

SPSD II

BIODIVERSITY OF THREE REPRESENTATIVE GROUPS OF THE ANTARCTIC ZOOBENTHOS: COMPARATIVE STRUCTURE, DISTRIBUTION AND FUNCTION (BIANZO)

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PART 2

GLOBAL CHANGE, ECOSYSTEMS AND BIODIVERSITY



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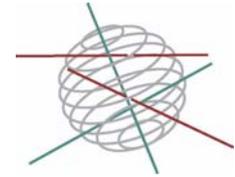
NORTH SEA



ANTARCTICA



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Part 2:
Global change, Ecosystems and Biodiversity



FINAL REPORT

**Biodiversity of three representative groups of the
Antarctic Zoobenthos:
Comparative structure, distribution and function
(BIANZO)**

EV/24

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ABSTRACT

The main goal of the BIANZO project was to investigate, at different structural and functional levels, the nature, distribution and role of the Antarctic benthos biodiversity through three representative faunal groups of different and complementary size categories: the nematodes (principal component of the meiobenthos), the amphipod crustaceans (one of the most speciose and diverse group of macrobenthos), and the echinoids (an important and widely distributed component of megabenthos).

BIANZO efforts concentrated on the exploration of unknown habitats, in particular the continental slope, abyssal plains and trenches of the Atlantic sector of the Southern Ocean, in the framework of the ANDEEP programme. On the other hand, comprehensive syntheses of the biodiversity and distribution knowledge of the target groups were developed and completed, and new identification tools designed. These two approaches allowed describing and analyzing the biodiversity of the three target groups and discussing their large-scale biogeographic and macroecological patterns and driving processes.

To contribute to understand the role of biodiversity in the functioning of the Southern Ocean benthic ecosystems the BIANZO project focused on the identification and description of the functional niches occupied by representatives of the three target groups, in particular their trophic niches and their integration in the benthic food web, as well as other functional aspects such as the role of size and biomass, habitat component, mode of life or mobility.

Three comprehensive biodiversity databases have been developed in the BIANZO framework to contribute to develop an information system for the Antarctic benthic biodiversity. The “Nemys” database is an information system for improving identification, classification and description of Antarctic nematode species. The “Ant’Phipoda” database holds exhaustive information on taxonomy, geographic and bathymetric distribution, and bio-ecology of all Antarctic and sub-Antarctic amphipod crustaceans. The “Antarctic Echinoids” database comprises complete information on all Antarctic echinoid species and includes illustrated identification keys, information about species morphology and ecology, distribution records and sources (bibliography, collections and expeditions). As a result of its experience in Antarctic biodiversity data management, the BIANZO consortium successfully proposed to establish a SCAR Information Network on Antarctic Marine Biodiversity, SCAR-MarBIN.

1. INTRODUCTION

Polar regions experience greater rates of climate change than elsewhere in the world. Their biota is highly adapted to their extreme environment and appears vulnerable to shifts in climate. Because of the key role of the Southern Ocean in the Earth system and the growing impact of global environmental change, it is crucial to establish comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. It is equally important to gain a better understanding of the role of biodiversity in the functioning of the Southern Ocean ecosystems.

The main goal of the BIANZO project is to investigate, at different structural and functional levels, the nature, distribution and role of the Antarctic benthos biodiversity through three representative faunal groups of different and complementary size categories: the nematodes (principal component of the meiobenthos), the amphipod crustaceans (one of the most speciose and diverse group of macrobenthos), and the echinoids (an important and widely distributed component of megabenthos).

The meiofaunal nematodes are in terms of abundance the most important metazoan group in marine sediments. As their communities contain a large number of species, usually an order of magnitude greater than any other major meiobenthic taxon, they are particularly suitable for tackling biodiversity and biogeography issues. Crustacean amphipods appear to be the second most speciose animal group in Antarctic seas, showing a remarkable diversity in terms of modes of life, habitats, trophic types, and size spectra. Finally, echinoids constitute an often abundant and widely distributed component of the Antarctic benthic communities, and offer important opportunities for symbiotic diversity.

These three target groups occupy different positions in the structure of the benthic Antarctic ecosystem where they play different roles. Their study has already been initiated during the former phases of the Belgian Antarctic Programme (Antar 3 & 4) (De Broyer *et al.*, 2003b; Vanhove *et al.*, 2003).

Objectives

Relying on the exploration of unknown Antarctic regions and habitats and on new comprehensive syntheses of the present biodiversity and biogeography knowledge of the target groups, the **first objective** of the study is to improve the understanding of the patterns and processes describing and explaining the nature and distribution of the Southern Ocean benthic biodiversity. Taxonomic inventories and assessment of local species richness are performed in unknown Antarctic areas such as the deep Scotia and Weddell seas and taxa distribution patterns are analysed with respect to several gradients (depth, basin or latitude).

The **second objective** aims at better understanding the ecofunctional role of biodiversity by analysing - at the scale suitable to the three faunal components - different dynamic features such as niche diversity, trophic types, trophic structure and respective role in food webs, reproduction patterns or biomass turnover. A special attention is also paid to symbiotic associations which can be source of biodiversity increase, especially in resource-limited environments such as deep sea.

The **third objective** concerns the development of a Biodiversity Information System for the Antarctic zoobenthos to make more effectively available to the scientific community and the society, the biodiversity knowledge acquired during previous Antarctic studies or newly gained from the present research. This information system relies on the extant or developing comprehensive databases in the three target groups and includes identification tools and mapping applications.

The BIANZO project was an integral part of the SCAR programmes EASIZ (Ecology of the Antarctic Sea Ice Zone) and EVOLANTA (Evolution in the Antarctic), now merged within the SCAR EBA programme (Evolution and Biodiversity in the Antarctic, a response of life to change). It contributed actively to the ANDEEP (Antarctic benthic deep-sea biodiversity), BENTART (Spanish Antarctic Benthos project), IBMANT-LAMPOS (Interactions between the Antarctic and the Magellan region), and BENDEX (Antarctic Benthos Disturbance Experiment) projects. Its results also directly contributed to CAML (Census of Antarctic Marine Life), SCAR-MarBIN (SCAR-Marine Biodiversity Information Network), OBIS (Ocean Biogeographic Information System) and GBIF (Global Biodiversity Information Facility) as well as to the Catalogue of Life.

This report presents an integrated review of the main results in three sections according to the three research objectives: Nature and distribution of biodiversity, Ecofunctional role and Biodiversity information system.

2. NATURE AND DISTRIBUTION OF BIODIVERSITY

2.1. INTRODUCTION

Current knowledge of the Antarctic benthic biodiversity is highly patchy in terms of coverage of geographical areas, bathymetric zones, habitats, taxonomic groups, ecofunctional groups, or size spectra. Vast areas of the High Antarctic continental shelf remain untouched and the Antarctic deep-sea fauna is hardly known.

A recent survey of the Antarctic macrozoobenthos revealed that over 4100 species are presently described (Clarke & Johnston, 2003) but reliable extrapolations estimated a number of potential species comprised between 11000 and 17000 for the entire Antarctic shelf without considering the deep sea (Gutt *et al.*, 2004).

Patterns and driving processes of the Southern Ocean benthic biodiversity are still partly understood. Despite the relative homogeneity of the Southern Ocean in terms of physical environmental factors, the species richness patterns are quite distinct between the various zones or belts surrounding the continent, between the successive bathymetric zones or between the diverse macrohabitats. Moreover, at a geological scale, the progressive isolation of Antarctica and the successive glaciations events have lead to the evolution of a peculiar fauna wherein some groups are under- or over-represented when compared to other seas (Arntz *et al.*, 1997). This indicates that evolutionary questions concerning the origin, diversification or extinction of the Southern Ocean marine fauna will have no single answer; the evolutionary history of each group appears to reflect a different response to the tectonic, climatic and oceanographic changes to which they have been subject through history (Clarke & Johnston, 2003).

Until the early 90's, hardly anything was known about the ecology and diversity of **meiobenthic communities** in the Antarctic. Since then, information has been gathered on diversity and distribution patterns of meiobenthos in general, and nematodes in particular, mainly in the Atlantic sector of the Southern Ocean (Herman & Dahms, 1992; Vanhove *et al.*, 1995, 1999). Temporal and spatial patterns in diversity and composition of subtidal and shelf communities have been unraveled (Vanhove *et al.*, 2000; Lee *et al.*, 2001a, b), and community shifts along bathymetric gradients from shelf to upper slope were analysed (Herman & Dahms, 1992; Vanhove *et al.*, 1995, 1999). Meiobenthic life in the Antarctic deep sea beyond 2000 m water depth however, remained completely unknown, and was studied for the first time during this project. Emphasis was put on meiobenthic communities along bathymetric gradients from the lower continental slope down to hadal depths (6300 m) and on spatial variability in the Weddell Abyssal Plain.

Nematode communities were until recently only studied at genus level and no indication of the existence of an autochthonous fauna was available (Vanhove *et al.*, 1999, 2000). A completely different picture may arise however when looking at the species level. Antarctic nematode species have hardly been studied, and their diversity and distribution patterns in Antarctic marine environments are unknown. Only a small number of nematode species have been described, mostly before 1960 (see Fig. 1), without any indication on their biogeography or bathymetric distribution patterns. Nematode species diversity and distribution patterns in a number of selected dominant genera in the Antarctic marine

environment was investigated and compared with communities in marine sediments in other oceans. This should allow assessing the degree of endemism at species level in comparison with other parts of the world.

Contrasting with the very limited knowledge of diversity and distribution of Antarctic meiobenthos, **macro- and megabenthos** received some attention from the beginning of the Antarctic biological exploration. The composition of the **amphipod crustacean fauna** of the Southern Ocean was progressively described over various periods showing however no recent slow-down (Fig. 1).

These investigations have revealed that the amphipod crustaceans are one of the most speciose animal groups in the Antarctic and sub-Antarctic waters (De Broyer & Jazdzewski, 1996; Clarke & Johnston, 2003). It has been suggested that their high species diversity may be primarily related to the high habitat heterogeneity and to a large variety of ecological niches, which remain in most cases to be described and understood, as shown from our previous results. In the Southern Ocean, amphipods count among the most diversified groups in terms of life styles, trophic types, habitats and size spectra, (Dauby *et al.* 2001, De Broyer *et al.* 2001a; Chapelle 2001).

The biogeography of the Southern Ocean amphipods was investigated by Knox & Lowry (1977) and more recently by Watling & Thurston (1989) and De Broyer & Jazdzewski (1993, 1996). Their distribution patterns mostly fit into the broad scheme of Southern Ocean biogeographic provinces established by Hedgpeth (1970) and Dell (1972). However, distribution data of benthic species in general have increased enormously during the last two decades. Moreover extensive biogeographic databases are now being built for some species-rich groups and new insights are progressively provided by molecular analyses. For example, a number of potential cryptic species has been detected in Antarctic isopods and molluscs (Held, 2003; Held & Wägele, 2005; Page & Linse, 2002; Raupach & Wägele, 2006) and these results may question our current estimation of species richness and our widely accepted view of circum-Antarctic distribution pattern for benthic species (De Broyer *et al.*, 2003a).

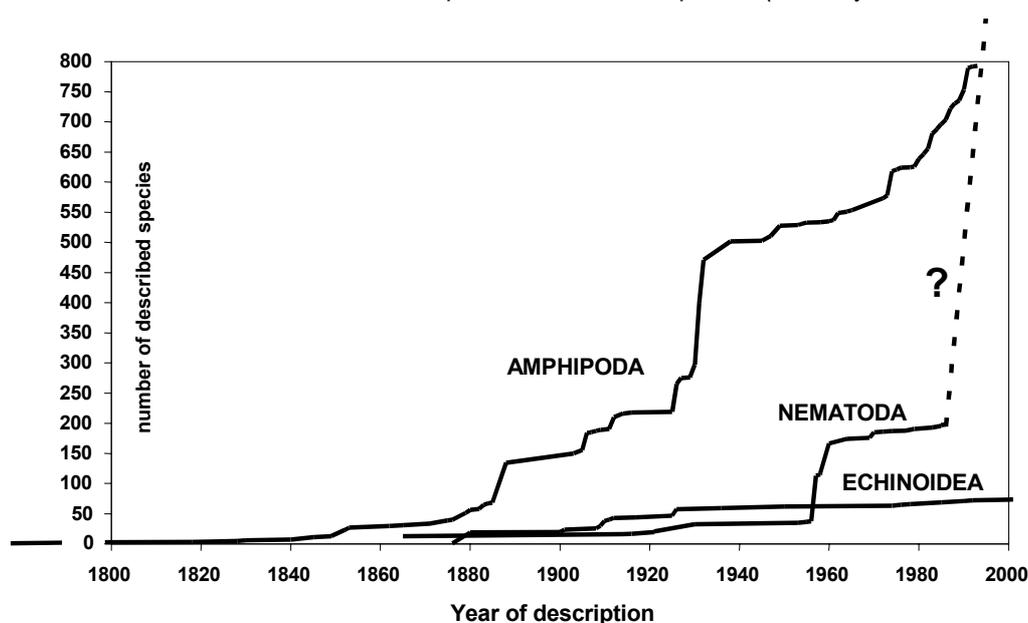


Fig. 1. Evolution of the number of species described from the Southern Ocean s.l. (Antarctic + sub-Antarctic regions) for the three target groups.

Three potential origins have been suggested for peracarid crustaceans, as well as for the marine fauna of the Antarctic shelf in general (Knox & Lowry, 1977; Knox, 2007; Crame, 1999): (1) a relict autochthonous fauna, which radiated *in situ*, possibly from the late Cretaceous time (supported by the high levels of endemism and by several phylogenetic studies), (2) a fauna derived from the adjacent deep sea (demonstrated in few groups), and (3) a fauna immigrated from South America *via* the Scotia Arc (suggested *e.g.* by Sieg, 1992, for tanaids). Too few phylogenetic studies (*e.g.* Watling & Thurston, 1989; Lörz & Held, 2004; Lörz & Brandt, 2004) have been conducted so far to allow elucidating the origins of most of the Antarctic amphipod taxa.

On the other hand, pioneer molecular studies on polar submergence in Antarctic serolid, arcturid and aselotte isopods (Held, 2000; Raupach, Held & Waegele, 2004) indicated several invasions into the deep sea from the Antarctic shelf, all of which occurred independently. These polar submergence events may be closely related to the glaciation history in Antarctica. How far these trends may apply to amphipod crustaceans and other macro/megabenthic taxa remains to be established.

Antarctic echinoid species have been documented by more than a century of Antarctic expeditions (David *et al.*, 2001; see Fig. 1). Echinoids count about 800 species in the World Ocean and 78 of them occur south of the Polar Front. These Antarctic species belong to 7 of the 19 post-Paleozoic echinoid orders and are represented by 9 families. With 10% of the world echinoid species, the Antarctic is considered a hot spot for echinoid biodiversity. This richness falls within the ranges for tropical regions as illustrated by the comparison with the Mediterranean Sea (25 species), the eastern North Atlantic (30 species) and the Australian waters (ca. 115 species). The Antarctic echinoid fauna shares a common story of about 50 My and started to isolate from the Australian stock in the Paleocene. Antarctic echinoids seem then to have evolved from previously existing forms (and not from recurrent migratory events) as soon as a deep-water barrier separated Australia from Antarctica, preventing planktonic larval dispersal (Clarke & Crame, 1989; Pawson, 1994). This means that the present day Antarctic echinofauna originated from warmer-water ancestors, and has also experienced a long independent evolution. The great species diversity (and endemism) and the low family number recorded on the continental shelf result from the extinction of planktotrophic taxa during glacial extremes, and from the diversification of lecithotrophic groups which brooding habits reduce dispersal and gene flow. In the Subantarctic, the echinofaunas are either allied with exclusively Antarctic taxa, or descended from northern temperate groups, or drifted from an island to another in the Antarctic Circumpolar Current.

BIANZO efforts concentrated on the **exploration of unknown habitats**, in particular the Antarctic deep sea (continental slope, abyssal plains and trenches of the Atlantic sector). The biodiversity of the meiobenthic nematodes, the macrobenthic amphipods and the megabenthic echinoids from these habitats is described and analysed and their geographic and bathymetric distribution patterns and driving processes are discussed. On the other hand, **comprehensive syntheses of the biodiversity and distribution** knowledge of the target groups were elaborated, and **new identification tools** designed.

2.2. MATERIAL AND METHODS

2.2.1. Study sites and sampling campaigns

Deep-sea meio- and macrobenthos samples were collected in the Weddell and Scotia seas, in the Drake Passage and in the South Sandwich Trench during the RV *Polarstern* campaigns ANDEEP I-III (Fütterer *et al.*, 2003; Fahrbach *et al.*, 2006). Continental shelf samples were taken along the Scotia Arc, around the Antarctic Peninsula and in the eastern Weddell Sea by the *Polarstern* LAMPOS and BENDEX cruises (Arntz & Brey, 2003, 2005). In addition, some meio- and macrobenthos samples taken during the *Polarstern* EPOS and EASIZ I-III campaigns (Arntz *et al.*, 1990; Arntz & Gutt, 1997, 1999, 2001) in the framework of previous Antarctic programmes (ANTAR 3 and 4) have been further analysed.

Figure 2 shows all the stations sampled and/or investigated during the BIANZO project.

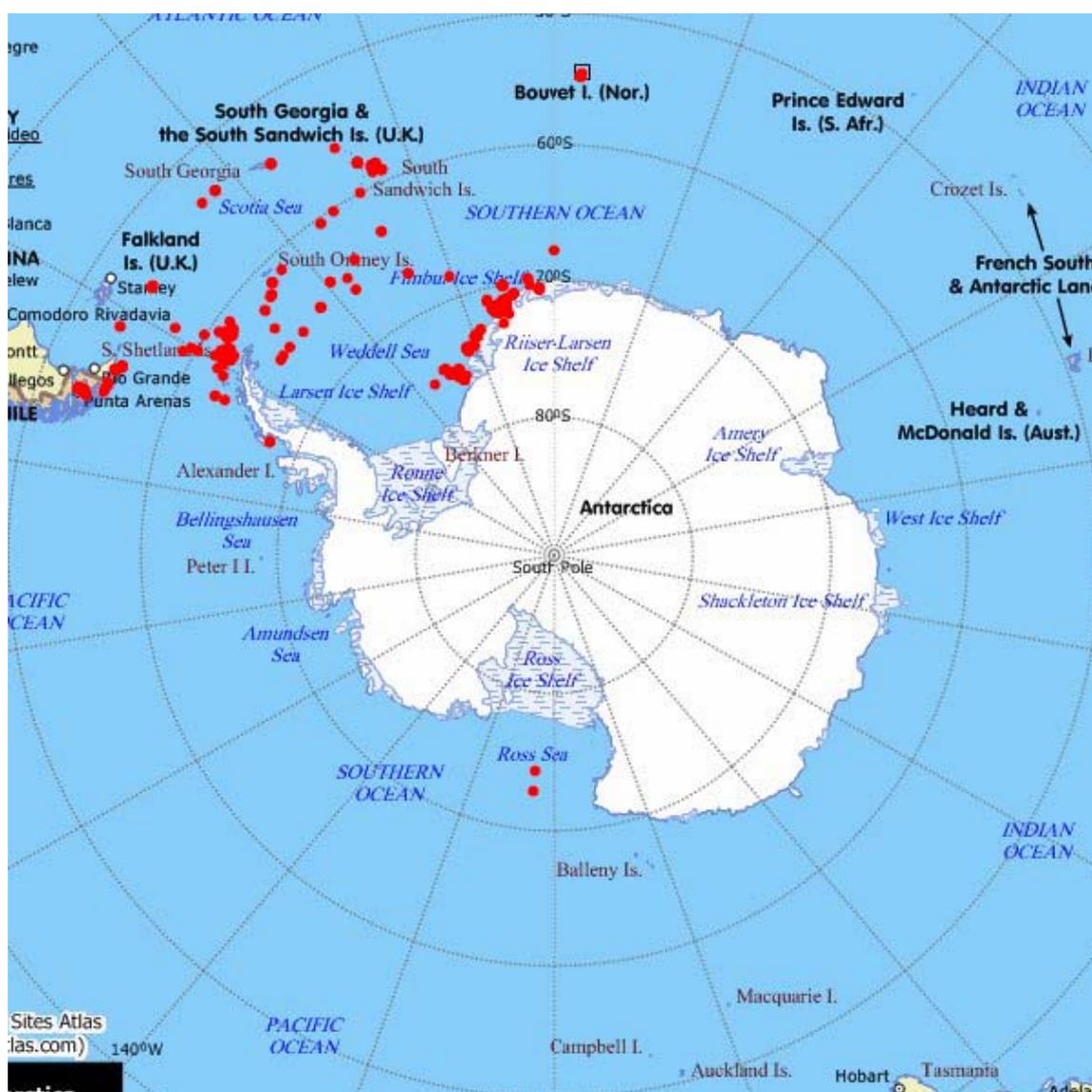


Fig. 2. Map of stations investigated by the BIANZO project (mainly from *Polarstern* ANDEEP I-III, LAMPOS, and BENDEX campaigns).

2.2.2. Sampling methods

Meiobenthos samples were taken with the multicorer (MUC) equipped with 12 cores with an inner diameter of 57 mm. When the sediment composition or weather conditions did not allow using the MUC, samples were collected with the Multibox corer (MG) (Vanreusel & De Mesel, 2003; De Mesel & Ingels, 2006).

Macro- and megabenthos were collected by a variety of gears: epibenthic sledge (EBS), baited traps (AT), Agassiz trawl (AGT), Bottom trawl (BT), Rauschert dredge (RD) and boxcorers (GKG) (De Broyer *et al.*, 2003c, 2004, 2006). Extensive sampling with EBS in the deep sea allowed covering roughly 85,000 m² of seafloor (Brandt & Hilbig, 2004).

2.2.3. Analysis of samples

Processing of meiobenthos samples. Sediment cores from multicorer (MUC) were sliced (0-1 cm, 1-3 cm, 3-5 cm, 5-10 cm and 10-15 cm) and preserved on a buffered formaldehyde solution (4%) for meiobenthic analysis. At each station, at least 1 core was sliced (0-0.5 cm, 0.5-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm) and frozen (-20°C) to determine organic carbon and nitrogen content, pigments and sediment grain size, and during the ANDEEP and LAMPOS expeditions one was preserved on acetone for molecular analysis. In case of Multibox corer samples, each box was sub-sampled with 3 cores for meiofauna community analysis, 1 core for environmental variables, and 2 cores for molecular analysis.

Meiofauna community analysis. Meiofauna communities were studied in the upper cm (transect towards South Sandwich Trench), upper 3 cm (Weddell Abyssal Plain) or down to 15 cm (Scotia Arc) sediment depth. Meiofauna was extracted from the sediment using standard Ludox-centrifugation procedures (Heip *et al.*, 1985). Nematodes were picked out and mounted into Cobb-slides for further identification.

Analysis of environmental variables in sediments. Photoplastic pigments were extracted in 90% acetone and their concentration was measured photometrically with a reversed phase HPLC. Organic carbon and nitrogen concentrations were determined with a Carlo Erba NA-1500 elemental analyzer. Sediment grain size was analysed with a Coulter LS&100 Particle Size Analyser.

Processing of amphipod samples. Amphipod samples were usually sorted onboard, fixed either in 4% buffered formalin or in pre-cooled 96% or absolute ethanol for molecular analysis, and identified to species level. Composition and relative abundance of accompanying fauna in trawl catches were recorded. Detection of microhabitat of symbiotic species was done by direct visual observation on living or fresh material of host species (*e.g.* ascidians or sponges). Determination of life style, mobility pattern and to some extent habitat was performed onboard on the basis of direct ethological observations of living specimens in cooled aquaria (volume: 6 to 30 l) at a temperature of -1°C ($\pm 1^\circ\text{C}$) permanently fed with fresh sub-surface seawater and provided with various biological or inorganic substrates.

