitas 1996. Diversitas: An International Programme of Biodiversity Science. Operational Plan Diversitas, Paris: 1-8.

Gammie F., 1995. Breakaway iceberg 'due to warming'. *Nature*, 374: 108.

Giere, O. 1993. *Meiobenthology. The microscopic fauna in aquatic sediments*. Springer-Verlag Berlin Heidelberg, 328p.

Graf G., 1992. Benthic-pelagic coupling: a benthic view. *Oceanography and Marine Biology: an Annual Review*, 30: 149-190.

Grassle J.F. & Maciolek N.J., 1992. Deep-Sea species Richness: regional and local diversity estimates from quantitative bottom samples. *The American Naturalist*, 139(2): 313-341.

Gutt J. & Starmans A., 1998. Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biology*, 20(4): 229-247.

Gutt J., Starmans A. & Dieckmann G., 1996. Impact of iceberg scouring on polar benthic habitats. *Mar. Ecol. Prog. Ser.*, 137: 311-316.

Jarre-Teichmann A., Brey T., Bathmann U.V., Dahm C., Dieckmann G.S., Gorny M., Klages M., Pagés F., Plötz J., Schnack-Schiel S.B., Stiller M. & Arntz W.E., 1997. Trophic flows in the benthic community of the eastern Weddell Sea, Antarctica. In Battaglia B., Valencia J. & Walton D.W.H. (Eds.): Antarctic communities: species, structure and survival. Cambridge University Press, 118-134.

Jazdzewski K., Teodorczyk W., Sicinski J. & Kontek B., 1991. Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. *Hydrobiologia*, 223: 105-117.

Karentz D., 1991. Ecological considerations of Antarctic ozone depletion. *Antarctic Science*, 3(1): 3-11.

Lee H.J., Vanhove S., Peck L.S. & Vincx M., in press1. Recolonisation of meiofauna after a catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biology*.

Lee H.J., Gerdes D., Vanhove S. & Vincx M., in press 2. Response of meiofauna to disturbance by iceberg scouring on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea). *Polar Biology*.

Martinez N.D., 1996. Defining and measuring functional aspects of biodiversity. In Gaston K.J. 1996. Biodiversity. A Biology of Numbers and Difference. Blackwell Science Ltd: 114-148.

May R.M., 1992. Bottoms up for the oceans. *Nature*, 357: 278-279.

Muthumbi, A.W.N., 1998. Biodiversity of nematodes in the Western Indian Ocean (WIO): taxonomy and assemblages. PhD thesis, Ghent University, 287p.

Peck L.S., Brockington S., Vanhove S. & Beghyn M., 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Mar. Ecol. Prog. Ser.*, 186: 1-8.

Poore G.C.B., Just J. & Cohen B.F., 1994. Composition and diversity of Crustacea Isopoda of the southeastern Australian continental slope. *Deep Sea Research Part II. Topical Studies in Oceanography*, 41(4): 677-693.

Poore G.C.B. & Wilson G.D.F. 1993. Marine species richness. *Nature*, 361: 597-598.

SCAR, 1994. Coastal and Shelf Ecology of the Antarctic Sea-Ice Zone (CS-EASIZ), a SCAR programme of marine research for the coastal and shelf ecosystem of Antarctic. *SCAR Rep.*, 10: 1-20.

UNEP, 1995. Global biodiversity assessment. Cambridge University Press, 1140p.

Vanhove S, Arntz W. & Vincx M. 1999. Comparative study of the nematode communities on the southeastern Weddell Sea shelf and slope (Antarctica). *Mar. Ecol. Prog. Ser.*, 181: 237-256.

Vanhove S., Beghyn M., Van Gansbeke D., Bullough L.W. & Vincx M., 2000. A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure. *Mar. Ecol. Prog. Ser.*, 202: 13-25.

Vanhove S., Wittoeck J., Beghyn M., Van Gansbeke D., Van Kenhove A., Coomans A. & Vincx M., 1997. Role of the meiobenthos in Antarctic ecosystems. Belgian Research Programme on the Antarctic, scientific results of phase III (1992-1996): 59 p.

Wilmotte A., Demonceau C., Goffart A, Hecq J.-H., Demoulin V. & Crossley C., in press. Molecular and pigment studies of the picophytoplankton in a region of the Southern Ocean (47 to 54°S, 141 to 144°E) in March 1998. *Deep Sea Research II.*

Winston J.E., 1992. Systematics and Marine Conservation. In Eldredge N., 1992. Systematics, Ecology, and the Biodiversity Crisis. Columbia University Press, New York, pp. 144-168.