Amphipod biodiversity and distribution analyses were based, on one hand, on a comprehensive database (Ant'Phipoda, initiated during Antar 4) of all literature and original records (> 8000 recs) of Antarctic and sub-Antarctic species of gammaridean and corophiidean amphipods, and, on the other hand, on extensive original collections mostly held at RBINS, Brussels.

Echinoid biodiversity and biogeographical analyses. The biodiversity approach was based on a wide set of samplings and museum collections. The analysis referred to the present day biodiversity data updated and geo-referenced in the “Antarctic echinoids” database (David *et al.*, 2005). Only the echinoids occurring south of the Polar Front were considered here; their longitudinal, latitudinal and bathymetrical distributions were analyzed and local biodiversity was compared using the classical Jaccard’s (1908) index (Magurran, 2004). This index is considered as relatively robust (Brown & Lomolino, 1998) and, on the other hand, the echinoid data didn’t allow the use of other indexes based on abundance or repeated occurrence data.

2.3. RESULTS AND DISCUSSION: NATURE AND DISTRIBUTION OF BIODIVERSITY

2.3.1. EXPLORATION OF UNKNOWN HABITATS: THE ANTARCTIC DEEP SEA

The ANDEEP campaigns of RV *Polarstern* in 2002 and 2005 have systematically explored – for the first time - the Antarctic deep-sea basins of the Weddell Sea, the Scotia Sea and the Drake Passage, as well as the South Sandwich Trench. They provided the first extensive results on the biodiversity and biogeography of Antarctic deep-sea benthic communities (see Brandt & Hilbig, 2004; Farhbach *et al.*, 2006; Brandt *et al.*, 2007a,b). Selected results contributed by the BIANZO project are presented hereafter.

Meiofauna communities in the Weddell Abyssal Plain (Sebastian *et al.*, submitted).

A first assessment was made on genus diversity and community composition of nematodes in the Weddell Abyssal Plain. The average meiofauna densities ranged generally between 200 and 250 individuals per 10 cm² (Fig. 3). Only in one station (Sta. 138) located closest to the South Sandwich Trench, densities were considerably higher and reached on average 510 individuals per 10 cm².

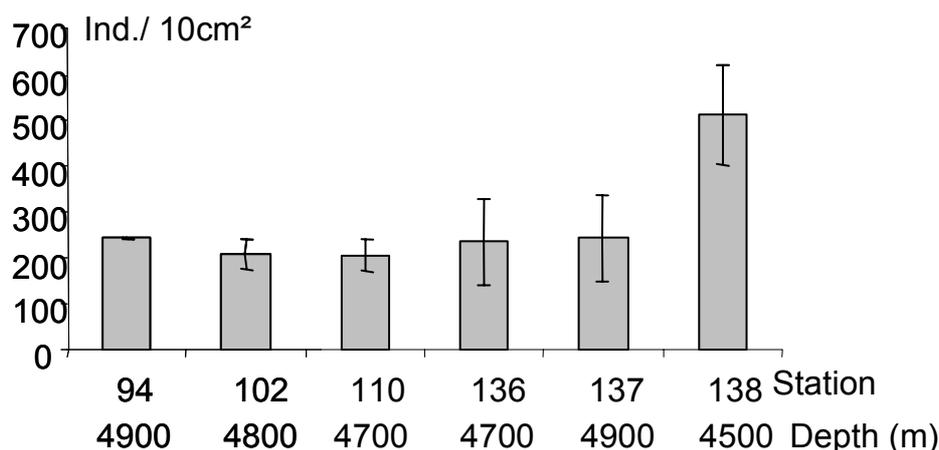


Fig. 3. Meibenthic densities per 10 cm² (mean \pm SE) in the Weddell Abyssal Plain.

Nematodes dominated the community in all samples representing more than 90% of the total community. Copepods are generally the second most abundant group. The number of taxa per sample varied from 5 to 11. In total, 19 different taxa could be distinguished. The nematode community was studied at genus level in the stations sampled during the ANDEEP II expedition (Sta. 136, 137 and 138).

All communities were dominated by typical deep-sea genera, such as *(Thalasso)Monhystera*, *Microaimus* and *Acantholaimus*. Also other genera commonly found in the deep sea – *Halalaimus*, *Desmoscolex*, *Dichromadora* – were quite abundantly present in most samples (Table 1). The nematode community in station 138 was characterized by lower genus numbers but higher dominance.

Since our main interest was to compare the Weddell Abyssal Plain with other abyssal areas worldwide a multivariate analysis was performed on genera composition from abyssal plains from different latitudes in the Atlantic Ocean and the Weddell Sea (Fig. 4). It is illustrated this way that the Weddell Abyssal Plain does not separate strongly from both Northern Atlantic areas (Porcupine and Cape Verde Abyssal Plain).

Table 1. Overview of the 10 most dominant nematode taxa in each ANDEEP II station (relative abundance).

64°S	136	63°S	137	62°S	138
<i>(Thalasso)Monhystera</i>	18,3	<i>(Thalasso)Monhystera</i>	26,5	<i>(Thalasso)Monhystera</i>	32,8
<i>Microaimus</i>	15,6	<i>Acantholaimus</i>	14,0	<i>Microaimus</i>	17,0
<i>Acantholaimus</i>	10,4	<i>Microaimus</i>	6,4	<i>Southerniella</i>	5,9
<i>Theristus</i>	8,6	<i>Dichromadora</i>	5,1	<i>Acantholaimus</i>	5,6
<i>Halalaimus</i>	5,5	<i>Theristus</i>	4,3	<i>Chromadorita</i>	5,5
<i>Desmoscolex</i>	4,0	<i>Desmoscolex</i>	3,7	<i>Theristus</i>	4,4
<i>Southerniella</i>	3,0	<i>Campylaimus</i>	3,0	<i>Dichromadora</i>	3,2
<i>Campylaimus</i>	2,1	<i>Chromadorita</i>	2,9	<i>Halalaimus</i>	3,0
<i>Dichromadora</i>	2,0	<i>Southerniella</i>	2,8	<i>Daptonema</i>	2,2
<i>Chromadorita</i>	1,8	<i>Halalaimus</i>	2,8	<i>Leptolaimus</i>	2,2

abyssal genera

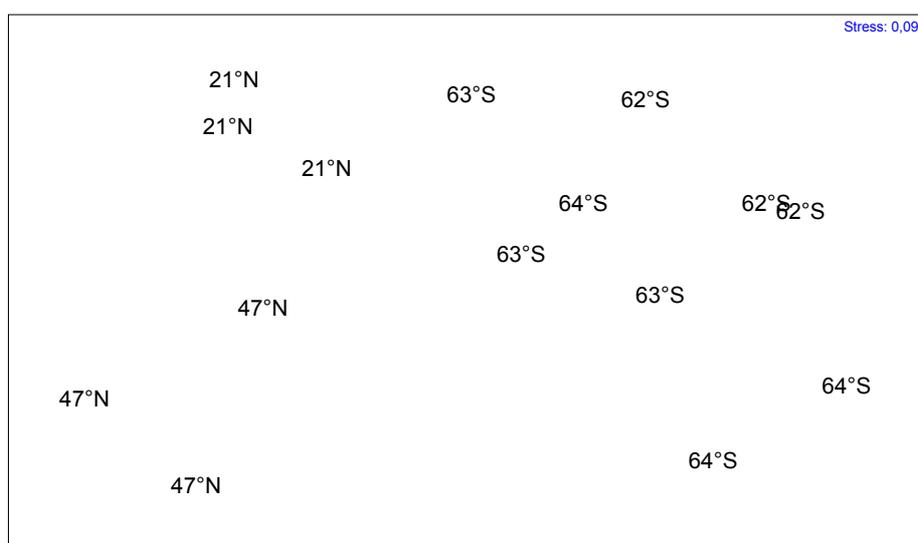


Fig. 4. MDS-plot based on relative abundance of different abyssal stations in the Atlantic sector indicated with their latitude.

Table 2 shows a relatively high similarity between the Weddell Abyssal Plain and other abyssal areas (> 44 %). The same dominant genera were found worldwide suggesting a high connectivity between the Weddell Sea and the Atlantic Ocean.

The diversity was calculated by means of expected number of genera for 100 individuals (Fig. 5). This index is density independent and allows comparison between different areas. The Weddell Sea biodiversity shows a high variability from very high to very low compared with both Northern Atlantic sites. The low diversity in station 138 at 62°S near the South Sandwich Trench is striking.

Table 2. % similarities within abyssal regions in bold; all other values give % dissimilarities between abyssal regions.

	64°S	63°S	62°S	47°N	21°N
64°S	63.8				
63°S	40.84	65.21			
62°S	39.38	39.64	66.72		
47°N	57.84	52.60	61.30	58.71	
21°N	56.28	44.45	53.50	43.84	71.40

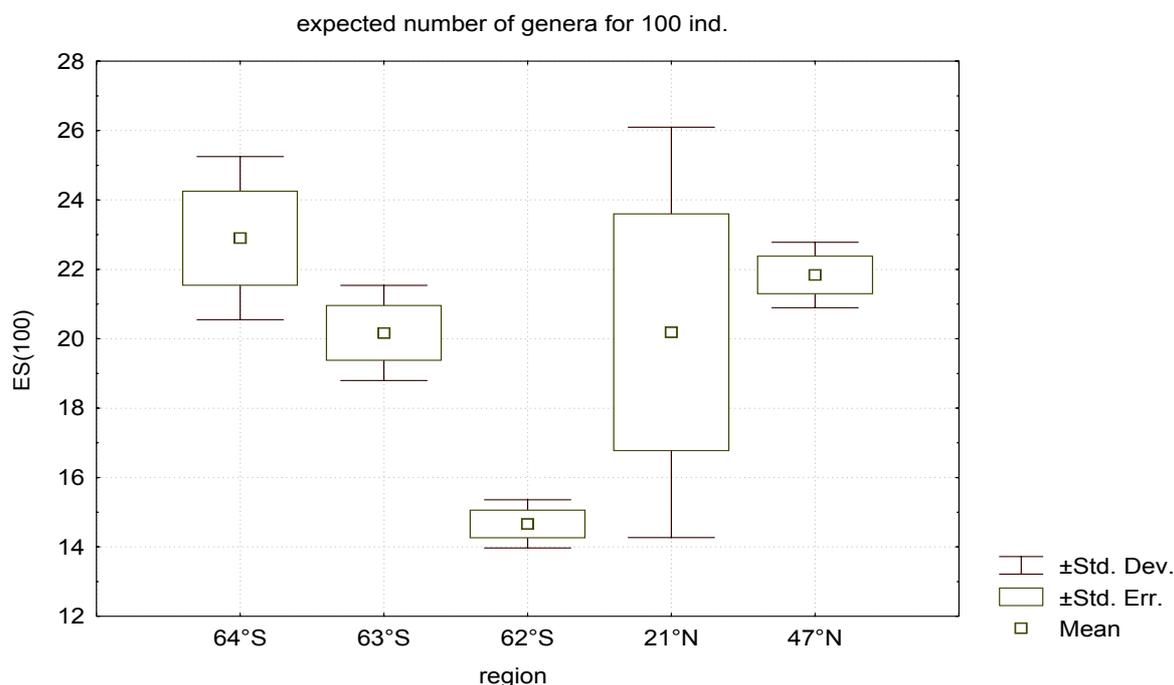


Fig. 5. Mean; SD and SE for the expected number of genera for 100 individuals ($ES(100)$) per sampling station in the Southern Ocean and the North Atlantic stations are indicated with their latitude.

Discussion. The ecology of deep-sea meiofauna in all world oceans has received quite some attention over the last decades (e.g. Vincx *et al.*, 1994). Only the Southern Ocean has been unknown for a long time. Gutzmann *et al.* (2004) were the first to publish higher taxon composition within the meiofauna on the lower continental slope and in the abyssal plain of the Weddell Sea. Similar to their

study, we found a community composition at higher taxon level which was very similar to what had been reported on the Antarctic continental slopes (Herman & Dahms, 1992; Vanhove *et al.*, 1995) and on deep sea sediments all over the world (Shirayama, 1984; Heip *et al.*, 1985; Pfannkuche, 1985; Tietjen *et al.*, 1989). Nematodes dominated the communities with relative densities of > 90%, followed by copepods with up to about 5% of the total community and sporadic occurrence of 17 other taxa with very low abundance. Densities in the Antarctic samples were generally slightly higher to those in other parts of the world. In one station, abundances were considerably higher (510 ind. per 10 cm²) and within the same range as those found at comparable depths along the transect towards the South Sandwich Trench (see below). The station with the higher densities in our study was also situated near the South Sandwich Trench. This area is an upwelling zone, characterized by high primary production (Howe *et al.*, 2004). The sedimentation of these micro-algae might have facilitated the co-existence of higher meiobenthic densities.

For the first time, nematode community structure was analysed in Antarctic abyssal plain sediments at genus level. The dominant genera were the same as those found in other oceans. (*Thalasso*)*Monhystera* was the most abundant genus in all samples, but their relative densities were considerably higher in Sta. 138 (32.8%) than in both other stations (18.3% and 26.5% in respectively Sta. 136 and 137). Monhysteridae are considered general opportunists that occur at sites with high organic input. They might have taken advantage of the higher food input close to the SST (see also above). Other dominant and typical deep-sea taxa found here were *Acantholaimus* and *Microlaimus*, and to a lesser extent *Halalaimus*, *Desmoscolex* and *Dichromadora*. In contrast to many macrofaunal taxa, no endemic genera were found in the Weddell Abyssal Plain; the same finding was reported in studies on shelf and slope communities in Antarctica (Vanhove *et al.*, 1998, 1999, 2000).

Meiofauna communities along a transect towards the South Sandwich Trench (Vanhove *et al.*, 2004)

A bathymetric transect from the continental slope over the abyssal plain towards the South Sandwich Trench (SST) was sampled, covering depths from 747 to 6319 m. (see also Vanhove *et al.*, 2004).

Highest meiobenthic densities were observed at 1100 m water depth (Fig. 6a). From this point densities decreased with increasing and decreasing depth. In total 23 meiobenthic taxa were found over all samples, with 7 to 11 taxa per sample. Free living nematodes were the dominant taxon making up 85 to 97% of the total community, followed by harpacticoid copepods (1 to 6%). Other taxa – such as Ostracoda, Halicarida, Cumacea, Kinorhyncha, Bivalvia – represented between 0.002 and 1.5% of the meiobenthos (Fig. 6b).

Three station groups could be distinguished based on similarities in terms of genus composition (Fig. 7): (1) the samples from 750 m water depth, (2) the samples from 1100 and 2300 m water depth, and (3) the samples from 4000 and 6000 m water depth, with the 3000 m samples scattered over the latter 2 groups. The genus *Tricoma* showed preference for the abyssal and hadal sites (from 4000 m on), whereas *Daptonema*, *Dichromadora* and *Molgolaimus* had a slight preference for depths shallower than 3000 m. Other dominant genera – *Paracanthonus*, *Halalaimus*, *Monhystera*, *Microlaimus*,

Acantholaimus – were proportionally equally present over all sites. In general, similar genera were found all over the sites, though with changing relative abundances.

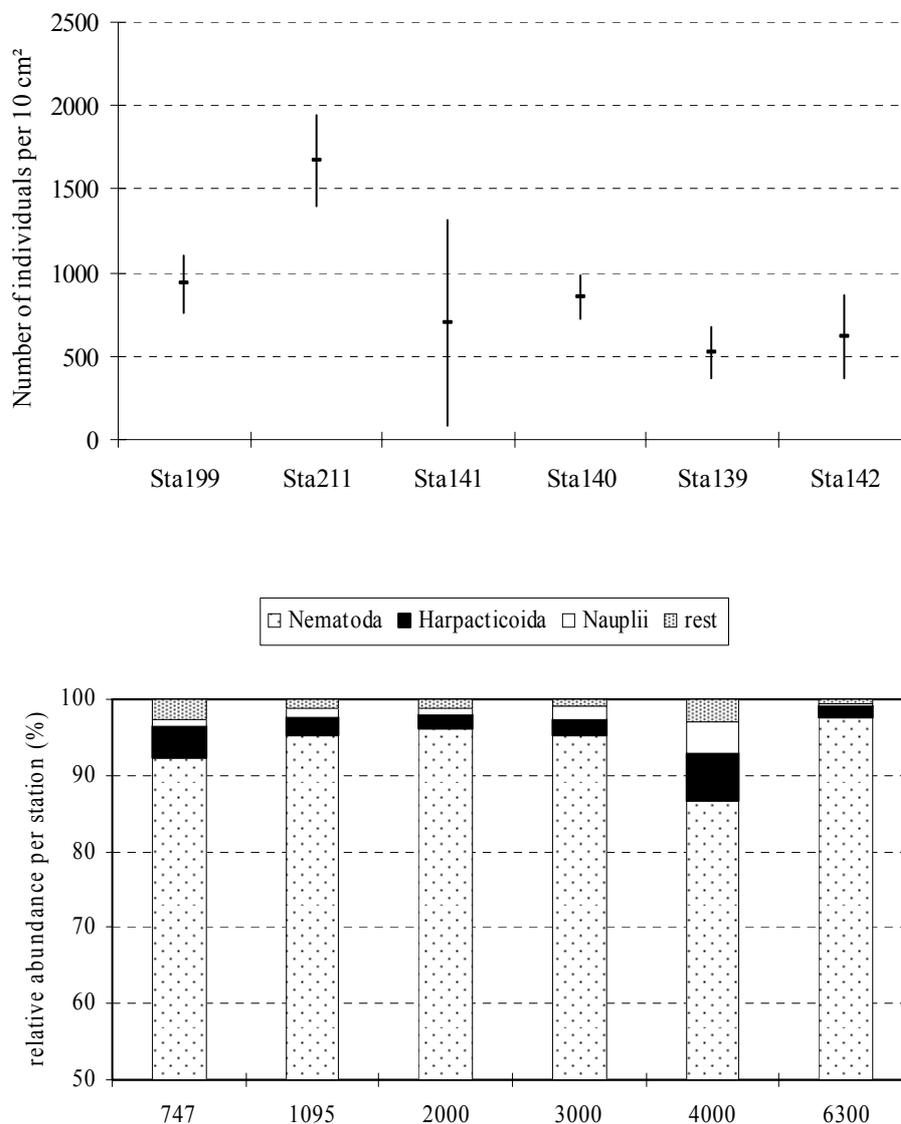


Fig. 6. Nematode densities and composition along the bathymetric gradient in the South Sandwich Trench (Stations are identical arranged from shallow to deep in both figures).

Discussion. Although the South Sandwich Trench area is highly productive (Howe *et al.*, 2004), food availability in the sediment was extremely low, with signals below 1% carbon and 0.1-1.6 ng g⁻¹ pigments (data not shown). These values are 20 – 450 times lower than those in the Atacama Trench at similar depths (Danovaro *et al.*, 2002). Therefore, a highly depauperate fauna was expected; however bathyal and abyssal densities from the South Sandwich Trench are situated above world oceans' regression line of meiobenthic stocks against water depth (Soltwedel, 2000) and confirm earlier results

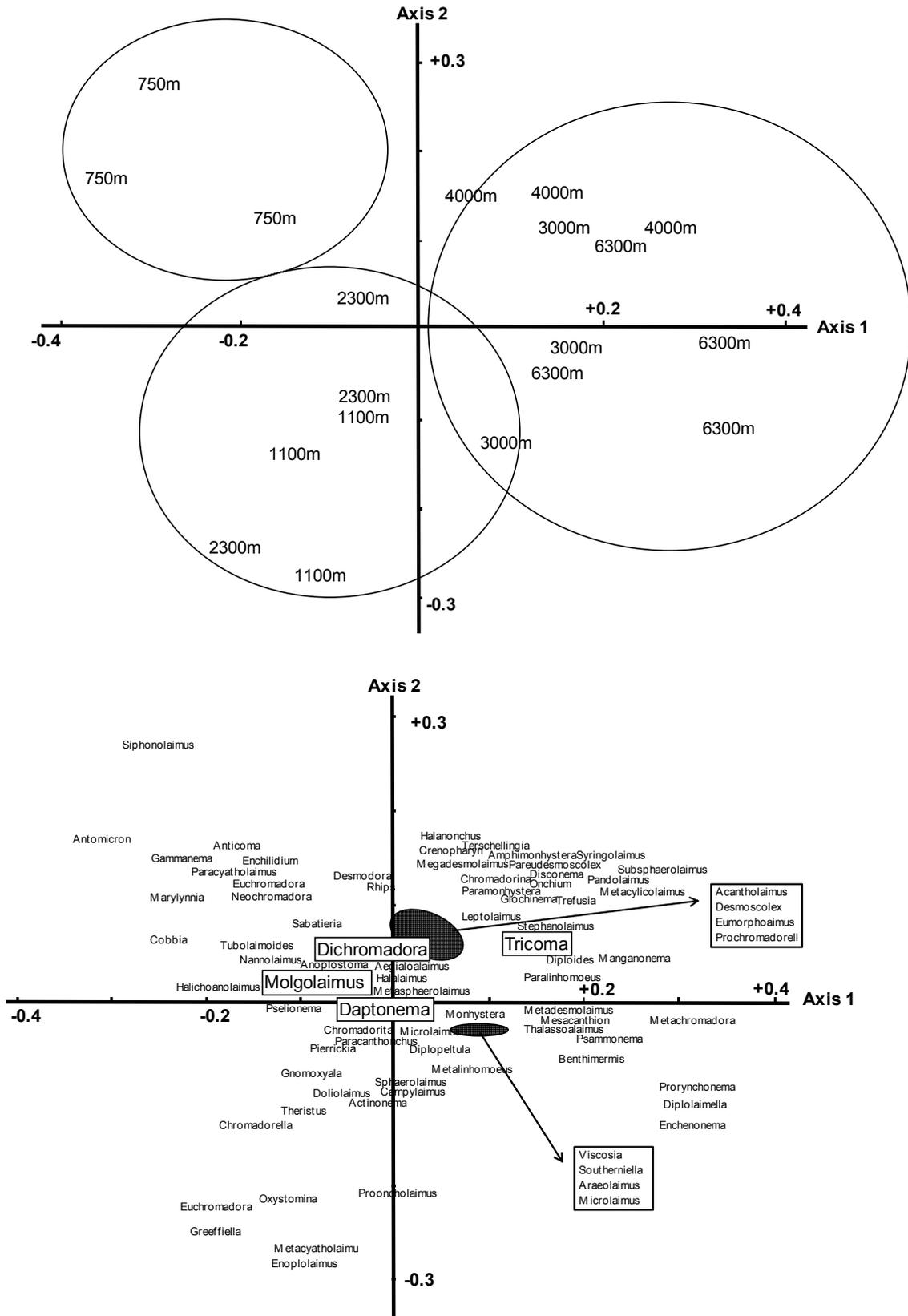


Fig. 7. PCA for genus relative abundances along the South Sandwich Trench transect.

from the Antarctic continental margins (Vanhove *et al.*, 1995) that the Southern Ocean is among the most productive offshore areas worldwide. Abundance on the trench floor (354-930 ind. per 10 cm²) is also higher than at similar depths in other oceans' trench regions (Soltwedel, 2000). Exceptions are Atacama Trench which holds very high concentrations of nutritionally rich organic matter (Danovaro *et al.*, 2002) and Barbados Trench, where meiofaunal abundances are indirectly linked to highly enhanced biological production – particularly due to bacterial activity – from the mud volcanoes (Olu *et al.*, 1997).

The discrepancy between high meiofaunal stocks and seemingly low food markers in the sediments cannot directly be explained with the current data. It seems likely that the Antarctic trench meiofauna utilizes incoming food very efficiently so that no clear traces of organic sources are left behind, explaining the low food content of the sediments.

The nematode assemblages along the bathymetric gradient generally contained the same genera, however their relative abundance differed considerably between the “shallow” (750-1100 m) and “deep” (4000-6300 m). The intermediate stations (especially at 3000 m) form a transition with changing overlap with both extremes. The “shallow” communities resemble those from the Weddell Sea continental margin (Vanhove *et al.*, 1999). The sediments at 2300-6300 m show a composition similar to abyssal nematode communities worldwide. These assemblages are consistently dominated by a few genera with abundances over 5% leading to a clustering of all abyssal sites with depths varying from 2000 to as much as 8000 m rather than grouping them on a geographical basis (Soetaert & Heip, 1985). The deepest assemblages at the South Sandwich Trench are very alike to those from the Puerto Rico (Tietjen, 1984) and Atacama Trench (Gambi *et al.*, 2003). Depth is clearly important in dominance distribution at genus and family level, though forms no barrier to the presence of most taxa. Downward and subsequent horizontal movement of nematode genera and families, despite strong geographic separation of sites, is seemingly no problem. The wide distribution of families and genera suggests that radiation of nematodes in abyssal depths occurred relatively long ago, or modern-day dispersal of nematodes over vast distances has been quite efficient. Current radiation of deep-sea nematodes probably occurs at species level (Tietjen, 1989).

The amphipod taxocoenosis of the Antarctic deep-sea

The ANDEEP exploratory campaigns allowed collecting the largest amphipod crustacean samples ever taken in the world deep sea. More than 10,000 specimens of benthic and benthopelagic amphipods were collected by a variety of gears between 1000 and 4934 m, which, according to the ongoing identifications, may belong to over 200 different species from 38 families including a majority of new taxa (De Broyer *et al.* 2003b, 2004, 2006; Berge & Vader 2003; Berge, pers. com.; Thurston, pers. com.; Brandt *et al.*, 2007a). The families particularly well represented in the Antarctic deep sea are the various lysianassoid families (in particular Eurytheneidae, Lysianassidae (Tryphosinae), Scopelocheiridae and Uristidae), as well as Eusiridae, Ischyroceridae, Phoxocephalidae, and Podoceridae. ANDEEP results showed that Amphipoda contributed up to 32% of the large material collected by the epibenthic sledge (EBS), ranking second after Isopoda (38%) (Fig. 8). This is in sharp contrast with deep-sea benthic samples from other oceans where amphipods are usually much less abundant (Dahl, 1954; Brandt *et al.*, 2007a).

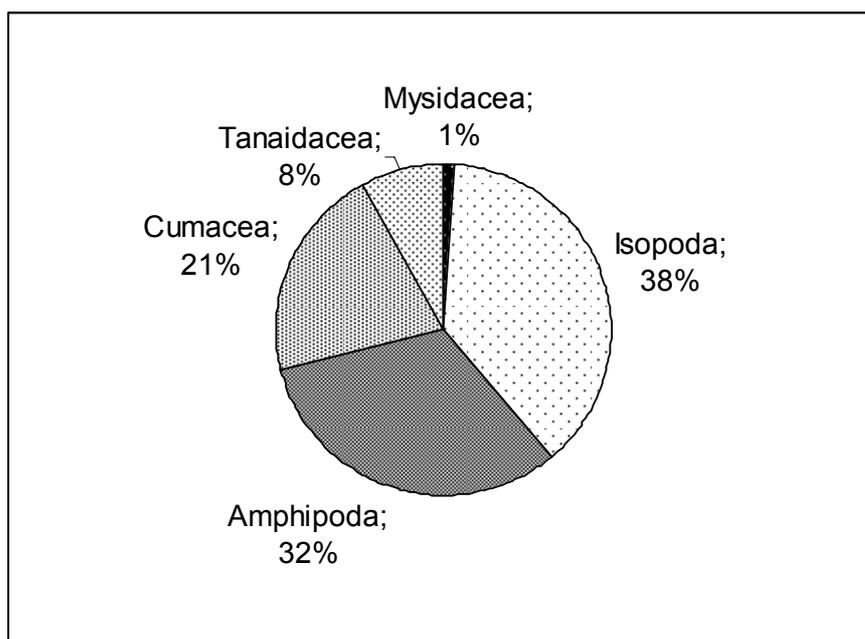


Fig. 8. Share of peracarid crustaceans collected by EBS during ANDEEP I-II campaigns.

On the basis of still incomplete taxonomic and distribution data, some patterns of geographic and bathymetric distribution were detected (De Broyer *et al.*, 2004; 2006; Brandt *et al.*, 2007a):

- The newly discovered Antarctic abyssal fauna shows high apparent endemism and has more affinities with peripheral abyssal basins than with the Antarctic shelf fauna. Among the amphipod scavenger guild (see hereafter), all but 10 of the strictly benthic deep-sea species are restricted to the Southern Ocean. The ten bathyal and abyssal species also occurring outside the Southern Ocean have been recorded in only one other basin peripheral to the Southern Ocean (Argentinian, Cape, or Eastern Australian Basin).
- Part of the shelf fauna extends along the upper slope to 1500/2000 m and the abyssal fauna appears below 2000 m (Fig. 9). This trend is shared by some other groups such as isopods and part of the molluscs but is not consistent among the various taxonomic groups (Brandt *et al.*, 2007a).
- The few cases of very wide eurybathic distribution possibly indicate the presence of cryptic species. Among the scavengers, *Eurythenes gryllus* is the only species found on the Antarctic shelf, the slope and in the abyssal zone. It is known as a panoceanic bathyal abyssal and hadal stenothermal species that can occur far above the sea floor (Thurston, 1990). Concerning the two other widely eurybathic species (*Orchomenopsis cavimanus* and *Abyssorchomene scotianensis*), small morphological differences have been detected between their shelf and deep-sea populations and a molecular analysis is required to detect potential cryptic species before confirming this very wide eurybathy.

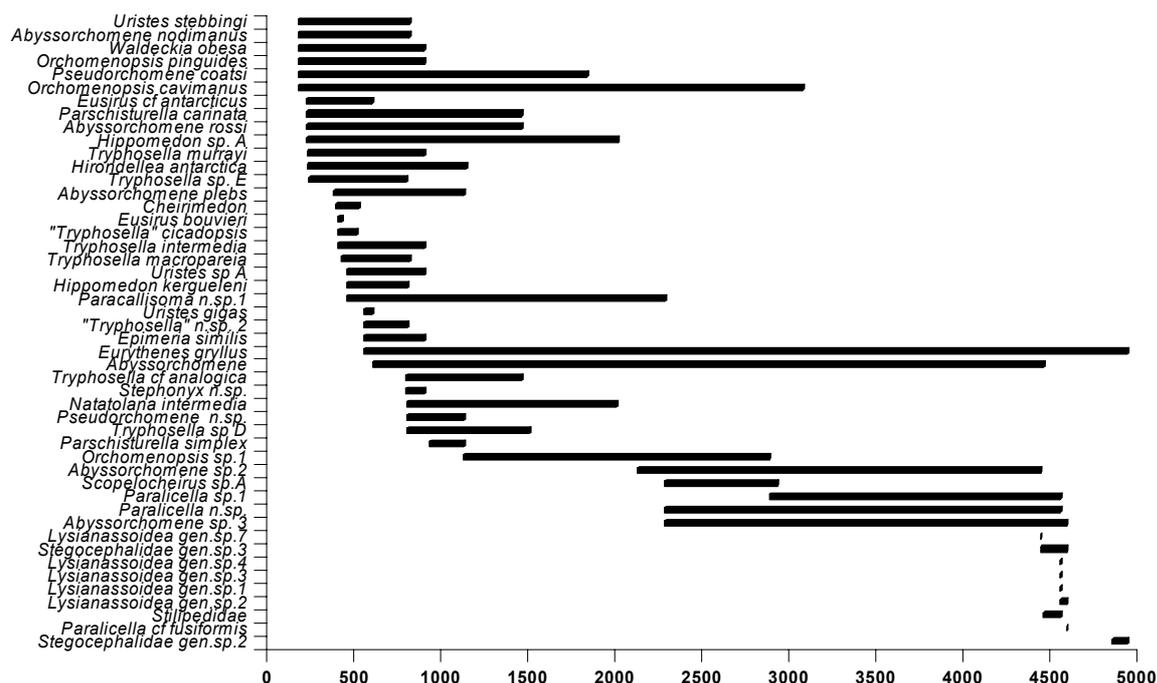


Fig. 9. Depth zonation exemplified by the scavenging amphipod species.

The deep-sea crustacean scavenger guild

Well represented in the deep sea, the scavenger guild (collected in baited traps) received particular attention during the (still ongoing) analysis of the rich ANDEEP amphipod material (see De Broyer *et al.*, 2004, 2006). Twenty-two baited trap operations were performed at bathyal and abyssal depths in the Weddell Sea, the Scotia Sea, the South Sandwich Trench and the Drake Passage. They provided about 5300 crustaceans of 51 species, one gastropod and few fishes. Both at slope and abyssal depth the bulk of the catches consisted of amphipod crustaceans (46 spp), in particular lysianassoids (39 spp from 18 genera and 8 families). New species of *Alicella*, *Hirondellea*, *Lepidepecreella*, *Orchomenopsis*, *Paracallisoma*, *Paralicella*, *Pseudorchomene*, *Stephonyx*, *Tryphosella*, and *Valettioopsis* were discovered. A few representatives of other amphipod families (Epimeriidae, Iphimediidae, Stegocephalidae) were collected, as well as other crustacean groups, namely Copepoda, Mysidacea, and cirrolanid Isopoda (Table 3).

The relation between species richness of necrophagous amphipods and depth is shown in Fig. 10. It clearly shows the variability of amphipod richness in coastal and shelf traps and its relatively limited reduction from the shelf down-slope to the abyssal zone.

In terms of bathymetric distribution, a number of species occurred on both the shelf and the slope (Fig. 9) showing in some cases an apparent quite extended level of bathymetry (see supra).

Table 3. Composition of the amphipod scavenger guild in the Antarctic deep sea (Atlantic sector).

	EASIZ I	EASIZ II	ANDEEP	Depth range
LYSIANASSOIDEA				
Lysianassidae and Uristidae				
<i>Abyssorchomene rossi</i> (Walker, 1903)		T11		1453
<i>Abyssorchomene scotianensis</i> (Andres, 1983)	T6	T11-12	100,114,131	1136-3070
<i>Abyssorchomene sp.A</i>			114	2754
<i>Hippomedon sp.A</i>	T6			2009
<i>Hippomedon sp.B</i>		T11		1453
<i>Orchomenopsis cavimanus</i> (Stebbing, 1888) var.A		T11-12	100.131	1136-3070
<i>Orchomenopsis n.sp.1</i>			46	2926
<i>Parschisturella carinata</i> (Schellenberg, 1926)		T11-12		1136-1453
<i>Pseudorchomene coatsi</i> (Chilton, 1912)		T11	100	1453-2280
<i>Pseudorchomene n.sp.1</i>		T11		1453
<i>Stephonyx n.sp.1</i>		T11-12		1136-1453
<i>Tryphosella cf analogica</i> K.H. Barnard, 1932		T11-12		1136-1453
<i>Tryphosella sp.C</i>		T12		1136
<i>Tryphosella sp.H</i>			100	2280
<i>Tryphosella sp.I</i>			100	2280
<i>Tryphosella sp.J</i>			100	2280
" <i>Tryphosella</i> " n.sp.2		T11		1453
<i>Tryphosinae gen. sp.A</i>		T11		1453
Alicellid family group				
<i>Alicella n.sp.1</i>			100	2280
<i>Paralicella cf caperesca</i> Shulenberg & Barnard, 1976			46	2926
<i>Paralicella n.sp.1</i>			100.114	2280-2754
Eurytheneidae				
<i>Eurythenes gryllus</i> (Lichtenstein, 1822)	T6	T11-12	46,100,114, 131,139	1453-3739
Hirondelleid family group				
<i>Hirondellea antarctica</i> (Schellenberg, 1926)		T12		1136
<i>Hirondellea n.sp.1</i>			100	2280
Scopelocheridae				
<i>Paracallisoma n.sp.1</i>			100	2280
<i>Scopelochirus sp.A</i>			46,100,114	2280-2926
IPHIMEDIOIDEA				
Epimeriidae				
<i>Gen. sp.A</i>			46	2926
Iphimediidae				
<i>Iphimediella sp.A</i>	T6			2009
Stegocephalidae				
<i>Gen.sp.C</i>	T6			2009
<i>Gen.sp.D</i>	T6			2009

Discussion. In terms of composition, the scavenger guild in the Antarctic deep sea shows some peculiarities in comparison with other oceans and with the Antarctic continental shelf. In contrast to lysianassoid amphipods, commonly caught in baited traps everywhere, there is only two previous record of Epimeriidae in baited traps: *Epimeria cf cornigera* (Jones *et al.*, 2003) and *Epimeria similis* (Dauby *et al.*, 2001a). The few Iphimediidae taken in traps were probably accidental as they are known as specialised micropredators (Coleman, 1989a,b; Dauby *et al.*, 2001a). Few Eusiridae are regular scavengers. Some *Eusirus* species have been recorded in traps (Takeuchi *et al.*, 2001; De Broyer,

unpubl.). Examination of feeding behaviour and stomach contents showed that *E. cf antarcticus*, for instance, is a selective macropredator able to feed partly on carrion (Dauby *et al.*, 2001a). Stegocephalidae are mostly micropredators associated with diverse benthic sessile invertebrates, while some species of *Andaniotes* and *Austrocephaloides* have been reported to be occasional scavengers (Berge and Vader, 2001, 2003). The second usually dominant group of scavengers on the Antarctic shelf, the cirrolanid isopods, was not represented significantly in the deep-sea samples. Besides crustaceans, nemerteans, gastropods and echinoderms (asteroids, ophiuroids, echinoids and holothuroids) frequently occur in traps at depths of less than 100 m (*e.g.* Presler, 1986; De Broyer, unpubl.). These groups were not represented in our catches at shelf, slope or abyssal depths except for five specimens of echinoderms and a single gastropod respectively found on the Weddell Sea shelf and slope.

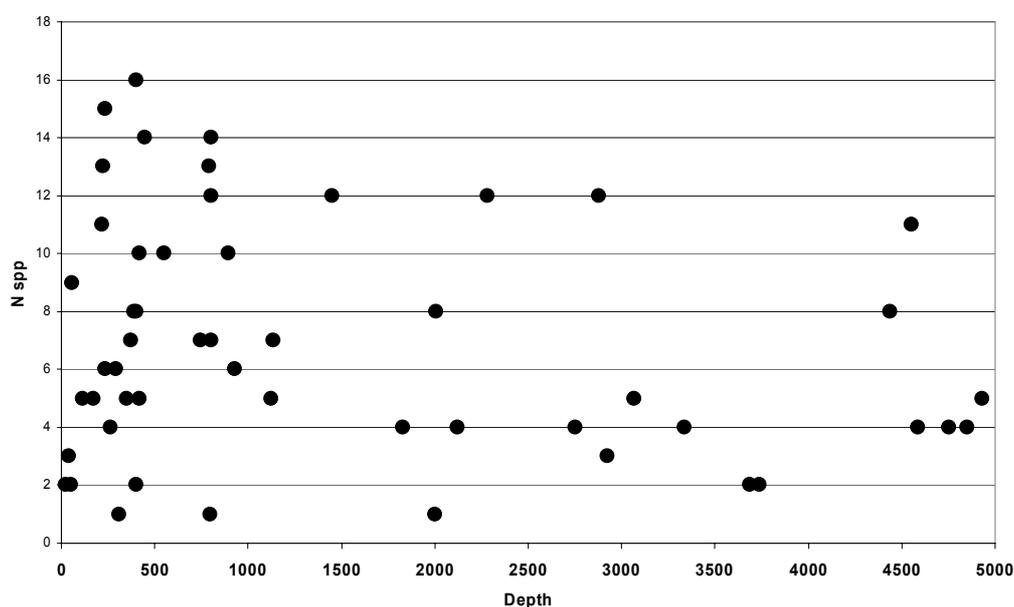


Fig. 10. Species richness vs. depth in scavenging amphipod species.

These first results on the Antarctic deep sea scavengers show that the Antarctic slope (1000–3000 m) appears to be richer in scavenger species than elsewhere in the world at similar depth range. Thirty-one amphipod species have been collected (18 spp in the eastern Weddell Sea) vs. 11 amphipod species (9 lysianassoids, 1 eusirid, 1 synopiid) found in baited traps on the slope of the Norwegian Sea at 1690 m depth (Vinogradov, 1997), 6 amphipod species (all lysianassoids) on the Gulf of Biscay slope at 200–1800 m depth (Desbruyères *et al.*, 1985), or only 5 amphipod species (4 lysianassoids, 1 epimeriid) trapped in the deep Cretan Sea at 1511–2485 m depth (Jones *et al.*, 2003). The higher species richness on Antarctic continental slope may be due to the extension of the rich deep-shelf fauna on the upper slope (De Broyer *et al.*, 2004).

In the Antarctic abyssal waters (> 3000 m), the species richness of the scavenger guild appears also higher than in the abyssal trap collections elsewhere in the world. The 12 ANDEEP abyssal trap sets in the Weddell, Scotia and Drake basins provided 18 species of necrophagous amphipods (2 alicellids, 1 eurytheneid, 2 lysianassids, 1 scopelocheirid, 4 uristids, 5 undetermined lysianassoids; 2

stegocephalids; 1 stilipetid) which constitute the most diverse abyssal trap record (De Broyer *et al.*, 2004). In comparison, the second most diverse record (44 trap sets at 3144–5940 m in the northeastern and tropical Atlantic Ocean), yielded 15 different species: 3 alicellids, 1 cebocaridid, 1 eurytheneid, 2 hirondelleids, 2 lysianassids, 2 scopelocheirids, 3 uristids, 1 valettiettid (Thurston, 1990). Moreover, this Atlantic record concerned more distinct abyssal plains and a wider bathymetric range, prospected with more numerous trap sets.

Considering the numerous and diverse benthic fauna recorded on the Antarctic shelf (see Gutt *et al.*, 2000), it appears that relatively few species, mostly lysianassoid amphipods, are attracted to baited traps. Similar observations were made in the high Arctic (Legezynska *et al.*, 2000). Some species may however occur in huge numbers (sometimes tens of thousands, see *e.g.* Slattery & Oliver, 1986), which indicate either high local densities, or low chemosensory thresholds and high mobility allowing some species to congregate from large areas of bottom.

2.3.2. EXPLORATION OF UNKNOWN HABITATS: BOUVET ISLAND

Bouvet Island appears as one of the most isolated and poorly known spot in the Southern Ocean. Its location in the ACC and at the fringe of the Weddell Sea Gyre suggests that it may play or have played a key role in the colonization of the Southern Ocean (Arntz, 2006). Four trawling and dredging operations as well as one trap deployment were performed on the poorly known bottoms around Bouvet Island during the *Polarstern* BENDEX cruise (Arntz & Brey, 2005).

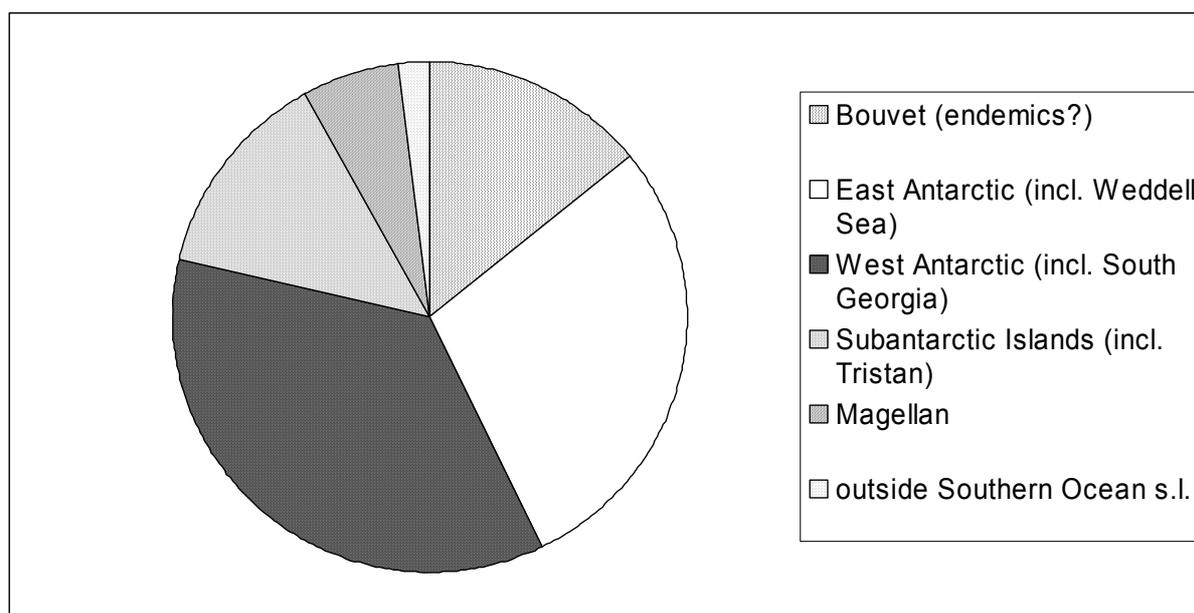


Fig. 11. Biogeographical affinities of Bouvet amphipod fauna.

These operations allowed collecting more than 67 amphipod species, including several new species, where only 5 benthic amphipod species were known before the cruise. The biogeographical affinities of the Bouvet amphipod fauna as presently known is shown in Figure 11.

The biogeographical links with the West Antarctic fauna (Antarctic Peninsula and Scotia Arc, excluding South Georgia) appear to be the strongest (24% of Bouvet species also occur in the West

Antarctic), followed by the Weddell Sea (18%) and the other East Antarctic fauna (16%). The comparison with other taxonomic groups shows that there is no consistent trend in the biogeographical affinities of Bouvet Island (Arntz *et al.*, 2006).

2.3.3. SPECIES DIVERSITY AND DISTRIBUTION PATTERNS: NEMATODA

Genus *Dichromadora* (Vermeeren *et al.*, 2004)

Species composition within the genus *Dichromadora* was studied at 1000 m and 2000 m sites in the Weddell Sea and adjacent areas (see Vermeeren *et al.*, 2004). Out of the 200 *Dichromadora* specimens studied, 8 different species were distinguished, of which 7 were new to science. At most, 6 congeneric species were found at one site (2000 m at Kapp Norvegia); on average 3.6 species were counted (see Table 4).

Five of the 7 new *Dichromadora* species have been described taxonomically (*D. weddellensis*, *D. southernis*, *D. parva*, *D. polarsternis*, *D. polaris*), two other have been described but were not named since they were only represented by 2 individuals (spec A and spec B). For the taxonomical descriptions, we refer to Vermeeren *et al.* (2004).

Discussion. Seven from a total of 8 *Dichromadora* species found in the Antarctic deep-sea samples around the Weddell Sea were new to science. Whether these species are unique for the Antarctic deep-sea can however not yet be assessed. Most ecological studies at nematode species level in marine environments, especially in the deep-sea do not include precise taxonomical information. This makes comparison between ecological studies, conducted by different scientists, difficult. Therefore, nematode samples from the Indian, Pacific, Arctic and Atlantic Oceans (1000 – 2000 m), available at the Marine Biology Section of the Ghent University, have been reconsidered for identification at species level within the genus *Dichromadora*, thus allowing a valuable comparison with Antarctic *Dichromadora* species.

In total, more *Dichromadora* species were observed in the Southern Ocean (8 spp) than in the Arctic (2 spp) or Atlantic Ocean (3 spp), which might be related to their higher abundance in the Southern Ocean. Seven of the nine known Antarctic species did not occur in other deep-sea sites. This might indicate some endemism at species level in Antarctica, similar to the observations for macrofauna, however the low taxonomical efforts taken so far in free-living nematodes in the deep sea worldwide does not allow to draw solid conclusions. The Arctic and Atlantic species retrieved in our samples, for example, were also new to science.

Our results show that while some species are spatially restricted in their distributions, others are widespread over the Atlantic sector of the Southern Ocean. This seems to confirm that many nematode species have wide ranges over regional scales in the deep sea (Lamshead & Boucher, 2003).

Genera *Desmodora* and *Desmodorella* (Ingels *et al.*, 2006)

Samples from both sides of the Scotia Arc, from the Weddell Sea, the Magellan area and the Ross Sea were studied at species level within the genera *Desmodora* and *Desmodorella* (See Ingels *et al.*, 2006). Six *Desmodora* species were distinguished, of which 5 were new to science. The only known species was identified as *Desmodora campbelli* Allgèn, 1932, which had been described from the sub-Antarctic Campbell Island south of New Zealand and was later also found off the coast of Chile and

Argentina. Two new *Desmodorella* species were found and one species – *Desmodorella* aff. *balteata* – had previously been observed around hydrothermal vents in the East Pacific Rise.

From the 64 stations analysed, 25 were characterized by the presence of *Desmodora* and/or *Desmodorella*. In fifteen stations, only one species was found, while the maximum number of species per station was three. The two known species, *Desmodora campbelli* and *Desmodorella* aff. *balteata*, were each found in 12 of the 25 studied stations while the other species were restricted to 1 or 2 stations. *Desmodorella campbelli* was relatively widespread over the shallowest stations (100-405 m) and completely absent in the deeper samples. *Desmodorella* aff. *balteata* was present in all areas (including the Ross Sea) except for the South Sandwich Trench and the Magellan Region. The maximum depth observed for *D.* aff. *balteata* was 1028 m in the Drake Passage. *Desmodora* sp. A, sp. B and sp. C were only observed in the South Sandwich Trench samples at depths between 747 and 6315 m, while only *Desmodora* sp. D was found in the Weddell Sea as well as in the South Sandwich Trench. *Desmodora* sp. E, *Desmodorella* sp. A and *Desmodorella* sp. B are characteristic for the Weddell Sea. Finally, *Desmodora minuta* Wieser, 1954 was found in the Magellan region, but absent from the Antarctic samples. Distribution patterns are given in Table 4 and Figure 12.

A first molecular analysis on specimen of *Desmodora campbelli* from both sides of the Scotia Arc was done to test whether we actually deal with the same species. Preliminary results based on ten partial COI-gene sequences (primers JB2 and JB5) of *D. campbelli* from stations 177 and 242 showed little genetic divergence between populations from these stations, which could point to either a very slow “evolver” or an extremely high gene flow.

Discussion. The genus *Desmodora* occurred in all areas except for the Antarctic Peninsula, while *Desmodorella* was absent only from the South Sandwich Trench. Both genera occurred mainly at shallow depths, except for 3 *Desmodora* species which were confined to the deeper stations at the South Sandwich Trench.

Desmodora campbelli was found in the Atlantic and Pacific sector (Campbell Island) suggesting a circumpolar distribution. However, this species only occurred at shallower depths and was absent in deeper samples (South Sandwich Trench), presumably excluding its dispersion through the deep sea.

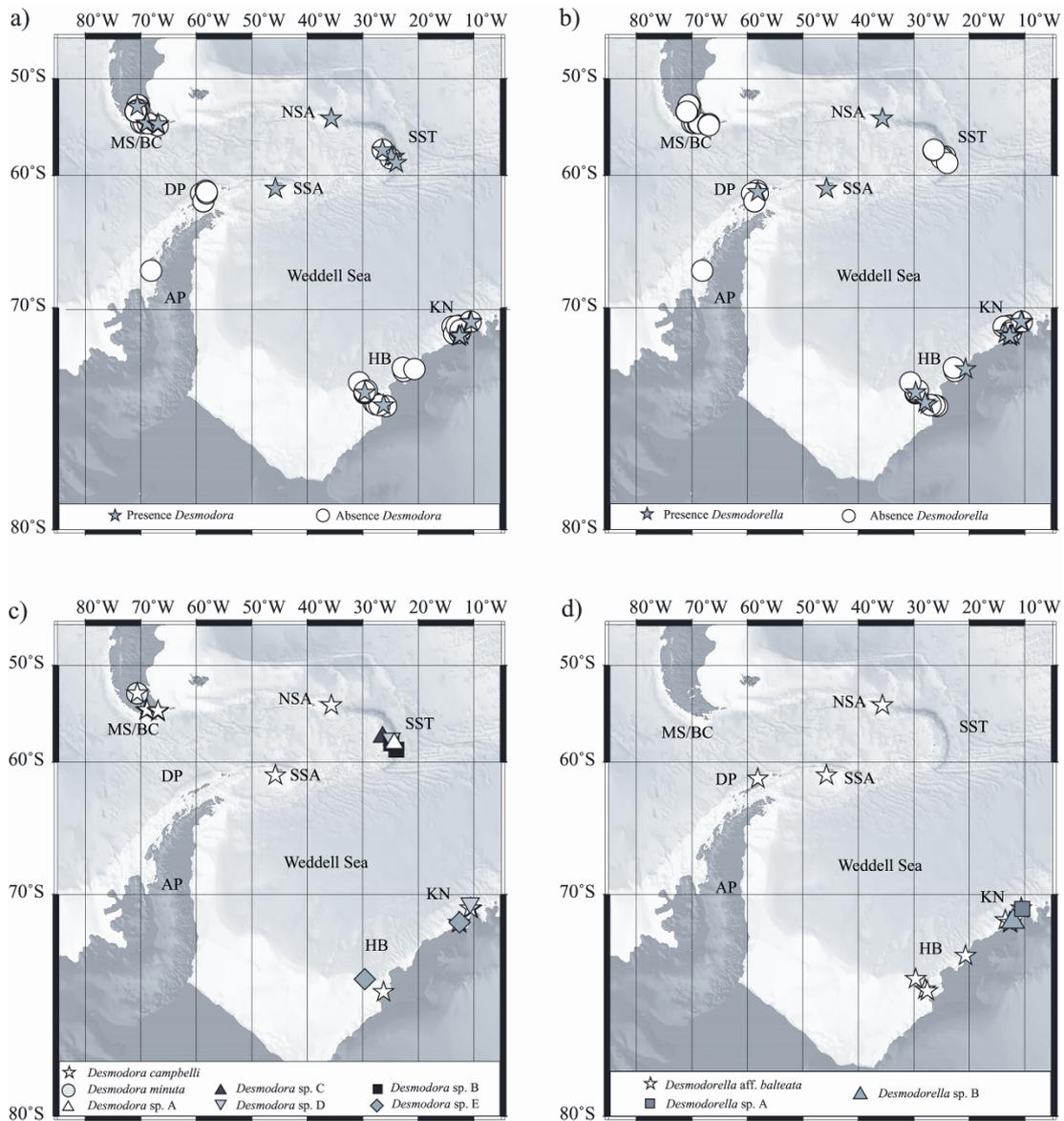


Fig. 12. Distribution of *Desmodora* and *Desmodorella* species in the Weddell Sea and Scotia Arc areas.

It was also absent around the Peninsula, possibly due to low food availability or sediment characteristics: samples from Rothera area were characterised by a relatively low silt-clay fraction. However, the absence of *D. campbelli* in a few samples does not necessarily mean that it is completely absent in the general sampling area. The Scotia Arc may very well have served as a migration path from or to the Antarctic for this species. Its dispersion could be influenced by hydrodynamics (Palmer, 1990) since dispersal of nematodes is assumed to be primarily by passive transport in the bedload and water column. Epigrowth-feeders such as *Desmodora* and *Desmodorella* prefer the surficial sediment and are most susceptible to erosion and transport (Commito & Tita, 2002, and references therein). Although the nematodes are assumed to be permanent sediment inhabitants, their occurrence in the water column is not exceptional in high-energy areas (Ullberg & Olafsson, 2003). Considering that Antarctic waters are characterised by a complex current system (ACC, East Wind Drift, Weddell Sea gyre, eddies, etc.) and movement of vast water masses (Antarctic Bottom Water, Circumpolar Deep

Water, Antarctic Surface Water, Sub-Antarctic Surface Water, etc.), the dispersion of benthic meiofauna cannot be excluded since turbulent water masses are encountered at considerable depth and have enough energy to transport small animals. Another explanation for the distribution of *D. campbelli* could be that it inhabited parts of South America and Antarctica before the two continents drifted apart, and remained unaltered ever since, partly due to a slow evolution rate which is typical in very cold conditions. This view is consistent with the assumption that the Antarctic fauna is very old. Preliminary molecular results based on 10 partial COI-gene sequences (primers JB2 and JB5) of *D. campbelli* from NSA 177 and SSA 242 show little genetic divergence between populations from these stations, which again could point to either a very slow “evolver” or an extremely high gene flow. Considering the large distance (ca. 960 km) between both stations, the latter may seem very improbable, but the complex hydrodynamic situation around the Scotia Arc leaves scope for discussion.

Genus *Acantholaimus* (De Mesel *et al.*, 2006)

Species diversity and distribution – in relation with biogeography, bathymetry and environmental characteristics – within the genus *Acantholaimus* were investigated on the shelf and slope (182-2009 m) in the Weddell Sea (Kapp Norvegia and Vestkapp) and near the Antarctic Peninsula (Drake Passage and Bransfield Strait) (see De Mesel *et al.*, 2006).

In contrast to previous studies, no link was observed between depth and relative and absolute densities. We did however find a link with chlorophyll a concentrations, with highest absolute and relative densities at lowest chlorophyll a concentrations (Fig. 13). The partial correlation analysis (controlling for depth) between chl a and the log transformed absolute and relative densities was significant ($p < 0.05$).

Very high morphological diversity within the genus *Acantholaimus* was found: 55 morpho-species could be distinguished within 450 specimens analysed in 15 stations. The morpho-matrix and morphological characteristics on which it is based are represented in De Mesel *et al.* (2006). The number of species (S) was highest in the Weddell Sea region, with in total 53 species vs 15 species found in the Antarctic Peninsula. This corresponds respectively with on average 5.9 and 2.67 species per station, indicating that the higher number of species in the Weddell Sea region is not only due to the higher amount of stations studied.

Discussion. In other oceans, *Acantholaimus* has mainly been found in sediments of continental slopes and the abyssal plain, often in high densities (Thistle & Sherman, 1985; Tietjen, 1989), increasing in relative importance with depth (Soetaert & Heip, 1995; Muthumbi & Vincx, 1997) and has as such always been considered a typical deep-sea genus (Tietjen, 1989; Soetaert & Heip, 1995; Muthumbi & Vincx, 1997). Members of this genus are found only sporadically on shelves and only one species has been described from shallow water sediments until now. In this study however, *Acantholaimus* species occurred in all samples from the continental shelf and slope (depths between 182 and 2008 m).

In total, 39 species were found on the shelf (200-500 m water depth), of which 14 had a distribution extending to the lower slope. This kind of wide bathymetric distribution patterns is considered typical for the Southern Ocean (Brey *et al.*, 1996). It has mainly been described within macrofauna, e.g. for gastropods, molluscs, decapods, amphipods, sponges, holothurians and sea urchins.

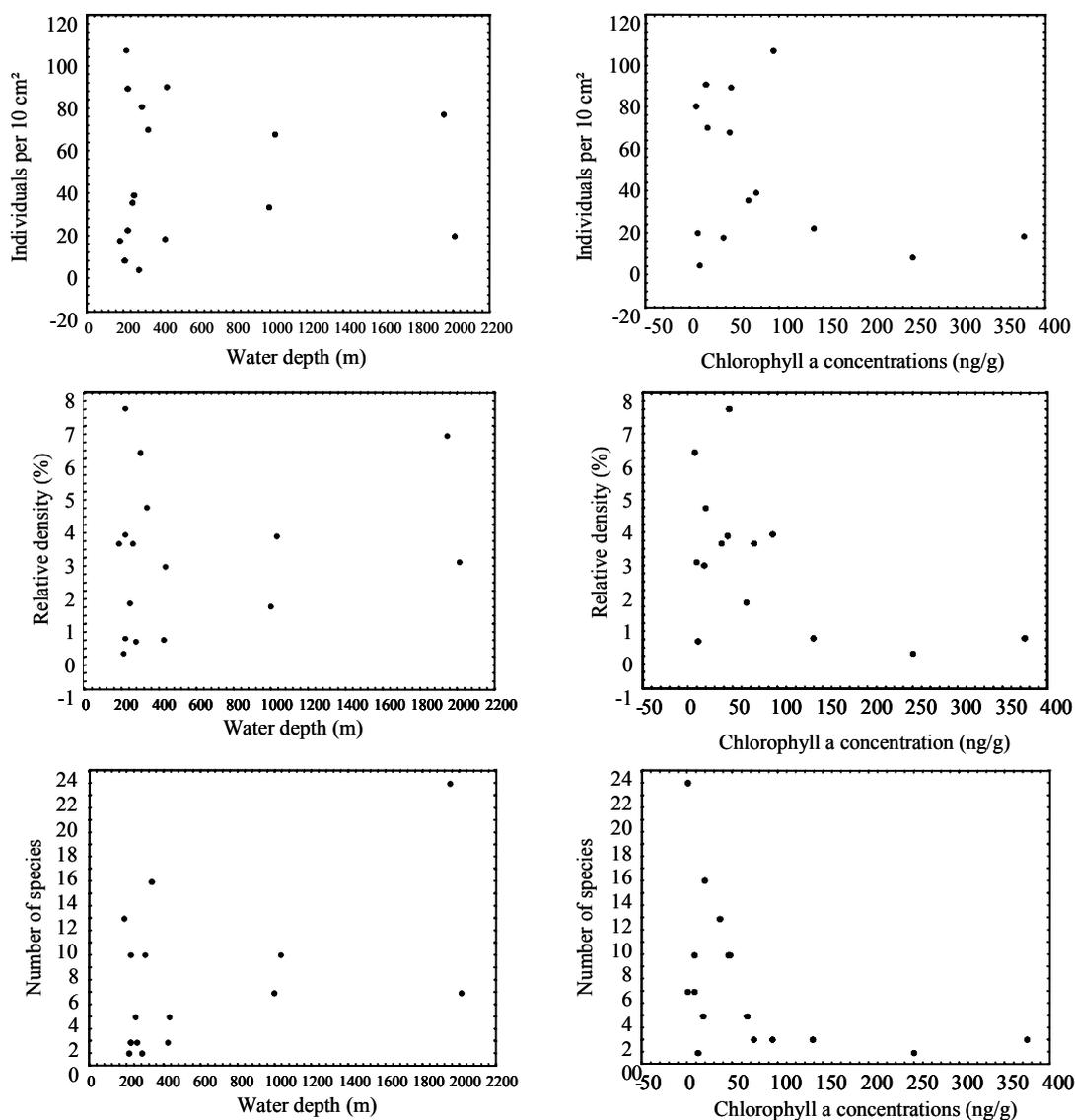


Fig. 13. Scatterplot of absolute and relative proportions and species richness of the genus *Acantholaimus* against water depth and chlorophyll concentrations in the Weddell Sea and adjacent seas.

The occurrence of typical deep-sea foraminifera in shallower water has been reported a number of times (Gooday *et al.*, 1995; Bowser *et al.*, 1995; Mikhalevich, 2004). The physical similarities (such as environmental stability and temperature) of the shelf and upper slope in Antarctica and the deep sea worldwide have been mentioned as possible explanation for the invasion of deep water species (Gooday *et al.* 1995; Bowser *et al.*, 1995). We should however be careful with drawing too general conclusions on eurybathy within the genus *Acantholaimus*. The distribution patterns of *Acantholaimus* along a bathymetric gradient can only be compared with one similar study in the Indian Ocean

(Muthumbi & Vincx, 1997). In contrast with our observations, *Acantholaimus* was not found shallower than 500 m water depth and they found 18 species occurring over a depth range from 500 m to 2000 m. The comparison of distribution patterns in both areas supports the evidence for eurybathy in Antarctica.

The relative importance and the number of species of *Acantholaimus* generally increase with depth (Soetaert & Heip, 1995; Muthumbi & Vincx, 1997). Because so many environmental factors co-vary with depth, it is mostly not feasible to assess the main factor responsible for the changes. In our study area however, considerable variation in environmental factors, mainly in chlorophyll a concentration, was found in stations at comparable depths. This allowed separate evaluation of both effects.

In contrast with the above mentioned studies, no link was found with depth in our study area. We did however observe a significant negative impact of chlorophyll a concentrations on the absolute and relative *Acantholaimus* densities, and their diversity. Chlorophyll a is a measure of the phytoplankton concentration in the sediment, and therefore of one of the most important food sources in the benthic food web, especially for assumed epistratum feeders such as *Acantholaimus*. *Acantholaimus* seems however not to rely on fresh food supply, but is able to sustain dense and diverse communities at low phytoplankton concentrations. It thus seems likely that *Acantholaimus* utilises other food sources, such as bacteria, and that their trophic classification based on their buccal cavity is not completely adequate. This negative link with chlorophyll a, together with the observations of Lee *et al.* (2001a and b) who found restricted colonisation abilities of *Acantholaimus* after iceberg scouring, suggest they can be considered “persisters” rather than colonisers. These findings also suggest that the relative importance of *Acantholaimus* might increase in winter when the light regime and the sea ice cover inhibit primary production and the input of pelagic and ice algae to the sea bed are very low.

Genus *Molgolaimus* (Fonseca *et al.*, 2006)

The genus *Molgolaimus* was studied at 7 locations around the Weddell Sea. In total, 17 stations were sampled between 200 m and 4000 m water depth (see Fonseca *et al.*, 2006). 17 *Molgolaimus* species were found of which 16 were new to science. For the taxonomical description of these species and a polytomous identification key to species level for the genus *Molgolaimus*, we refer to Fonseca *et al.* (2006).

In order to unravel possible relationships between *Molgolaimus* species from shallow water and the deep sea, the distribution of species belonging to the same morpho-group – as identified by the polytomous key – was analysed in relation to bathymetry and geography (Fig. 14). Samples from other parts of the world were included for this investigation. No bathymetric restriction of the morpho-groups was found: species from each of the morpho-groups appeared from coastal zones to the deep-sea. To test for geographical restrictions of the morpho-groups, their occurrence was plotted on a world map. It appeared that very similar species of *Molgolaimus* occurred in the same or adjacent geographical areas.

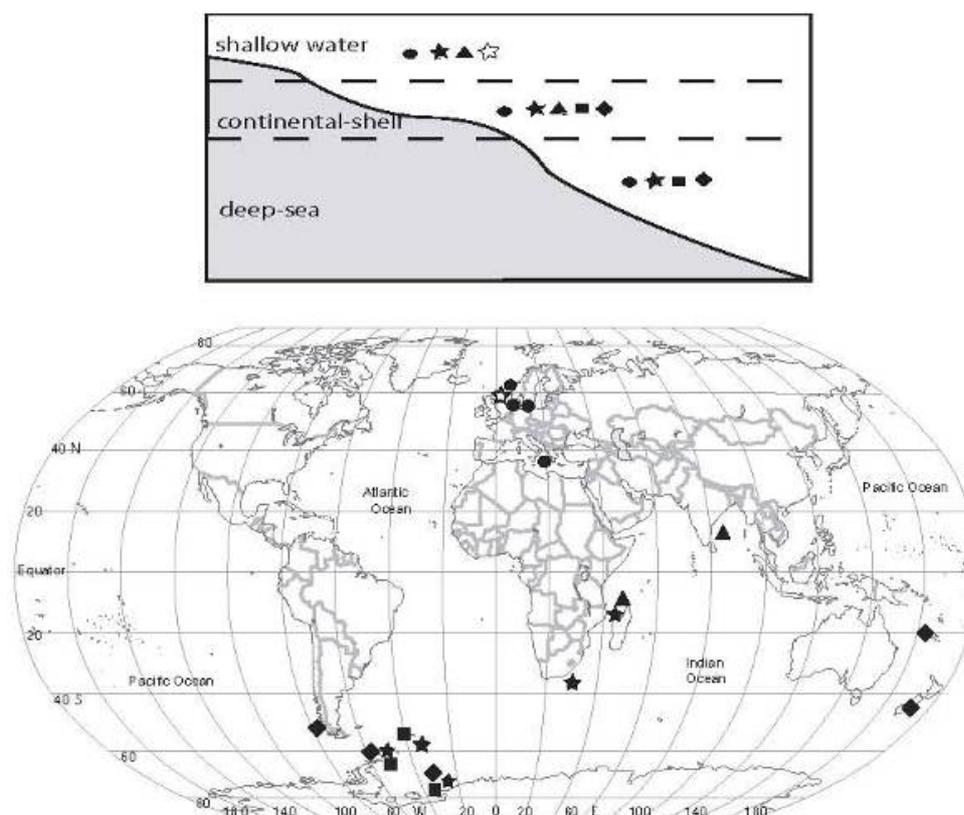


Fig. 14. **a.** Environmental distribution, and **b.** world spatial distribution of the different morphological groups of *Molgolaimus* species, where: ● = group 1a, ★ = group 1b, 1c & 2, ■ = group 3, ▲ = group 4a, ◆ = group 4b + *M. gigaslongincus*, ☆ = outliers species: *Molgolaimus allgeni* and *M. minutus*.

Discussion. Proponents of a theory suggesting a recent shallow origin of the current deep sea fauna include Fonseca *et al.* (2006). The present study shows that geographical rather than environmental clustering of “morphologically” similar *Molgolaimus* species does not support the idea of a common origin of deep-sea nematode species. Possibly, the distribution of nematodes can be explained on a global scale by means of paleogeographical events, such as the movements of tectonic plates. However, paleogeographical events by themselves are not the only explanation for the current distribution pattern of deep-sea benthic organisms, and recent migration from shallow water towards the deep sea is apparently also occurring.

Although based on limited samples and a small genus, this study is the first attempt to discuss global patterns for marine nematodes. Hopefully, confirmation of this hypothesis will come in the future with the combination of morphological and molecular evidence from phylogeographic studies.

2.3.4. SPECIES DIVERSITY AND DISTRIBUTION PATTERNS: AMPHIPODA

Amphipod biodiversity survey

A comprehensive census of Antarctic and sub-Antarctic species of gammaridean and corophiidean amphipods has been completed (De Broyer *et al.* 2007), based on a complete survey of taxonomic and ecological literature (935 references), and on new data collected during BIANZO and previous projects. The Southern Ocean fauna includes 815 described species. In addition, 70 taxa of known genera have been recorded but not identified to the species level.

Among the described species, 536 occur in Antarctic waters south of the Polar Front and 407 in sub-Antarctic waters between the Polar Front and the sub-Tropical Front zone. Both regions share 128 species, i.e. 24% of the Antarctic fauna or 31% of the sub-Antarctic fauna. Detailed information on geographic and bathymetric distribution is given for all species (>8000 distribution records), completed with the available habitat data.

The whole amphipod fauna of the Southern Ocean (*s.l.*) comprises 723 gammaridean, 92 corophiidean and 69 hyperiidean species (the latter - exclusively holoplanktonic - are not further treated herein; see De Broyer & Jazdzewski, 1993, for a checklist). An overview of the gammaridean and corophiidean amphipod fauna of the Southern Ocean is given in Table 5, which summarizes for the different biogeographic regions, sub-regions and bathymetric zones the number of taxa of the whole fauna and its benthic, benthopelagic and pelagic components as well as the semi-terrestrial fauna (Talitridae) and the cetacean ectoparasites (Cyamidae).

In terms of composition, the Antarctic and sub-Antarctic amphipod fauna is mostly dominated by representatives of Lysianassoidea (158 spp in 57 genera and 18+ families), Eusiroidea (108 spp in 27 genera and 4 families), Stenothoidae (66 spp in 16 genera), Ischyroceridae (49 spp in 7 genera), Iphimediidae (46 spp in 13 genera), Phoxocephalidae (34 spp in 18 genera) and Epimeriidae (26 species in 5 genera).

The total *benthic and benthopelagic* fauna presently counts 772 species in the whole Southern Ocean (*s.l.*), 502 species in the Antarctic region and 388 species in the sub-Antarctic region. The benthopelagic species, which have been recorded in the water column at some distance from the bottom in the neritic or oceanic zones, count 24 Antarctic and 7 sub-Antarctic species, respectively. Despite their non-permanent occurrence on the bottom, they have been included in the benthic fauna as they play a role - which may be significant - in the benthic ecosystem (*e.g.* the benthopelagic and demersal lysianassoid scavengers). They belong to some dominantly pelagic families: alicellids (*Paralicella*), Eurytheneidae (*Eurythenes*), Hyperiopsideae (*Hyperiopsis*) and to dominantly benthic families: Epimeriidae (*Epimeriella*), Eusiridae (*Eusiroides*, *Eusirus*, *Rhachotropis*), Lysianassidae (*Cheirimedon*, *Orchomenella*), Pagetinidae (*Pagetina*), Pardaliscidae (*Halice*), Pleustidae (*?Atylopsis*), Scopelocheridae (*Paracallisoma*, *Scopelocheirus*), Stegocephalidae (*Parandania*), and Uristidae (*Abyssorchomene*, *Uristes*).

A clear distinction both in species richness and composition can be made between the different bathymetric zones. The Antarctic *shelf* fauna (0-1000 m; see Clarke & Johnston, 2003) comprises 474 benthic and benthopelagic species, with 427 species restricted to shelf depths. On the other hand, 164

benthic and benthopelagic species occur between 500 m (average depth of the continental shelf break) and 3000 m, but only 56 spp between 1000 and 3000 m. This clearly indicates that part of the shelf fauna extends its distribution to the upper slope.

The *deep-sea* fauna (found below 1000 m) amounts 96 benthic and benthopelagic species in the whole Southern Ocean, 91 species in the Antarctic and 21 species in the sub-Antarctic region. These numbers do not include the preliminary results from the recent *Polarstern* ANDEEP cruises. When included, the number of Antarctic deep-sea species may surpass 200 species (De Broyer *et al.*, 2004; Brandt *et al.*, 2007a).

The presently known *abyssal fauna*, below 3000 m, counts 19 benthic and benthopelagic species in the Antarctic and only 4 species in the sub-Antarctic region. This low species richness mostly reflects the lack of deep-sea exploration in the Antarctic, but, again, the number of Antarctic abyssal species will substantially increase due to the recent ANDEEP discovery of numerous species in the abyssal basins of the Atlantic sector of the Southern Ocean.

The *pelagic fauna* of the neritic or/and oceanic Antarctic waters is composed of 26 gammaridean species belonging to purely or dominantly pelagic families (Cyphocarididae: *Cyphocaris*, Eurytheneidae: *Eurythenes*, Hyperlopsidae: *Hyperlopsis*, thorellids: *Chevreuxiella*, *Danaella*), and also to dominantly benthic families: Calliopiidae (*Stenopleura*), Eusiridae (*Cleonardo*, *Eusirella*, *Harcledo*), Pagetinidae (*Pagetina*), Pardaliscidae (*Halice*), Pleustidae (?*Atylopsis*), Scopelocheridae (*Scopelocheiropsis*, *Scopelocheirus*), and Stegocephalidae (*Parandania*).

In terms of *endemism*, the Antarctic fauna show a level of 72,3% of endemic species (all components) or 66,6% if only benthic and benthopelagic species are considered. The Antarctic faunule is characterized by the presence of three (small) endemic families: Clarenciidae, Didymocheliidae and Pagetinidae, the latter two also occurring in the sub-Antarctic region. The sub-Antarctic region is characterized by a much lower level of species endemism: 45,7% (all components) and 47,9% for the benthic component, reflecting the links with adjacent regions (e.g. South America for the Magellan province and New Zealand for the New Zealand sub-Antarctic islands). If the whole Southern Ocean *s.l.* is considered, the level of species endemism reaches 79,8% for all components and 83,6% for the benthic and benthopelagic species.

Synopsis of Southern Ocean Amphipoda

An international network of 17 specialists from 12 countries (the "Antarctic Amphipodologist Network", AAN) was established to undertake the taxonomic revision of the Antarctic fauna of gammaridean and corophiidean amphipods, to synthesize their biogeographical and ecological traits and to elaborate the highly-needed identification guides and electronic interactive identification keys.

The revision of the first group of families (Acanthonotozomellidae, Amathillopsidae, Dikwididae, Epimeriidae, Iphimediidae, Ochlesidae and Vicmusiidae) was completed (Coleman, 2007) and an interactive illustrated key of the Southern Ocean families and subfamilies was elaborated (Lowry, 2007).

The high species richness of amphipods and isopods

The high species richness of some Antarctic macrozoobenthic groups has been attributed to different evolutionary and ecological factors: the long evolution in isolation of the southern polar ecosystem, the glaciological history and the oscillations of the ice sheet (the “climatic pump of biodiversity”; Clarke & Crame, 1989, 1992, 1997), and at smaller time scales, the regular seasonality or predictability of the system, the role of disturbance (by ice in particular), the high spatial heterogeneity, and the energy input (e.g. Arntz *et al.*, 1994; Clarke, 2003a; Clarke *et al.*, 2004). Some particular determinants of the high species diversity in Antarctic amphipods have been discussed by De Broyer *et al.* (2003a).

Amphipods, like most peracarid crustaceans, feature some characters that obviously may reduce gene flux between populations and facilitate speciation. Their diversification success can be attributed first of all to their *brooding habit*, which implies limited dispersal of juveniles and enhanced reproductive isolation. Many peracarids have a rather *low mobility*, with the exception of the typical pelagic and hyperbenthic swimmers among amphipods and mysids. A substantial part of the amphipod species for instance are known to be bottom crawlers, burrowers, nestlers, tube-dwellers, clingers, or endo- or ectosymbionts of algae or benthic sessile suspensivores. They are sedentary or weakly motile or have very limited swimming periods. On the other hand, amphipods are known to be primarily a *cold-water adapted group*, which radiated more successfully in cold conditions (Barnard & Barnard, 1983). The importance of the *habitat heterogeneity* has been stressed by several recent studies (e.g. Clarke & Johnston, 1996; De Broyer *et al.*, 2001a). In the eastern Weddell Sea some 230 amphipod species have been recognised so far. This high species richness has been mainly attributed to the diversity of habitats offered by the biogenic sediments such as the sponge spicule mats and bryozoan debris, the ubiquitous dropstones providing hard substrates even in the deep sea, and the abundant and diverse sessile epibenthos which provide tri-dimensional substrates, food resources and opportunities for symbioses.

Another potential factor of diversification is the *emergence of new adaptive zones* due to the faunal extinction events during the Tertiary cooling of the Southern Ocean. In particular, the extinction of many decapod crustaceans may have allowed some peracarid crustaceans to fill their vacant ecological niches (Clarke & Crame, 1989; De Broyer & Jazdzewski, 1996; Brandt, 2000). Part of the success of the “reptant” iphimedioid amphipods or serolid isopods might be due to the absence of reptant decapods through reduced predation and competition. Moreover, decapod scarcity may have allowed a widening of the size spectrum among the Antarctic amphipods and isopods which comprise many large species (De Broyer, 1977; Chappelle, 2001; De Broyer *et al.*, 2003a).

A possible *co-evolution with the Antarctic Notothenioides* was suggested by different studies (Wägele, 1992b; Brandt, 2000). Like some peracarid crustaceans, notothenioids have experienced an adaptive radiation in the Southern Ocean during the Tertiary (e.g. Eastman & Clarke, 1998). As many of them

Table 5. The Gammaridean and Corophiidean Amphipod fauna of the Southern Ocean.

	All fauna	Benthic & benthopelagic taxa	Benthopelagic taxa only	Pelagic taxa	Cetacean ectoparasites (Cyamidae)	Semi-terrestrial taxa (Talitridae)
Antarctic Region						
Total spp. (N endemics)	536 (388)	502 (376)	24 (16)	26 (11)	7 (1)	1 (0)
Total gen. (N end.)	205 (53)	192 (53)	16 (1)	14 (0)	2 (0)	1 (0)
Total fam. (N end.)	67 (1)	65 (1)	13 (1)	9 (0)	1 (0)	1 (0)
<i>East (High) Antarctic province</i> N spp. (N end.)	291 (104)	262 (89)	20 (4)	20 (7)		0 (0)
<i>West Antarctic (Scotia) province</i> N spp. (N end.)	414 (149)	401 (145)	19 (3)	12 (3)		1 (0)
<i>Antarctic deep sea</i> N spp. (N end.) (>500 m)	201(136)	182 (134)	16 (10)	19 (5)		
N spp. (N end.) (>1000 m)	92 (57)	74 (53)	11 (7)	18 (4)		
N spp. (N end.) (>3000 m)	31 (14)	19 (13)	6 (4)	12 (2)		
Sub-Antarctic Region						
Total spp. (N end.)	407 (186)	388 (186)	7 (0)	7 (0)	4 (0)	8 (2)
Total gen. (N end.)	200 (30)	192 (30)	6 (0)	5 (1)	1 (0)	5 (0)
Total fam. (N end.)	67 (1)	65 (1)	4 (0)	4 (0)	1 (0)	1 (0)
<i>Subantarctic Islands province</i> N spp. (N end.)	226 (72)	216 (71)	4 (0)	2 (0)]		5 (1)
<i>Magellan province</i> N spp. (N end.)	210 (95)	203 (94)	4 (0)	3 (0)		4 (1)
<i>Subantarctic deep-sea</i> N spp. (N end.) (>200 m)	133 (42)	129 (42)	5 (1)			
N spp. (N end.) (>500 m)	59 (14)	58 (14)	4 (1)	4 (1)		
N spp. (N end.) (>3000 m)	7 (0)	4 (0)	2 (0)	3 (0)		
Southern Ocean (s.l.)						
Total spp. (N end.)	815 (651)	772 (646)	24 (19)	28 (13)	7 (1)	8 (2)
Total gen. (N end.)	301 (106)	291 (104)	16 (1)	21 (0)	2 (1)	5 (0)
Total fam. (N end.)	81 (4)	79 (4)	12 (1)	11 (0)	1 (0)	1 (0)
Southern Ocean deep sea N spp (N end.) (>500 m)	216 (126)	196 (120)	32 (11)	20 (6)		
N spp (N end.) (>1000 m)	96 (59)	78 (55)	19 (9)	18 (4)		
N spp (N end.) (>3000 m)	31 (17)	19 (15)	7 (5)	12 (2)		
Total unidentified spp. (not included)	70	69	0	1		

predate on peracarid crustaceans, Brandt (2000) suspected some links between the notothenioid evolution and the success of some peracarid taxa. Several amphipod and isopod families possess body ornamentation of teeth and spines, sometimes strongly developed. On the other hand, some detailed analyses of the feeding habits of notothenioids by Gröhsler (1992) and Olaso *et al.* (2000) showed that the peracarid preys were mostly composed of species lacking this strong body ornamentation. Relying on these results and on a similar Baikal Lake example (Bazikalova, 1954), Brandt (2000) postulated that the development of such spiny ornamentation in some isopods such as Serolidae and in some amphipods such as Iphimediidae and Epimeriidae could confer some selective advantage in terms of avoiding or limiting predation. In the same line, it may be suggested that the very successful radiation of the Antarctic iphimerioid and stenothoid amphipods could be in some way related to the radiation of the abundant sessile suspension feeders that constitute their prey or their hosts. Iphimediidae and related families are mostly specialized micropredators on sponges, bryozoans, hydrozoans or cnidarians and Stenothoidae are known as associates to diverse benthic organisms (Coleman, 1989a,b; Dauby *et al.*, 2001; De Broyer *et al.*, 2001a, 2003a).

2.3.5. SPECIES DIVERSITY AND DISTRIBUTION: ECHINOIDEA

Southern Ocean echinoid biodiversity

Among the 78 species recorded in the Southern Ocean s.s., 21 belong to the Cidaridae and 30 to the Schizasteridae, *i.e.* most (*ca* 65%) Antarctic echinoids species only belong to 2 families. Obviously, diversification occurs at species and not at genus level. In contrast, all other Antarctic echinoid families are much less diversified and represented by a lower number of species and genera (Table 6).

Table 6. Echinoid biodiversity in the Southern Ocean

Orders	Families	Number of genera	Number of species	<i>Endemic genera</i>	<i>Endemic species</i>
Cidaroida	Cidaridae	5	20	60%	81 %
Echinothurioida	Echinothuriidae	1	1	0	0
Phyrosomatoida	Arbaciidae	1	1	0	0
Temnopleuroida	Temnopleuridae	1	3	0	0
Echinoida	Echinoidea	3	7	0	57 %
Holasteroida	Plexechinidae	1	2	0	50 %
	Pourtalesiididae	6	8	17 %	62 %
	Urechinidae	4	6	25 %	50 %
Spatangoida	Schizasteridae	8	30	37 %	67 %
7 orders	9 families	30	78	27 %	64 %

An outstanding feature of the Cidaridae and the Schizasteridae is the brooding behavior displayed by most of their species (Table 7). Indeed, 70% of the Cidaridae and more than 83% of the Schizasteridae are brooders. The large yolky eggs are kept on the body surface of females in apical or oral depressed areas (Cidaridae) or in ambulacral deep depressions where direct development occurs leading to

juvenile individuals. This behaviour has also evolved in Urechinidae but it is only restricted to a few species.

Table 7. Biodiversity of brooders

Families	Number and (%) of brooding species	% of brooders among endemic species
Cidaridae	14 (70%)	71%
Urechinidae	2 (33%)	100%
Schizasteridae	25 (83%)	95%

Longitudinal patterns of regional biodiversity

Four longitudinal regions were considered. They corresponded to the Atlantic Ocean sector (range: ca.70°W-20°E), the Indian Ocean sector (range: 20°E-120°E), the Australia-New Zealand sector (120°E- 180°), and the Pacific Ocean sector (180°-70° W). The comparison of these four main longitudinal sectors resulted in an expected pattern (Table 8).

Table 8. Shared echinoid species and similarity indexes between longitudinal sectors

	Total spp	Atlantic Ocean	Indian Ocean	Australia + New Zealand	Pacific Ocean
Atlantic Ocean	54		32 (0.44)	14 (0.23)	21 (0.35)
Indian Ocean	50			20 (0.40)	20 (0.35)
Australia + NZ	20				13 (0.38)
Pacific Ocean	27				

According to the straits opening chronology, the land masses distribution, and the direction of main currents, we may predict the lowest similarity between the Atlantic and Pacific, and the highest similarity between the Atlantic and Indian regions. Although, similarity between contiguous regions is fairly constant, its lowest (35%) and highest (44%) values were as expected.

Latitudinal patterns of regional biodiversity

Four latitudinal zones were compared: Zone A: from the coastline to 75° S (this zone is restricted to the Weddell and Ross seas); Zone B: from 75° to 70° S; Zone C: from 70° up to the Antarctic Divergence (at ca. 65° - 60°S); Zone D: from the Divergence to the Polar Front (Antarctic Convergence) at ca. 55° - 50° S. The Jaccard similarity indexes are respectively of 60% between zones A and B, 63% between zones B and C, and 45% between zones C and D (Table 9).

Along this latitudinal cline, the echinofauna appears relatively homogeneous up to the Antarctic Divergence (C-D boundary) where a drop of 18% occurs. Slightly more than half of the echinoid species (55%) are affected by the C-D boundary.

Table 9. Matrix of similarity between latitudinal geographic zones (The diagonal terms - bold italic digits - indicate the number of species recorded in each zone. The lower part of the matrix gives the numbers of shared species between the zones, and the upper part the corresponding Jaccard indexes).

	Zone A	Zone B	Zone C	Zone D
Zone A	25	0.60	0.46	0.24
Zone B	24	39	0.63	0.39
Zone C	25	36	54	0.45
Zone D	15	26	33	53

There are 13 species restricted to the southernmost latitudes and they belong to only three orders (Spatangoida, Cidaroida and Holasteroida), while the 19 species restricted to the northernmost latitudes belong to the full set of Antarctic echinoid orders (Spatangoida, Holasteroida, Echinoida, Temnopleuroida, Phymosomatoida, Echinothuroida and Cidaroida). Translatitudinal species (26 species) mostly belong to Spatangoida or Cidaroida, and to a lesser extent to Holasteroida, and Echinoida (Fig. 15). Among the 13 species restricted to the south, 10 spp (77%) are brooders; among the 18 species reported exclusively north to the Divergence 9 spp (50%) are brooders; 19 (73%) of the translatitudinal species are brooders.

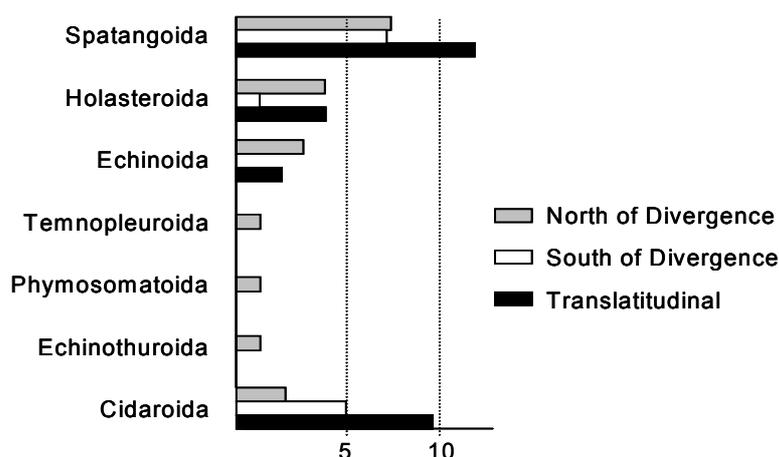


Fig. 15. Latitudinal distribution of echinoid orders.

Bathymetric patterns of regional biodiversity

As expected, the relationships between depth ranges display stronger similarities between the shelf fauna from the shore to 500 m in depth (upper shelf area) and from 500 to 1000 m (lower shelf area and upper slope) rather than between the shelf and the deep-sea (below 1000 m) (Table 10). The shelf fauna is thus homogenous (with 73% of the species occurring in the two considered shelf depth ranges). In contrast, only ca. 30% of the deep water species (below 1000 m) are also present on the lower shelf. The shelf and the deep-sea echinoid fauna are consequently distinct. This pattern is observed all around Antarctica, in the four longitudinal sectors.

Table 10. Shared echinoid species and similarity indexes according to depth ranges

	Total species	0 – 500 m	500 – 1000 m	> 1000 m
0 – 500 m	52		43 (0.73)	21 (0.29)
500 – 1000 m	50			24 (0.36)
> 1000 m	41			

Endemism

The echinoid endemism is particularly high as 64% of the species are endemic to the Southern Ocean s.s. (Table 6). Once again, the Cidaridae and the Schizasteridae are remarkable as most of the species for both families are endemic, namely, 81% of the Cidaridae species and 67% of the Schizasteridae species. High level of endemism is also observed for Pourtalesiidae and Urechinidae; however, these families are less diversified at species level.

Discussion. Echinoids are free-living epi- or endobenthic animals that range from the intertidal zone to the abyssal depths. There are 78 Antarctic species (7 orders, 9 families), with 64% of the species (27% of the genera) endemic to the Southern Ocean. About 65% of the Antarctic echinoid species belong to 2 families, the Cidaridae and the Schizasteridae, whose endemic species count respectively 70% and 83% of direct developers. The remarkable predominance of brooders in Antarctic Cidaridae and Schizasteridae has been explained by the glacial conditions that have counter-selected indirect developers and therefore have limited their diversification (e.g. Poulin & Féral, 1996). This could have resulted in the extinction of taxa with planktonic larvae during glacial extremes and in the diversification of taxa with lecithotrophic eggs. As brooding habits reduce dispersal and gene flow, it must have increase speciation rates. This is supported by the fact that most endemic species of Cidaridae (71%) and Schizasteridae (95%) are brooders. Interestingly the Cidaridae and Schizasteridae are also the oldest families to occur in Antarctica; there are fossils records from Mesozoic for Cidaridae and from Cenozoic for Schizasteridae (Hotchkiss, 1982; McKinney *et al.*, 1988; Pawson, 1994; Néraudeau *et al.*, 2000). This has given some time for speciation to occur in these two groups.

3. ECOFUNCTIONAL ROLE OF BIODIVERSITY

3.1. INTRODUCTION

The role of biodiversity in the functioning of the Southern Ocean benthic ecosystems remains poorly understood. The high species richness, which characterizes many benthic groups, implies that a large variety of ecological niches has to be expected, and their spatial and functional components have to be described to assess their respective role(s).

The knowledge of the habitats and microhabitats (including symbioses) occupied by many benthic species from the Southern Ocean is still limited, despite recent progresses (*e.g.* Gutt & Starman, 1998; Gutt & Schickan, 1998; De Broyer *et al.*, 2001a). On the other hand, there are still large gaps in our knowledge of the trophic regime of many species or the composition and role of the various trophic guilds, and few attempts have been done so far to synthesize the role of biodiversity in the energy fluxes of the Southern Ocean benthic ecosystems (*e.g.* Jarre-Teichmann *et al.*, 1997).

The BIANZO project focused on the identification and description of the functional niches occupied by representatives of the three target groups, in particular the habitat component, the size, mode of life and mobility, the trophic niches and their integration in the benthic food web.

The **trophic position of meiobenthos** in general and nematodes in particular in the benthic food web and the importance of their biodiversity in the functioning of the marine systems are still not well understood. Based on the morphology of their buccal cavity, nematodes have been subdivided in trophic groups (Wieser, 1953). The trophic composition of the nematodes might be an indication of the food sources used in the seabed; however this approach is not always straightforward in shelf and slope communities (Vanhove *et al.*, 1998; 1999), but had never been tested in the Antarctic deep sea. A further attempt to refine this classification, as was originally planned in this project, did not seem the best option, especially since biochemical methods have now proven to be very useful in food-web investigations. First attempts have been made to analyse stable isotope ratios in nematodes from deep-sea environments. These data were complemented with feeding experiments in which ¹³C labelled food items – bacteria and diatoms – were added to sediment cores and their uptake by the nematodes was followed over 2 weeks.

Biomass spectra are useful tools in assessing functional changes in nematode communities as a result of a changing environment (Vanaverbeke *et al.*, 2003). A striking characteristic of the Antarctic nematode communities is the shift towards higher sizes in deeper water along the continental slope, in contrast to other parts of the world (Vanhove, 1997). We studied the individual and total biomass at abyssal and hadal depths and compared with other oceans.

Within the Antarctic macrobenthic communities the **amphipod crustaceans** appear to be probably the most diversified group in terms of trophic types, life styles, habitats and size spectra (De Broyer & Jazdzewski, 1996; Dauby *et al.*, 2001; De Broyer *et al.*, 2001a; Chappelle, 2001). The first analysis of the trophic diversity of an Antarctic benthic amphipod community was performed in the eastern Weddell Sea (Dauby *et al.*, 2001a). Almost all known feeding types were encountered, with a notable exception for macroherbivory, likely because of the apparent absence of macroalgae in that area. Eight main different types were described, from suspension-feeding to obligate necrophagy. More specialized trophic types

can be expected as inquilinous and symbiotic species have not been systematically investigated so far. The amphipod trophic impact on the different available food items was also estimated (Dauby *et al.*, 2001b), with plankton particles and crustaceans being the more preyed ones. The diversity of the amphipod feeding modes is likely to be partly related to the diversity of habitats and microhabitats as shown by De Broyer *et al.* (2001a).

To compare with the eastern Weddell Sea food web, the trophic structure of the macrobenthic community of the Antarctic Peninsula region was investigated by relying on stable isotopes as trophic biomarkers. Within the macrobenthic food web, the trophodiversity of the amphipod taxocoenosis was analysed in detail by a multi-proxy approach (stomach content analysis, morphology of feeding appendages, feeding experiments, stable isotopes and lipids as trophic biomarkers) (Nyssen *et al.*, 2002, 2005; Nyssen, 2005). On the other hand the significance of benthic and pelagic amphipods as a food resource for the higher trophic levels of the Southern Ocean has been reviewed (Dauby *et al.*, 2003).

A systematic analysis of the amphipod size spectra revealed that the Antarctic contains the greatest percentage of giant species. Comparison with other marine and freshwater ecosystems of the world showed that oxygen availability rather than temperature was responsible for this tendency towards gigantism (Chapelle & Peck, 1999; 2007). New datasets were analysed in order to validate the "oxygen hypothesis" (Chapelle & Peck, 2004).

Echinoids can feed on a variety of food resources. Irregular echinoids are primarily deposit-feeders feeding on the organic matter that settles on the sea floor, while regular echinoids are usually opportunistic browsers feeding on vegetal or /and animal materials (De Ridder & Lawrence, 1982). Do particular feeding categories characterize the Antarctic echinoids? The question was tentatively answered in this project.

During the last decades, symbiosis has been described as a pervasive and evolutionary significant biological phenomenon, as it widens the set of available niches in the environment and thus may increase biodiversity. It has been well documented that in benthic communities, substratum space is often limited and that competition is intense (*e.g.* Key & Barnes, 1999). The opportunity to settle on other organisms (the hosts) can consequently be advantageous, and more particularly so if these hosts have permanent (not molted) external surface and if they are motile (the abiotic substratum being regularly disturbed in coastal areas). Echinoids are usual hosts for a wide range of procaryotic (bacteria) and eucaryotic symbionts (Barel & Kramers, 1977; Jangoux, 1990; De Ridder & Foret, 2001). Among Antarctic species, numerous ectosymbiotic organisms (from sponges to echinoderms) have been recorded (David *et al.*, 2001), the inventory of which is only starting. In the deep sea in particular, such symbioses with echinoids could constitute new ecological niches and increase the number of coexisting taxa. Cidaroids in particular are well diversified and abundant in the Antarctic waters where they are usually heavily coated by ectosymbionts.

Within the BIANZO project, we explored the importance of echinoids in the Antarctic ecosystems both as elements of trophic webs and as substrate providers for sessile ectosymbionts. A comprehensive study of the ectosymbioses occurring on cidaroids has been conducted (Hétériér, 2007).

3.2. MATERIAL & METHODS

Meiobenthos. Nematode size and biomass. Sediment cores were collected along a bathymetric transect (747 – 6300 m) towards the South Sandwich Trench and on the Weddell Abyssal Plain during the *Polarstern* LAMPOS and ANDEEP II campaigns (see Fig. 2). 150 nematodes from the upper cm in each station (*i.e.* 50 from each replicate) were mounted into Cobb slides. The nematodes were measured using a Quantimet 500+ image analysis system on a Leitz Dialux 20 microscope. The length and width of the nematodes was used to calculate their biomass with Andrassy's adjusted formula (Andrassy, 1956; Soetaert, 1989): WWT nematode (mg) = [largest body width (mm)² x body length (mm)] x 1.13g cm⁻³/1.9. Conversion to dry weight assumes a dry:wet weight of 0.25.

Nematode trophodiversity. Nematodes from the South Sandwich Trench transect were classified into four feeding groups according to Wieser (1953) linked to buccal morphology: selective (1A) and non-selective deposit feeders (1B), epistratum feeders (2A) and predators/omnivores (2B).

Trophic position of meiobenthos. Three replicate drops were performed. From each drop, 4 cores were sliced (0-1cm, 1-2cm, 2-3cm, 3-4cm, 4-5cm) of which one was preserved on 4% formaldehyde solution for community analysis (not presented) and 3 were frozen (-20°C) for respectively stable isotope analysis and fatty acid analysis (not presented). Six cores per drop were used for the incubation experiment (see Table 11).

Table 11. Use of the cores from each drop.

Core tube	Destination	Treatment (Diatoms/Bacteria)	Sampling time (days)	Storage
1	Experiment	Diatoms	1	Dark, -1°C
2		Diatoms	7	Dark, -1°C
3		Diatoms	14	Dark, -1°C
4		Bacteria	1	Dark, -1°C
5		Bacteria	7	Dark, -1°C
6		Bacteria	14	Dark, -1°C
7	Meiofauna community + densities			4% formalin
8	Natural stable isotopes			-20°C

Six cores per drop were incubated under controlled conditions in the dark at -1°C in a water bath and under permanent aerations. The cores were left to stabilize for 24 hours before the labeled food sources were added (Table 11). Three cores per drop were inoculated with ¹³C labeled bacteria and the 3 other cores with ¹³C labeled diatoms. *Thalassiosira rotula*, commonly used for this kind of experiments in other regions, was chosen for this experiment, while the bacterial inoculum consisted of an undefined mixture of bacteria. Samples were collected after 1, 7 and 14 days. Each time, 3 replicate cores – one from each drop – per treatment were sliced (0-1cm, 1-2cm, 2-3cm, 3-4cm, 4-5cm) and frozen (-20°C).

For the stable isotope analyses, the 0-1 cm and the 1-2 cm slices of each experimental sediment core, and from the core for natural stable isotope analysis, were decanted in a jar of 5 litres over a 125

and 32 µm sieve, respectively, to retrieve two different size classes of the meiofauna (32-125 µm and >125 µm). After repeating this procedure for 10 times, approximately 95% of the meiofauna was extracted, stored in Milli-Q water and immediately processed (Steyaert, pers. comm.). The isotope study is based on the > 125 µm size class fraction. Nematodes were handpicked with a fine needle, rinsed twice in MQ water to remove adhering particles, and finally transferred to a drop of MQ water in 2,5 x 6 mm aluminium cups (Van Loenen Instruments). The cups and needles were pre-combusted for 4h at 550°C to remove any contaminating organic carbon. The aluminium cups were oven-dried at 60°C overnight, pinched closed, and stored in air-tight Multi-well Microtiter plates. A minimum of 70 nematodes, depending on crude biomass estimates based on observations of length and width of selected specimens, were picked out for one reliable analysis (Moens, pers. comm.). Carbon was conservatively estimated at 10% of nematode wet weight (Sikora *et al.*, 1977; Heip *et al.*, 1985).

To obtain the natural $\delta^{13}\text{C}$ signatures of the organic carbon in the sediment samples, 20-40 mg sediment was weighed, dried and homogenized. The samples were then treated in silvercups with dilute HCl to solve the inorganic carbonate fraction. The cups were pinch closed, and stored in air-tight Multi-well Microtiter plates.

The carbon isotopic composition of the samples was determined with a high precision continuous flow IRMS Europa Hydra 20/20. The data are reported in the δ notation relative to the Vienna Pee Dee Belemnite standard and expressed in units of ‰, according to the standard formula following the procedure of Craig (1957):

$$\delta^{13}\text{C} = \frac{^{13}\text{C}/^{12}\text{C sample} - ^{13}\text{C}/^{12}\text{C standard}}{^{13}\text{C}/^{12}\text{C standard}} \times 1000$$

The δ values had a reproducibility of 0,17 ‰ (based on the standard deviation of the standards).

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

Lipid analysis. Samples stored in chloroform:methanol (2:1 by vol.) were evaporated with nitrogen to dryness and subsequently lyophilised for 48 h. Dry mass (DM) was determined gravimetrically. Total lipid mass (TL) was measured gravimetrically after lipid extraction from the freeze-dried samples using dichloromethane:methanol (2:1 by vol.), essentially after Folch *et al.* (1957). Fatty acid composition was analysed by gas-liquid chromatography (Kattner & Fricke, 1986). Fatty acids of the total lipid extracts were converted to their methyl esters by transesterification in methanol containing 3% concentrated sulphuric acid at 80°C for 4 hours. After extraction with hexane, fatty acid methyl esters were analysed with a Hewlett-Packard 6890 Series gas chromatograph with a DB-FFAP fused silica capillary column (30 m x 0.25 mm inner diameter; 0.25 µm film thickness) using temperature programming (160-240°C at 4°C min⁻¹, hold 15 min). For recording and integration Class-VP software (4.3) (Shimadzu, Germany)

was used. Fatty acids were identified with commercial and natural standard mixtures and if necessary, additional confirmation was carried out by gas chromatography-mass spectrometry.

Isotopic ratios. Muscle tissues or whole animals of small species were dried and ground with mortar and pestle into a homogenous powder. Isotopic ratios were measured individually in each specimen. Stable carbon and nitrogen isotope ratios were analysed with a nitrogen-carbon elemental analyser (Fisons, UK) directly coupled to an Optima (Micromass, UK) continuous flow isotope ratio mass spectrometer (CF-IRMS) for combustion and automated analysis. Isotopic ratios are expressed in ‰ values as the proportional deviation of the sample isotope ratio from that of an international Vienna Pee Dee Belemnite (V-PDB) standard according to the following formula:

$$\text{‰X} (\text{‰}) = \left[\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 1000$$
, where X is ^{13}C or ^{15}N , R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, and the appropriate standards were Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Inter-comparison materials were IAEA-N1 ($\text{‰}^{15}\text{N} = +0.4 \pm 0.2\text{‰}$) and IAEA CH-6 (sucrose) ($\text{‰}^{13}\text{C} = 10.4 \pm 0.2\text{‰}$). Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.3‰ for both carbon and nitrogen.

Megabenthos: Analysis of echinoid symbioses. Symbioses occurring on cidaroid hosts have been studied through 3 set of observations: (1) the ectosymbionts biodiversity (study #1), (2) the morphological features of the spines and their effects on colonization by ectosymbionts (study #2), (3) the ecological significance of symbioses in benthos biodiversity (study #3). Samples were obtained by dredging and kept in 70% ethanol. Observations of spines and ectosymbionts were done under a stereomicroscope (Leica MZ75). For the morphometric studies, the ectosymbionts were removed and the spines were photographed under the same microscope using a Nikon 9500 digital camera. For observations under scanning electron microscope (SEM), ectosymbionts were dehydrated in graded ethanol, dried by the critical point method using CO_2 as transition fluid, mounted on aluminium stubs, coated with gold in a sputter coater and observed with a JEOL JSM-35-C scanning electron microscope.

In study #1, ectosymbionts from 13 cidaroids species were inventoried and a detailed comparison was done on ectosymbionts associated with two morphologically contrasted cidaroid species: *Ctenocidaris spinosa* and *Rhynchocidaris triplopورا*. The samples origin for the global inventory is given in Table 12; for the detailed comparison of *C. spinosa* and *R. triplopورا*, 20 individuals of each species were collected in the Weddell Sea by the R/V “Polarstern” during the IX/3, XIII/3, XV/3 campaigns between 1991 and 1998 (depths ranges: 64 to 746 m). (see Hétérier *et al.*, 2005 for details). A distinction was made between oral, ambital and apical spines and two spines of each type have been selected for analysis; two zones per spine, a distal and a proximal one, were examined. The ectosymbionts (macroinvertebrates only) were identified up to the species or to morphological types. Ectosymbiont distribution and abundance were analyzed taking in account the host species, the position of spines on the sea urchin test, as well as the location along a given spine.

In study #2, the analysis of spine morphology and of its effect on the ectosymbiotic coating was performed on the 13 studied cidaroid species (Table 12). The relationship between the features of the spines and its ectosymbiotic coating was studied. The spines categories and zones were as in study #1. The ectosymbionts coating was estimated globally -without detailing the taxa- in terms of proportion (%)

of the spine surface coated) and classified into 4 classes (0-25%; 25-50%; 50-75%; 75-100%). Spines measurements were recorded directly on the digital pictures using OPTIMAS® (Version 6.51)

Table 12: Origin of the studied species.

Species	N specimens	Region	Depth (m)	Expedition
<i>Aporocidaris milleri</i>	10	Weddell Sea	405	ANT XXI/2
<i>Austrocidaris canaliculata</i>	10	Murray Narros	-	N°42 - 1895
<i>Ctenocidaris geliberti</i>	10	King George Island	120	Pnekoji II
<i>Ctenocidaris gigantea</i>	10	Kapp Norvegia	626	ANT XV/3
<i>Ctenocidaris nutrix</i>	10	Kapp Norvegia	150	ANT IX/3
<i>Ctenocidaris perrieri</i>	10	Kapp Norvegia	243	ANT XV/3
<i>Ctenocidaris rugosa</i>	10	South Shetland Islands	105	ANT XIII/4
<i>Ctenocidaris speciosa</i>	10	Weddell Sea	1681	ANT XV/3
<i>Ctenocidaris spinosa</i>	20	Kapp Norvegia	280	ANT XV/3
<i>Notocidaris hastata</i>	10	King George Island	417	ANT XV/3
<i>Notocidaris lanceolata</i>	10	Kapp Norvegia	506	ANT VI/3
<i>Notocidaris mortensenii</i>	20	Kapp Norvegia	437	ANT X/3
<i>Rhynchocidaris triplopora</i>	20	Kapp Norvegia	460	ANT XV/3

Two sets of parameters extracted from digital pictures were considered in 13 species: dimension parameters (maximal length, diameter, spinosity and area) (Fig. 16) and proportion-based parameters (“rectangularity”, circularity, and several ratios).

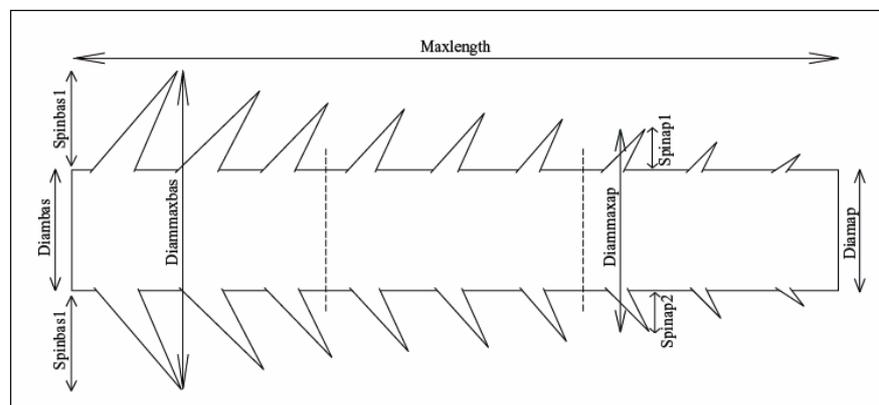


Fig. 16. Spines measurements: maximum length (maxlength), basal diameter (diambas), apical diameter (diamap), basal spinosity (spinbas), apical spinosity (spinap), area.

The morphological diversity (i.e. disparity) of spines has been investigated according to several complementary approaches. In a first step, empirical morphological spaces (Mc Ghee, 1999) have been built using a neutral exploratory technique: the Principal Components Analysis (PCA). In a second step, hierarchical ascendant classifications have been used to cluster the spines morphologies regardless of their taxonomic origin. This technique has been driven on the proportion-based parameters, and on the ambital plus oral spines that were supposed to be the most discriminant. In a third step, discriminant analyses allowed to test statistically the congruence between spines morphologies and taxonomy. Finally, disparity indexes based on variance have been calculated using the code MDA (developed under *MATLAB* by Navarro, 2003) and bootstrap procedures in order to appraise quantitatively the variety of supports offered by each species or each morphological cluster.

In study #3, the impact of ectosymbioses on local biodiversity was examined by comparing the epifauna found on the bottom (tillites pebbles) and on cidaroids collected in the Weddell Sea by the R/V "Polarstern" during the ANT XXII/3 campaign (2005). Two stations were investigated: Sta. 142-6 (62°9,93'S 40°30,47W) at 3403 m and Sta. 151-1 (61°45,46'S 47°7,57°W) at 1187 m. In both stations 300 tillites were collected; 32 individuals of *Aporocidaris milleri* were collected in Sta. 142-6 and 23 individuals of *Ctenocidaris speciosa* in Sta. 151-1. The distribution and abundance of ectosymbionts was estimated as in study #1; the sessile fauna attached to the tillite samples was identified taking in account their location (exposed versus buried part of the pebbles). Specific diversity, specific richness and similarities indexes were calculated as described in Chao and Chen (2003) and Chao *et al.* (2005). Such indexes correspond to extensions of classical parameters as they also consider the probability to have an under-sampling of rare species. In addition, they allow the computation of error bars. They have been processed using the software *SPADE*.

3.3. RESULTS AND DISCUSSION: ECOFUNCTIONAL ROLE OF BIODIVERSITY

3.3.1. MEIOBENTHOS

3.3.1.1. Nematode size and biomass

Along a bathymetric transect towards the South Sandwich Trench

Nematode length over 940 single measurements varied from 124 to 2991 μm (average 631, geometric mean 537 μm) within all measurements. Body width versus length (Fig. 17) showed two demarcated oval clusters representing two distinct morphological groups: comparably plump nematodes (L: 124-400 μm , W: 17-53 μm ; *Tricoma*) and mostly slender nematodes (L: >200 μm , W: mostly about 20-25 μm ; *Monhystera*, *Acantholaimus*, *Daptonema*, *Dichromadora*, *Molgolaimus*, *Paracanthochus*, *Microilaimus*). At the right side of this cluster a third less clear group was set off, combining very slender nematodes (*Halalaimus*; L: 500-2000 μm ; W: 10-20 μm) and the few very big nematode specimens from subdominant genera *Mesacanthion*, *Diplopeltula*, *Sabatieria*, *Viscosia* and some species of *Paracanthochus* (L: 1600-3000 μm ; W: 60-90 μm). The clusters were visible as two modes (e.g. at ratio 9 and 26, respectively) and a long tail in the L:W ratio frequency distribution towards the very slender nematode genera with L:W varying between 50 and 100 (Fig. 17). The frequency distributions of nematode L:W did not express a clear relationship with water depth (figures not depicted). Only Sta. 139 was clearly different in that it harboured much higher abundances (up to 20%) of plump nematodes

(with L:W ratios of 11). The nematodes from Sta. 142 (6300 m) had a higher average length (both harmonic and geometric) than those from Sta. 140 (3000 m) and Sta. 139 (4000 m). L:W morphometrics were negatively correlated with sand and positively with silt (Spearman Rank, $p=0.02$). There was no relation with food.

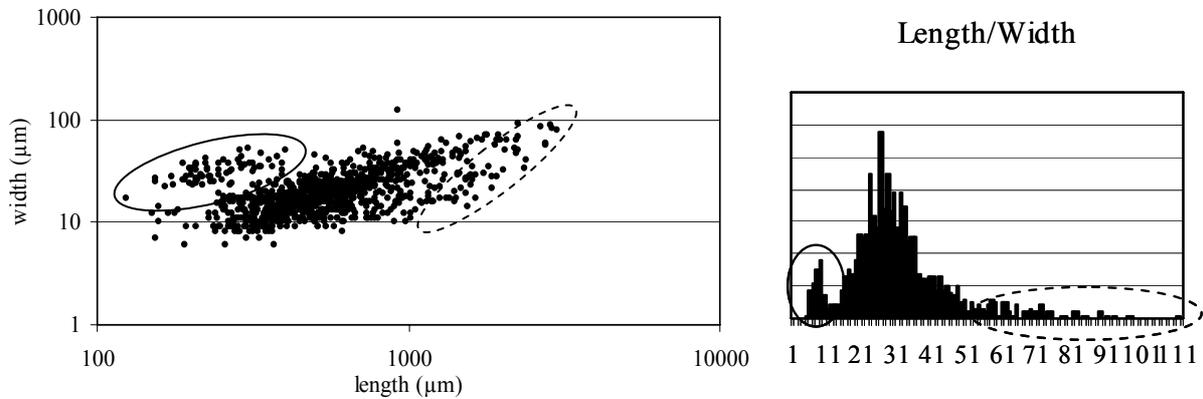


Fig 17. Nematode length/width scatterplots and frequency distributions in the Weddell Sea based on individual measurements.

Average nematode biomass displayed values between 0.076 and 0.140 µg dwt (harmonic mean) and 0.023-0.042 µg dwt (geometric mean), with a decreasing trend with depth for harmonic, but not for geometric mean (Fig. 18).

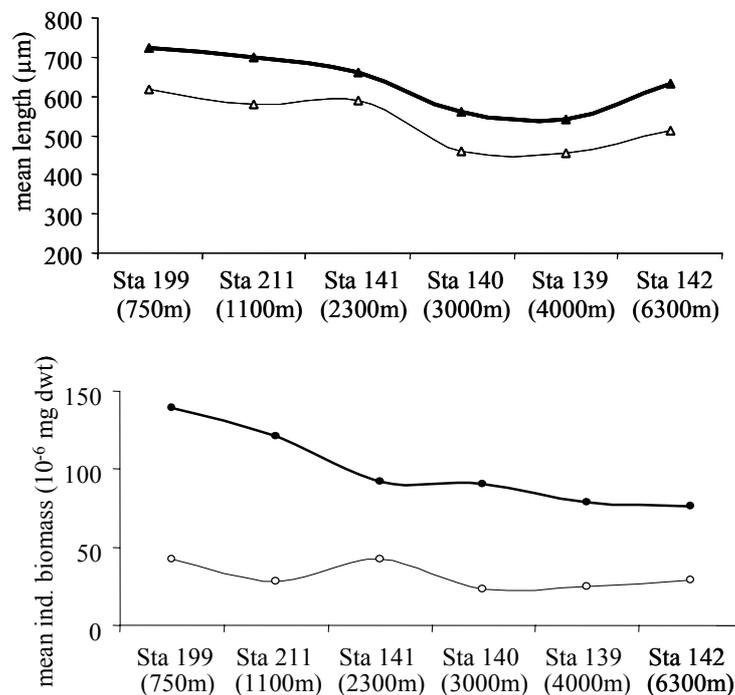


Fig 18. Bathymetric gradient in mean Nematode length and individual biomass in the South Sandwich Trench.

The nematodes from Sta. 141 and Sta. 142, particularly, deviated from a linear decrease. Nematode biomass spectra (Fig. 19) illustrated big differences between the stations, thus showing a highly different morphological nematode structure with depth.

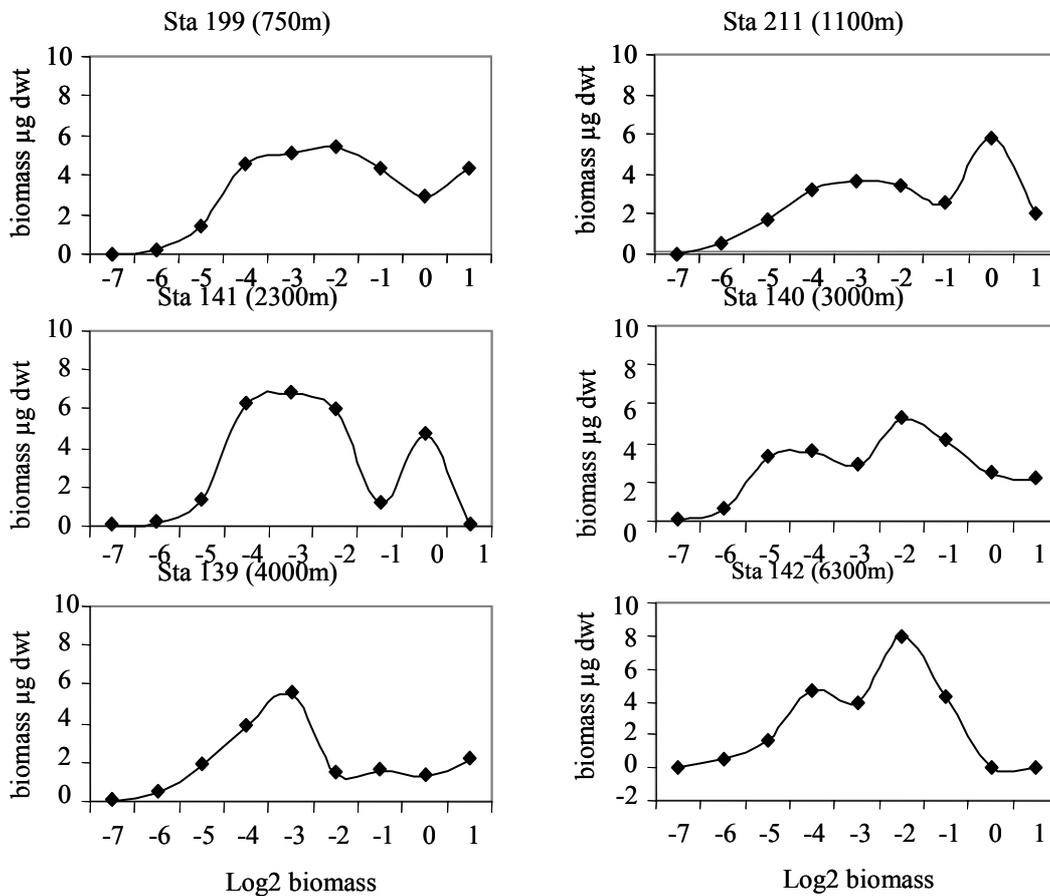


Fig 19. Biomass frequency distributions for distinct water depths in the South Sandwich Trench.

Differences were more pronounced in the higher biomass values of the spectrum. At stations 199, 211 and 141, a peak appeared in the higher size class 0 or 1, meaning that the few big nematodes at these sites (e.g. *Paracanthonus*) had a high impact on total biomass. Below 4000 m big nematodes disappeared and were substituted by nematodes in the size class -4 to -2 (*Tricoma*, *Acantholaimus*, *Dichromadora*, *Halalaimus*, *Daptonema*, *Microlaimus*, *Molgolaimus*). At 6300 m bigger nematodes were completely absent. Meiofaunal total biomasses were obtained from the product of nematode density and mean individual biomass, and ranged between 16 and 80 $\mu\text{gC}\cdot 10\text{cm}^{-2}$ (for harmonic mean), and between 5 and 19 $\mu\text{gC}\cdot 10\text{cm}^{-2}$ (for geometric mean). Juveniles dominated at all stations, ranging between 38% (Sta.142, 6300 m) and 55% (Sta. 140, 3000 m). Females were approximate as abundant (between 27% and 40%); males much less abundant (between 13 and 25%). The male to female ratio ranged between 1.1 and 3.0, the juvenile to adult ratio between 0.6 and 1.2. There was no relation of sex ratio to depth, sediment texture and food content.

Discussion. Over evolutionary timescales, selection in deep-sea sediments has led to 2 nematode morphologies within the smaller size range (<500 µm length). Short and corpulent “plump” nematodes (with small L:W ratios) are less susceptible to predation, but have a reduced mobility. Such nematodes are generally restricted to the most oligotrophic deep sea or to coarse sediments (Soetaert *et al.*, 2002). In our study plump nematodes occur predominantly (20%) at station 139 (4000 m). This site is characterized by sediments intensely bioturbated with many stones and coarse basalt grit. As in all stations the sediments are oligotrophic. These plump nematodes (L:W = 9) belong to the taxonomic similar selective deposit-feeding genera of the order Desmoscolecida (*Tricoma*, *Desmoscolex* and *Pareudesmoscolex*). Predation is avoided by the presence of protective desmen and cuticular protrusions. Selective deposit-feeding is needed for distinguishing between particles in different stages of decomposition (Vanhove *et al.*, 1999). “Slender” nematodes (L:W = 26; biomass size class -4 to -2) such as *Monhystera*, *Acantholaimus*, *Daptonema*, *Dichromadora*, *Molgolaimus*, *Microlaimus* and some species from *Paracanthochus*, mixed among mainly selective and epistratum feeding modes, show no preference for certain sites thus forming the bulk of the Trench community. As discussed by Soetaert *et al.* (2002) these long and slender nematodes are able to move swiftly through the fine sediment common for ocean margins. Apart from the stony station 139 (4000m), they occur in abundances between 43% (3000m) and 50% (1100m). The presence of sand burrows in some stations along the bathymetric profile seems not to have affected the presence of this morph type. A third less clear group of nematodes combines “very slender” taxa (*Halalaimus*; L: 500-2000µm; W: 10-20 µm; L:W = 60) and a few “very big” nematode specimens from subdominant genera *Mesacanthion*, *Diplopeltula*, *Sabatieria*, *Viscosia* and *Paracanthochus* (L: 1600-3000 µm; W: 60-90 µm; in the higher size class 0 or 1).

Average nematode biomass along the South Sandwich Trench displays values between 0.076 and 0.1396 µg dwt, with a decreasing trend with depth. However, this is not substantiated with geometric mean (where the effect of bigger nematodes is reduced due to logarithmation), neither by nematode size spectra, length measures or L:W ratios. It implies that there is not a general miniaturization tendency with depth, as introduced by Thiel (1975). Confirmed by later studies (Shirayama, 1983; Pfannkuche, 1985; Jensen, 1988; Shirayama & Horikoshi, 1989; Soetaert & Heip 1989; DeBovée *et al.*, 1990; Vanreusel *et al.*, 1995; Soltwedel *et al.*, 1996; Schewe & Soltwedel, 1999; Soetaert *et al.*, 2002; Gambi *et al.*, 2003), there is rather a decreasing abundance of bigger nematodes at greater depth. This, in turn, suggests a lower abundance of, for example, predating taxa (from the Enoplid, Leptosomatid, Oncholaimid, Halichoanlaimid families). The age-structure does not affect this trend as the percentage of juveniles is not a function of water depth.

Weddell Abyssal Plain

The total and individual biomass of the nematodes in the Weddell Abyssal Plain were compared with those of two North Atlantic sites (Vanreusel *et al.*, 1995)

The Porcupine Abyssal Plain (PAP at 47°N) is characterised by a high, seasonal input of organic matter derived from the overlying water column, while the other site (EUMELI at 21°N) receives low organic input. We noticed that nematodes with a similar length were considerably wider in the Southern Ocean than in both other sites. Also a higher proportion of long animals were found in the Weddell Sea.

Total biomass was highest in Sta. 138, while individual biomass was similar to the other Antarctic stations, or even a little lower (Table 13). Total biomass was about 3 to 6 times higher in all Antarctic sites compared to the PAP site, and 19 to 40 times higher than in the EUMELI site. The arithmetic mean is about 1.5 times higher for Antarctic nematodes than for the nematodes in the North Atlantic.

Table 13. Densities and biomass at different abyssal sites in the Atlantic Ocean and the Weddell Sea.

	Station n°	Total densities /10 cm ³	Total biomass (µg wwt/10cm ²)	Arithmetic mean ind. Biomass (µg dwt)
Southern Ocean	64°S	200	38.4	0.0480
	63°S	210	65.436	0.0779
	62°S	511	139.19	0.0681
North Atlantic	47°N	254	54.16	0.0511
	21°N	89	8.52	0.0241

Total biomass was similar to 2.8 times higher in Antarctica compared to the Porcupine Abyssal Plain and up to 16 times higher than in the Cape Verde Abyssal Plain. Differences between the Southern Ocean and the Atlantic Ocean are due to a combination of higher densities and higher individual biomass of the nematodes.

Discussion. Both total and individual biomass are considerably higher in the Southern Ocean than in the North Atlantic. This indicates higher food availability in Antarctica (Thiel, 1975; Pfannkuche, 1985; Jensen, 1988). Although the organic content of the sediment at the time of sampling, i.e. beginning of March, was rather low, we can assume that the food input during the past few months had been high. After the retreat of the ice edge at the beginning of the summer, a phytoplankton bloom occurred and a lot of this organic matter settled on the sea bed and became available for the benthos. It is likely that a different picture would arise immediately after winter, when food availability has been restricted for several months.

The higher total biomass in the Southern Ocean compared to the North Atlantic is due to a combination of high densities and high individual biomass. Also within the Southern Ocean, we observe a huge difference in total biomass between Sta. 138 at 62°S which is situated close to the upwelling zone of the South Sandwich Trench, and both other stations. This is solely due to the high densities (Vanhove *et al.*, 2004), since individual biomass is similar, or even somewhat lower, than in the other sites.

3.3.1.2. Nematode trophodiversity

Nematodes along the South Sandwich Trench were mainly selective deposit-feeders (1A: 36%), epistratum grazers (2A: 33%) and non-selective deposit feeders (1B: 27%). Predators/omnivores were well below 10%. There was no significant change in this composition with depth. Predators/omnivores were, however, extremely lowly represented at 2300 and 6300 m (Fig. 20).

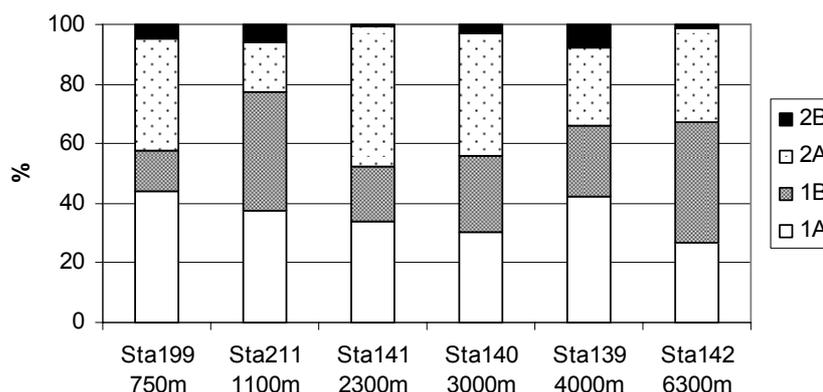


Fig 20. Nematode trophic composition along the South Sandwich Trench

The 1A group was negatively correlated with the mean particle size and sand fraction of the sediment in the burrows (Spearman Rank, $p = .0004$) and outside burrows (Spearman Rank, $p = .0006$). Inversely, 1B was positively correlated with these parameters (Spearman Rank, $p = .005$) and negatively with clay and silt (Spearman Rank, $p = .0005$). So were the 2A. No relation was found with food in the sediment.

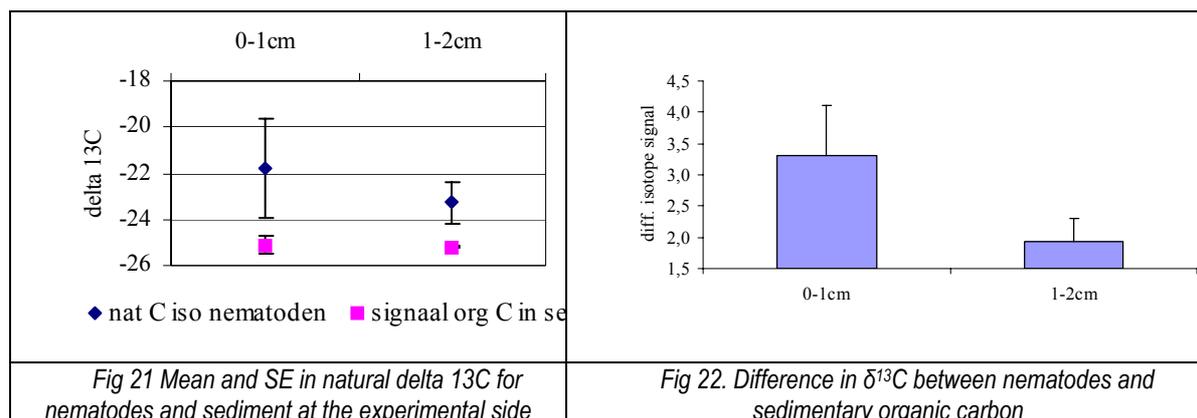
Discussion. The selective deposit-feeders with minute buccal cavity, presumably feeding on bacteria, are observed in highest proportions in the two shallowest stations with moderately sorted silts with thin fluff layer on top. Non-selective deposit (with big mouth cavity) and predatory/scavenging (with big teeth) feeding modes appear more at the shallow (750 and 1100 m) and burrow rich (2300 m) sites. Both feeding types are, generally, related to high energy labile organic matter levels: non-selectivity prevails over selectivity in circumstances of excess labile detritus (Vanhove *et al.*, 1999) and higher trophic complexity (with relatively more abundant higher trophic levels) is to be expected where food is trapped (Soetaert & Heip, 1995).

3.3.1.3. Trophic position of meiobenthos

Natural stable isotopes

The $\delta^{13}\text{C}$ signatures of the sedimentary organic carbon ($-25,2 \pm 0,14 \text{ ‰}$) remain constant over the vertical sediment profile (Fig. 21). The $\delta^{13}\text{C}$ nematode signatures are less depleted in comparison to the sedimentary organic carbon (Antarctic: $-22,5 \pm 1,68 \text{ ‰}$). Other meiofaunal taxa could not be analysed by means of stable isotopes because the densities at that water depth were too low to retrieve enough biomass for a reliable $\delta^{13}\text{C}$ signal.

Within the sediment, the averaged $\delta^{13}\text{C}$ signatures along the vertical profile exhibited considerable variation, and became lighter with increasing sediment depth. Unfortunately, the significance of this downward trend is masked by one outlier ($-23,34 \text{ ‰}$).



In all the replicates a clear isotopic shift (average $\Delta\delta^{13}\text{C} = +2,7 \text{ ‰}$) was found between the natural carbon isotopic signatures of the nematode communities and the natural ^{13}C signals of the bulk sedimentary organic matter (Fig. 22). Remarkable is the difference in $\Delta\delta^{13}\text{C}$ between the nematodes of the upper sediment layer (+3,3 ‰) in comparison with the nematodes of the deeper sediment layer (+1,9 ‰) for the Antarctic station.

Enrichment experiment

Assimilation of ^{13}C enriched bacteria by the nematodes was clearly visible in the upper centimetre layer of the sediment and the assimilation in nematode biomass was slightly variable among the replicates. The maximum ingestion of enriched material (highest observed $\delta^{13}\text{C}$) was measured after 7 days, after which the isotopic signals of the nematodes returned to more negative levels, comparable to the background signals (Fig. 23).

In the deeper sediment layer (1-2cm) of the bacteria treatment however, no enrichment of nematodes was observed in both experiments. It is possible that the duration of the experiments was too short for the ^{13}C enriched organic matter to reach deeper sediment layers. For the nematodes incubated with enriched diatoms, no enrichment whatsoever was observed. The nematode isotopic $\delta^{13}\text{C}$ signals were comparable with the corresponding natural isotopic signals earlier mentioned.

Discussion. The natural ^{13}C signals in the bulk sediment were much more depleted in the Southern Ocean than in other world oceans. A similar value was observed in the 2 sediment layers (about -25 ‰). The nematodes on the other hand did show a vertical profile. In the upper cm, larger $\Delta\delta^{13}\text{C}$ values (i.e. $\delta^{13}\text{C}_{\text{nematodes}} - \delta^{13}\text{C}_{\text{sediment}}$) in the upper cm (3.3‰ on average) than in the cm below (1.9‰ on average). This could be due to different dietary preferences in both sediment layers. The results suggest that nematodes from the deeper sediment layer feed more on bulk organic matter available in the sediment, while in the upper layer selectivity might occur.

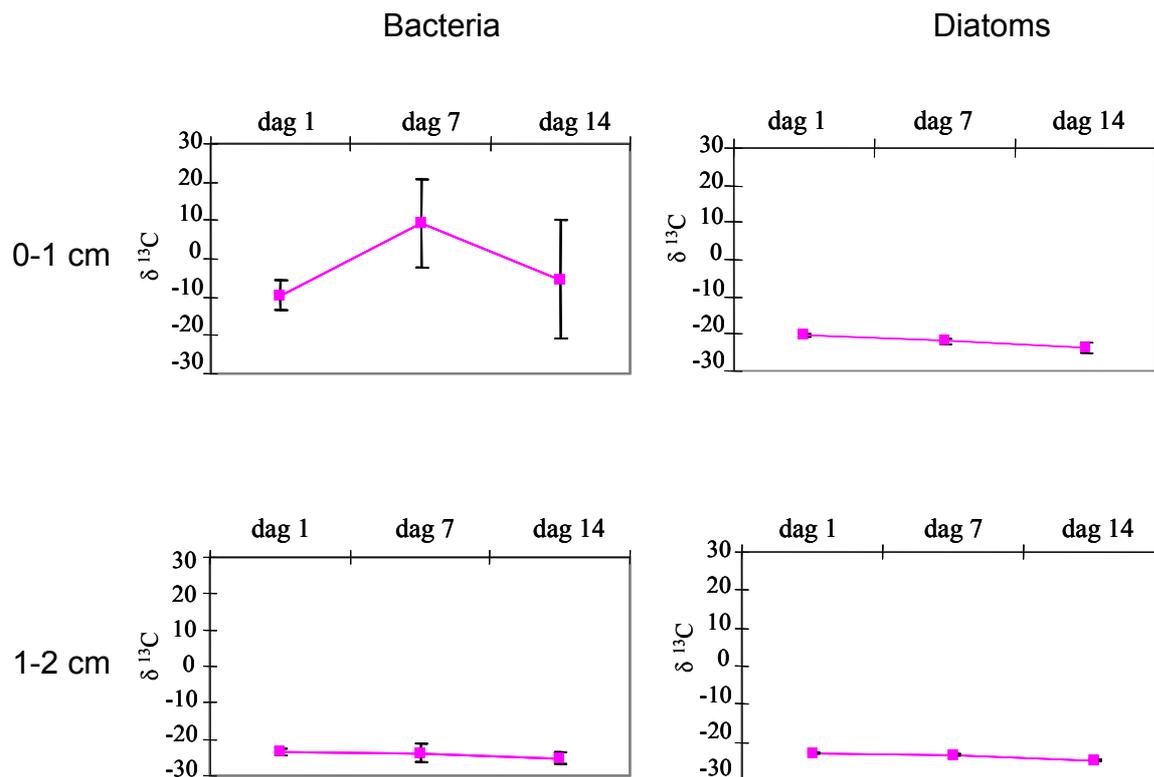


Fig. 23. Uptake in delta 13C through bacteria or diatoms by nematodes in experimental conditions at day 1, 7 and 14 (mean and SE).

The enrichment experiment showed that only bacteria were consumed by the nematodes. The maximum enrichment occurred after 7 days, but only in the upper cm. No response was measured for the ^{13}C -enriched diatoms over the whole sediment profile. Previous deep-sea studies have shown that the diatom species used in our experiment (*Thalassiosira rotula*) is well suited as food source for meiobenthos. It seems that nematodes in the Antarctic deep sea do not react directly on the input of microphytoplankton. Our data suggest that settled phytoplankton enters the food chain via a bacterial link. Bacteria might be a more reliable food source in the Antarctic deep-sea than diatoms which have a highly seasonal input.

3.3.2. TROPHIC SIGNIFICANCE OF AMPHIPODA IN ANTARCTIC BENTHIC COMMUNITIES

3.3.2.1. Trophodiversity

As they may explain part of the apparent discrepancies between seasonally limited food resources and the richness of benthic life, the feeding habits of benthic organisms have received considerable attention in the last decades (Arntz *et al.*, 1994). However, because of the large number of benthic and benthic-pelagic species and the wide and variable food spectra of many of these, there subsist many trophic interactions to clarify.

The trophic ecology of amphipod crustaceans has been approached in a multidisciplinary way, but the different methods lead to the same main conclusion: amphipod trophic ecology is diverse, rich and complex. Even in their feeding appendages morphology, and mandibles were investigated in particular because of their essential role in the nutrition, amphipods appear to have developed a multitude of morphological patterns. The mouthparts of ten species have been dissected and examined with scanning electron microscopy (SEM). From gut content composition, four main trophic categories were distinguished: (micro- and macro-) herbivores, opportunistic predator, specialist carnivore and opportunistic scavenger. However, the link between amphipod mandible morphology and feeding habits is often not sufficiently distinct to be considered as a reliable method of trophic classification. For example, according to their gut contents, *Epimeria similis* and *Iphimediella cyclogena* are both specialist consumers. The first is considered as a cnidarian-feeder and the second consumes mainly holothurians. However, if each species mandibles are compared with those of other Antarctic species which also feed exclusively on cnidarians or holothurians, as respectively, the iphimediid *Maxilliphimedia longipes* and the stilipedid *Bathypanoploea schellenbergi* (Coleman, 1989a, 1990b), totally different morphologies are observed. These different morphologies are summarized in Table 14.

Table 14. Summary of the mandible morphological differences between specialist consumers.

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

The evolution of the amphipod mandible morphology has not only been guided by its feeding functionality, but other factors did interfere also in the process. However, the global analysis of all mouthparts morphological features (maxillipeds, maxilla 1 and maxilla 2) would probably provide better insights to infer trophic type.

As demonstrated also by the other approaches (stable isotopic ratios and fatty acid composition analyses), few other benthic groups seem to cover a similarly wide trophic spectrum as amphipods do. Results indicate that benthic amphipods live at many trophic levels of the Weddell Sea food web. And, besides some highly specialized species as, for example, micro-grazers feeding on a single food item (*Echiniphimedia* species feed exclusively on sponges, as revealed by their guts full of hexactinellid spicules), there are numerous signs of opportunism in amphipod feeding behaviour.

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

3.3.2.2. The benthic food web in the Antarctic Peninsula and the role of amphipods

The presence of amphipods at all levels of the Weddell Sea benthic food web can be generalized to the other ecosystem considered in this project: the shelf of the Antarctic Peninsula. Based on stable isotope data of zoobenthos in the Antarctic Peninsula, an Antarctic food web including amphipods can be exemplified to figure out which position they occupy and how important they are among the zoobenthos. All analyzed organisms are listed in Table 15. Among amphipods, sixteen species have been considered. This collection gathers several feeding types, notably, suspension-feeder (*Ampelisca richardsoni*), deposit-feeders (*Byblis* sp., *Paraceradocus gibber*), micrograzers (*Echiniphimedia echinata*, *E. hodgsoni*, *Epimeria similis*), predator (*Iphimediella* sp.), scavengers (e.g. *Abyssorchomene plebs*, *Pseudorchomene coatsi*, *Waldeckia obesa*). Amphipods have been classified into hyperiids and gammarids because of their different habitats, hyperiid amphipods being exclusively planktonic.

Table 15. Carbon and nitrogen isotopic ratios (mean \pm SD, ‰) of all animals sampled on the shelf of the Antarctic Peninsula; TL corresponds to estimated trophic level.

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

PHYLUM	Class / Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL
	<i>Echiniphimedia hodgsoni</i>	-24.3 ± 1.3 (2)	10.6 ± 1.8 (2)	5.3
	<i>Iphimediella</i> sp.	-21.7 ± 1.0 (6)	11.8 ± 1.0 (6)	5.8
	<i>Pseudorchomene coatsi</i>	-22.7 ± 0.3 (3)	9.3 ± 0.3 (3)	4.7
	<i>Waldeckia obesa</i>	-22.8 ± 0.9 (4)	7.3 ± 0.7 (4)	3.9
	<i>Eurythenes gryllus</i>	-27.3 ± 1.1 (9)	8.5 ± 0.5 (9)	4.4
	<i>Abyssorchomene plebs</i>	-26.5 ± 0.4 (6)	9.5 ± 0.8 (6)	4.8
	<i>Epimeria georgiana</i>	-22.9 ± 1.9 (9)	7.9 ± 0.4 (9)	4.1
	<i>Epimeria similis</i>	-25 ± 1.4 (15)	7.6 ± 0.5 (15)	4.0
	<i>Leucothoe spinicarpa</i>	-22.7 ± 0.6 (6)	8.3 ± 0.8 (6)	4.3
	<i>Paraceradocus gibber</i>	-23.5 ± 0.7 (12)	5.0 ± 0.5 (12)	2.9
	Euphausiacea			
	<i>Euphausia superba</i>	-28.6 ± 1.1 (6)	2.8 ± 0.4 (6)	2.0
	Decapoda			
	<i>Notocrangon antarcticus</i>	-23.6 ± 0.3 (4)	9.3 ± 0.2 (4)	4.7
	<i>Chorismus antarcticus</i>	-24.0 ± 1.8 (2)	7.4 ± 1.3 (2)	3.9
BRYOZOA	<i>Reteporella</i> sp.	-26.9 ± 0.0 (1)	6.5 ± 0.0 (1)	3.5
ECHINODERMATA	Crinoidea	-26.1 ± 0.0 (1)	7.9 ± 0.0 (1)	4.1
	Holothuroidea			
	<i>Psolus</i> sp.	-26.6 ± 1.4 (3)	8.0 ± 0.8 (3)	4.2
	<i>Bathyploetes fusviculum</i>	-24.8 ± 0.3 (2)	8.8 ± 0.7 (2)	4.5
	<i>Echinocucumis</i> sp.	-29 ± 0.3 (2)	7.5 ± 0.2 (2)	4.0
	Ophiuroidea			
	<i>Astrotoma agassizii</i>	-23.9 ± 2.1 (3)	7.5 ± 0.9 (3)	4.0
	<i>Ophiosparte gigas</i>	-27.3 ± 1.6 (3)	5.5 ± 0.4 (3)	3.1
	<i>Ophionotus</i> sp.	-24.5 ± 1.5 (2)	6.7 ± 0.2 (2)	3.6
	Asteroidea	-24.0 ± 1.6 (4)	11.2 ± 1.3 (5)	5.5
CHORDATA	Osteichthyes			
	Channichthyidae			
	<i>Champsycephalus gunnari</i>	-25.1 ± 0.3 (5)	8.5 ± 0.3 (5)	4.4
	Nototheniidae			
	<i>Gobionotothen gibberifrons</i>	-24.3 ± 0.1 (5)	9.8 ± 0.4 (5)	4.9
	<i>Notothenia coriiceps</i>	-23.6 ± 0.8 (6)	9.9 ± 0.6 (6)	5.0
	<i>Notothenia rossii</i>	-24.4 ± 0.5 (6)	9.2 ± 0.3 (6)	4.7
	<i>Trematomus bernacchii</i>	-19.7 ± 2.0 (2)	12.6 ± 0.2 (2)	6.1
	<i>Trematomus pennellii</i>	-20.2 ± 0.6 (3)	11.0 ± 0.8 (3)	5.4
	<i>Trematomus nicolaii</i>	-20.5 ± 0.0 (1)	11.0 ± 0.0 (1)	5.4
	<i>Trematomus hansonii</i>	-21.9 ± 0.0 (1)	10.2 ± 0.0 (1)	5.1
	<i>Trematomus eulepidotus</i>	-24.5 ± 0.4 (5)	9.0 ± 0.6 (5)	4.6

The most striking features of the Antarctic Peninsula benthic ecosystem are, on the one hand, a general impoverishment in ^{13}C compared to other systems (e.g. tropical), probably originating from a depleted food source but transferred throughout the food web. This pronounced depletion in ^{13}C at the base of Antarctic food web has been observed before. The SPOM isotopic ratios are considerably lower than values previously recorded for other regions but within the range of Antarctic as well as Arctic values (Wada *et al.*, 1987; Hobson *et al.*, 1995; Dunton, 2001; Corbisier *et al.*, 2004). Polar SPOM is in general depleted in ^{13}C as compared with predominantly temperate SPOM ($-22 \pm 3\%$) (reviews in Rau *et al.*, 1982; Fischer, 1991; France, 1995). Low temperature (below 2°C), low light intensity and high water $[\text{CO}_2(\text{aq})]$ values lead to very low ^{13}C content in the phytoplankton (Rau *et al.*, 1989, 1991a). Thompson & Calvert (1994) also suggest a substantial role of irradiance in the process of ^{13}C incorporation in marine diatoms.

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

3.3.2.3. Benthic-pelagic coupling

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

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

Isotopic investigations support the hypothesis that a major part of the benthic community is supported primarily by phytoplanktonic POM reaching the benthos. Carbon evidence for this is the similarity in $\delta^{13}\text{C}$ values between pelagic POM-based feeders (*e.g.* *Euphausia superba*, *Themisto* sp.) and benthic filter feeders (*e.g.* *Echinocucumis* sp., *Ampelisca richardsoni*); (Table 15, Fig. 24). Similar results have been found in isotopic investigations of Arctic marine food webs (Dunton *et al.*, 1989; Hobson *et al.*, 1995). Benthic organisms in systems exhibiting weaker benthic-pelagic coupling would be expected to be substantially enriched in ^{13}C relative to both POM and POM grazers.

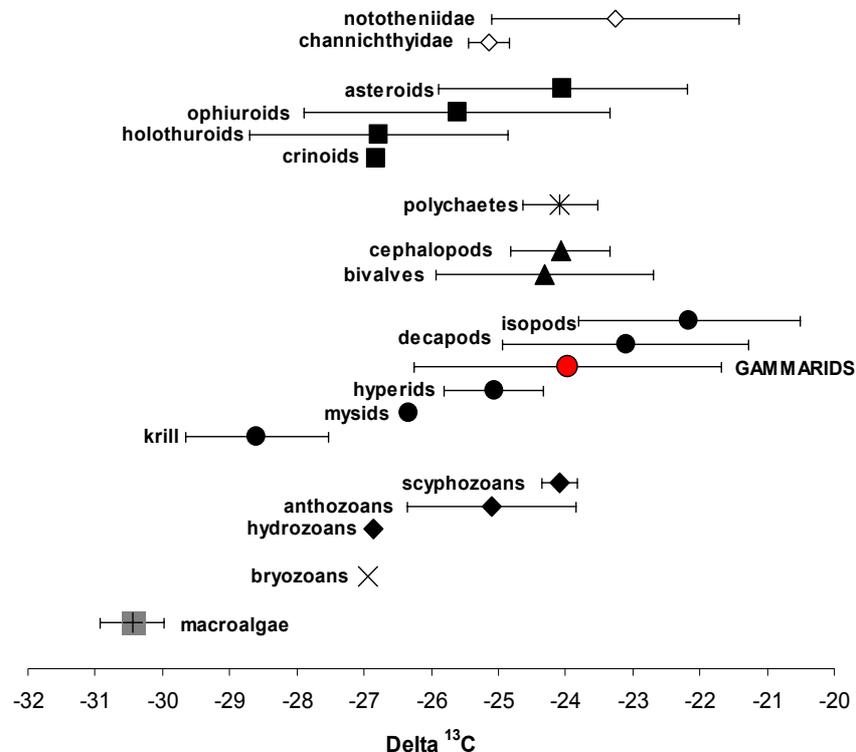


Fig. 24. Distribution of stable-carbon isotope ratios (mean \pm SD) among benthic food web components in Antarctic Peninsula.

In this case, the possible sources of significant primary production were POM, macroalgae and ice algae. The coastal waters along the west side of the Antarctic Peninsula and nearby islands are characterized by a rich and dense macroalgal flora composed of annual and perennial species (Zielinski, 1990; Chung *et al.*, 1994; Klöser *et al.*, 1994; Amsler *et al.*, 1998). Large amounts of algae are degraded, so they become a suitable food resource for benthic organisms (Richardson, 1979; Brouwer, 1996; Iken *et al.*, 1997, 1998). Detached algae can be decomposed by biological and hydrodynamical processes (Reichardt & Dieckmann, 1985; Rakusa-Suszczewski, 1993) and some may drift into deeper waters to provide food for benthic deposit and suspension feeders (Fischer & Wiencke, 1992). The recorded macroalgae $\delta^{13}\text{C}$ values range from -31 to -30‰. Owing to the strong similarity with POM isotopic ratios (Nyssen *et al.*, 2002), it was impossible to distinguish between these two primary producers on a carbon isotopic base. On the contrary, the difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between SPOM and ice algae, generally more enriched (e.g. $\delta^{13}\text{C} = -18.5\text{‰}$, $\delta^{15}\text{N} = 8.3\text{‰}$; Hobson *et al.*, 1995; Fischer *et al.*, 1991; Rau *et al.*, 1991; Kennedy *et al.*, 2002) permit further insight into the relative input of these sources to the food web. While the enrichment in ^{13}C from POM to some POM grazers may point towards some contribution of ice algae, $\delta^{15}\text{N}$ values clearly indicate direct feeding on POM and not on the isotopically heavier ice algae. Low $\delta^{13}\text{C}$ values were generally maintained through the food web, including fishes and benthic invertebrates, again confirming the importance of POM as a major food source for the entire food web. It has to be mentioned that those conclusions are based on isotopic ratios only and then, the contribution of macroalgae as a primary carbon source in the food web cannot be totally excluded.

From the nitrogen stable isotopic ratios of euphausiids (2.8‰) and the mean value of 0.4‰ used by Dunton (2001) for Antarctic phytoplankton, a "per-trophic-level" ^{15}N enrichment factor of about 2.4‰ was applied to obtain trophic level estimates according to the relationship: $TL = (D - 0.4)/2.4 + 1$, where D is the $\delta^{15}\text{N}$ value of the organism, 0.4 refers to the mean value of SPOM, and TL is the organism's trophic level. Assuming that POM is the first trophic level, the range of $\delta^{15}\text{N}$ values in Antarctic Peninsula fauna reflects a food web characterized by 6 trophic levels, the highest level being occupied only by the demersal emerald rockcod *Trematomus bernachii*. Other fish range over two trophic levels from planktivorous species such as *Champsocephalus gunnari* and *Trematomus eulepidotus* (TL 4.4 to 4.6) through *Trematomus pennellii* and *T. nicolai* (TL 5.4), which are predatory on larger benthic invertebrates and fishes (Gon & Heemstra, 1990; Barrera-Oro, 2002). They share these levels of the food web (4th and 5th levels) with asteroids, cephalopods, polychaetes and some amphipod and decapod crustaceans (see Fig. 25). The sixteen species of amphipods considered in this study range over 3 trophic levels from herbivorous species (*A. richardsoni*, *D. furcipes*, TL 2.5 and 2.9, respectively) to scavengers (*E. gryllus*, *A. plebs*, TL 4.4 to 4.8) and predator (*Iphimediella* sp, TL 5.8). One can be surprised by the trophic levels estimation which put species between two consecutive trophic levels. Those calculations have to be considered with caution. Indeed, as they are based on assumptions (SPOM isotopic ratio, exclusive trophic link between SPOM and krill ...), one can suppose that they are probably biased. Those trophic level estimations then provide only a rough idea of each group relative position in the food web.

Among amphipods in general, the trophic relationships predicted by $\delta^{15}\text{N}$ are in good agreement with information in the literature and with results obtained previously (see Nyssen *et al.*, 2002, 2005). For example, the well established trophic link between the species *Epimeria similis* and hydrozoans is confirmed by their carbon and nitrogen isotopic ratios (see Table 15). However, for species such as the iphimeriids *Echiniphimedia echinata* and *E. hodgsoni*, some clarifications are needed. Although gut contents indicate an exclusive reliance on sponges for both species, their carbon and nitrogen isotopic ratios differ respectively by 3‰ and 4‰, resulting in a difference of 2 trophic levels between them. This can be due to the consumption of different sponge species, as wide range of isotopic ratios have been recorded for these sessile organisms ($\delta^{13}\text{C}=-26.5$ to -23.2 ‰ and $\delta^{15}\text{N}=3.9$ to 9.9 ‰). These isotopic values are also coherent with the classification of another amphipod species, *Leucothoe spinicarpa* ($\delta^{13}\text{C}=-22.7\pm 0.6$ ‰ and $\delta^{15}\text{N}=8.3\pm 0.8$ ‰) as sponges consumer. These results confirmed known trophic relationships among Antarctic Peninsula organisms and revealed their position in the food web (Table 15). The analysis also demonstrated that many consumers occupy similar trophic levels, but derive their carbon from different sources. For example, as first level consumers, both amphipods species *A. richardsoni*, *P. gibber* have similar $\delta^{15}\text{N}$ values (4.1‰ – 5.0‰), but their $\delta^{13}\text{C}$ values differ by 6‰ suggesting different carbon sources. Revealed as deposit-feeder from gut content analyses, *P. gibber* derives probably its carbon from microbially reworked organic matter that forms a thin layer on the sediment, whereas *A. richardsoni* feeds exclusively on phytoplankton (Dauby *et al.*, 2001; Nyssen *et al.*, 2002; Nyssen *et al.*, 2005).

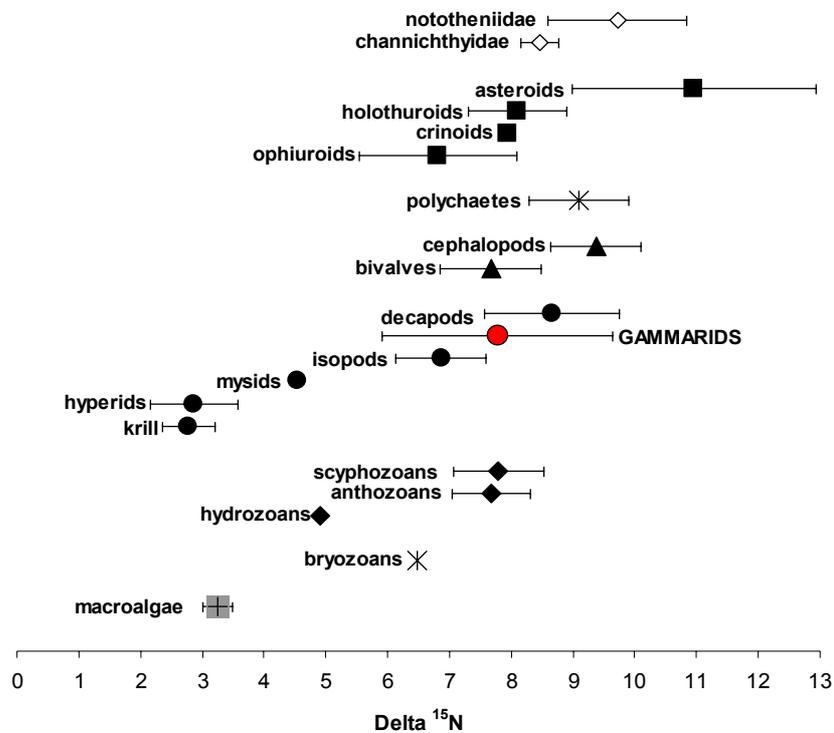


Fig. 25. Distribution of stable-nitrogen isotope ratios (mean \pm SD) among benthic food web components in Antarctic Peninsula.

3.3.2.4. An evaluation of the efficiency of stable isotopes and fatty acids as natural trophic biomarkers

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

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

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

Cluster analysis of the fatty acid composition separated the amphipod species into 5 trophic groups; suspension feeders (C5), macro-herbivores (C4), omnivores (C3), scavengers (C2) and exclusive scavengers (C5) (Fig. 26). The suspension feeder was isolated due to an important proportion of 18:4(n-3), fatty acid biomarker of phytoplankton. Macro-herbivores were found to rely heavily on macroalgal carbon, containing a high percentage of arachidonic acid 20:4(n-6). Scavenger amphipods revealed a unique fatty acid composition dominated by one single fatty acid, 18:1(n-9), probably the result of a very intensive de novo biosynthesis to cope with starvation periods.

The **combined use of stable isotopes and fatty acids as trophic biomarkers** has effectively facilitated the understanding of the trophic relationships between the different organisms in Antarctic ecosystems. Indeed, it seems impossible to separate different primary producers (phytoplankton and macroalgae) based on their carbon isotopic signatures, but based on their distinct fatty acid composition. Thus, the presence or absence in consumers of fatty acid biomarkers of phytoplankton or of macroalgae

has allowed assessing the contribution of each primary producer to higher trophic levels. For example, from their similar isotopic values, the amphipod species *A. richardsoni* and *D. furcipes* were both classified as primary consumers. Their respective fatty acid profiles reveal that, even if they were at the same trophic level, they did not rely on the same primary producers: the former being a suspension-feeder and the latter a macroalgae consumer. On the other hand, isotopic data did assist in the correct interpretation of fatty acid compositions, too. Indeed, significant proportions of mono-unsaturated fatty acids typical of dominant Antarctic copepods (Hagen *et al.*, 1993; Kattner *et al.*, 1994; Hagen *et al.*, 2000) in the amphipod *Iphimediella* sp. would have classified this species as a zooplankton feeder. However, its $\delta^{15}\text{N}$ value (highest value for amphipod ever recorded so far in the Antarctic, to our knowledge) as well as its known predatory behaviour strongly indicates that there exists an additional trophic level between copepods and *Iphimediella* sp.

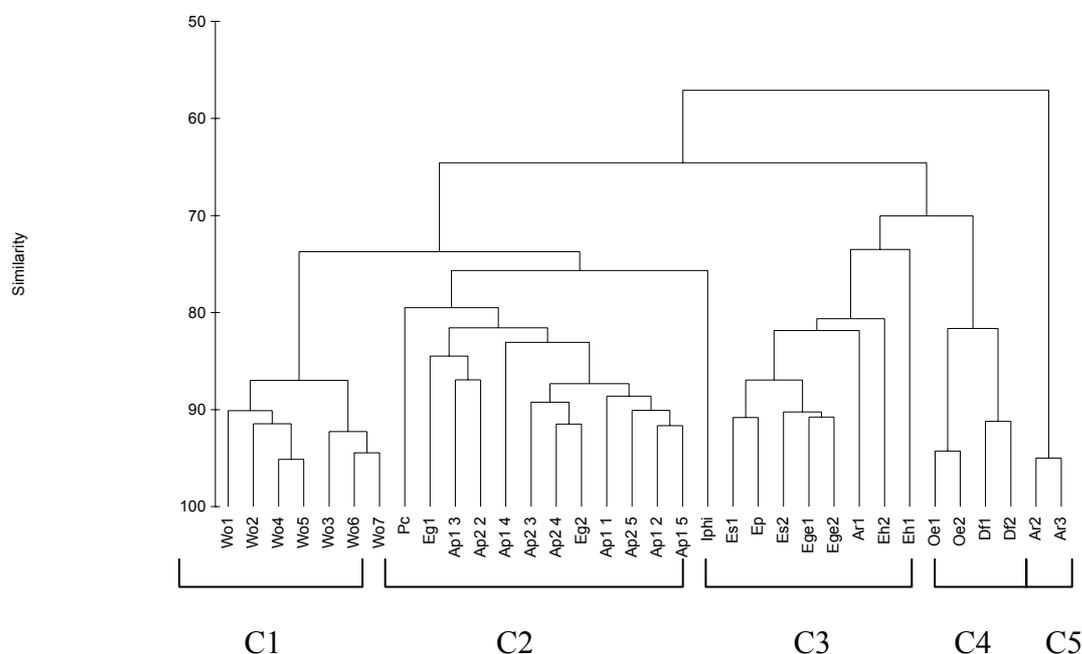


Fig 26. Hierarchical cluster analysis of fatty acid composition (%) of the total lipid extracted from 12 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorhomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorhomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Eh—*Echiniphimedia hodgsoni*, Ep—*Eusirus perdentatus*, Df—*Djerboa furcipes*, Oe—*Oradarea edentata* (data from Graeve *et al.* (2001), Ar—*Ampelisca richardsoni*, Iphi—*Iphimediella* sp.

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

The combination of both approaches creates a 2-dimensional biomarker assay with higher accuracy and better trophic resolution. In the same line, another interesting approach that could be used in the future to characterize carbon fluxes between prey and predators as well as to validate the applicability of both methods, involves feeding experiments with ^{13}C -enriched experimental diets. Such studies would

provide information on carbon accumulation, transfer and turnover rates as well as biosynthesis of lipids and individual FA (e.g. Albers, 1999).

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

3.3.2.5. Amphipods as food sources for higher trophic levels in the Southern Ocean

The significance of amphipods in Antarctic trophodynamics has also been approached in terms of potential food resources for higher trophic levels (Dauby *et al.*, 2003). This review was based on an exhaustive dataset collected from about 310 references concerning the Southern Ocean *sensu lato i.e.* including the sub-Antarctic islands (south of the Sub-Tropical Front) but excluding here the Magellanic Region. About 1500 "records" were registered in the whole dataset. A total of 176 amphipod species were listed in top predator stomach contents, *i.e.* more than 20% of the species known for this area. The best represented (super-)families are: lysianassoids, eusiroids and epimeriids for gammarideans, and hyperiids and vibilliids for hyperideans. Concurrently, 192 different predators were identified belonging to various zoological groups. The most numerous records concern fishes (101 species from 19 families, especially from the notothenioids) and seabirds (48 species from 12 families, mainly procellariids and spheniscids).

Amongst invertebrates, the more important amphipod predators are polychaetes and echinoderms (starfishes, sea-urchins and brittle stars) in the benthos, and several species of squids in the water column. Many species of the different notothenioid families feed on amphipods to a more or less broad range. All the Antarctic and sub-Antarctic seabird families have been reported to feed on (pelagic) amphipods. Among marine mammals, 10 species –4 baleen whales, 1 dolphin and 5 seals– have been found with amphipods in their stomach.

To synthesize the dataset, a tentative 'box-model' was built up which shows the relative importance of both pelagic and benthic amphipods in the diet of the Southern Ocean top predators. To construct this model, various published data were used: (i) the mean quantitative values of amphipod mass fractions in predators' diet, (ii) the standing stocks of the main groups of predators in the Southern Ocean, (iii) the feeding rates of these predators. The diagram (Fig. 27) shows the estimates of the different predation fluxes, expressed in millions of tons per year (Mt.yr⁻¹). It clearly appears that pelagic fishes (myctophids) are responsible for the biggest flux (50 Mt.yr⁻¹), which can easily be understood when considering the area and depth ratios of the oceanic vs neritic zones. The second group in importance is represented by benthic and benthopelagic fish (mainly nototheniids), whose predation on pelagic amphipods was not estimated but is likely at least one order of magnitude smaller than on benthic ones (8.6 Mt.yr⁻¹). The other predator groups (birds and mammals) consume a lower amount of amphipods (from 0.1 to 1.7 Mt.yr⁻¹) as their relative biomass is far weaker than that of fish. The total amphipod mass ingested per year is thus estimated at roughly 60 Mt. These values must however be cautiously regarded as they are tainted with biases and approximations for several reasons: (i) predator biomass data are usually widely scattered, available only either for areas of intensive scientific research or for species of commercial significance; (ii) just a few (characteristic) fish families were taken into

account, while other ones (such as *e.g.* zoarcids or muraenolepids) are also well represented in the Southern Ocean but less studied; (iii) seasonal variations in either predator standing stocks or feeding rates are likely to occur, the importance of which can hardly be weighed; (iv) the proportion of amphipods in predators' diet may considerably vary with respect to several parameters like *e.g.* age, sex or geographical location; (v) some maybe significant groups (*i.e.* benthic and pelagic invertebrates) were totally omitted; (vi) the circumscription of what is the 'Southern Ocean' (south of the Antarctic Polar Front, south of the Sub-Tropical Front, including or not the Sub-Antarctic islands) is not always clearly defined in the literature. This notwithstanding, values presented in Figure 27 can be considered to represent a rather realistic working hypothesis about the importance of amphipods for Southern Ocean top predators.

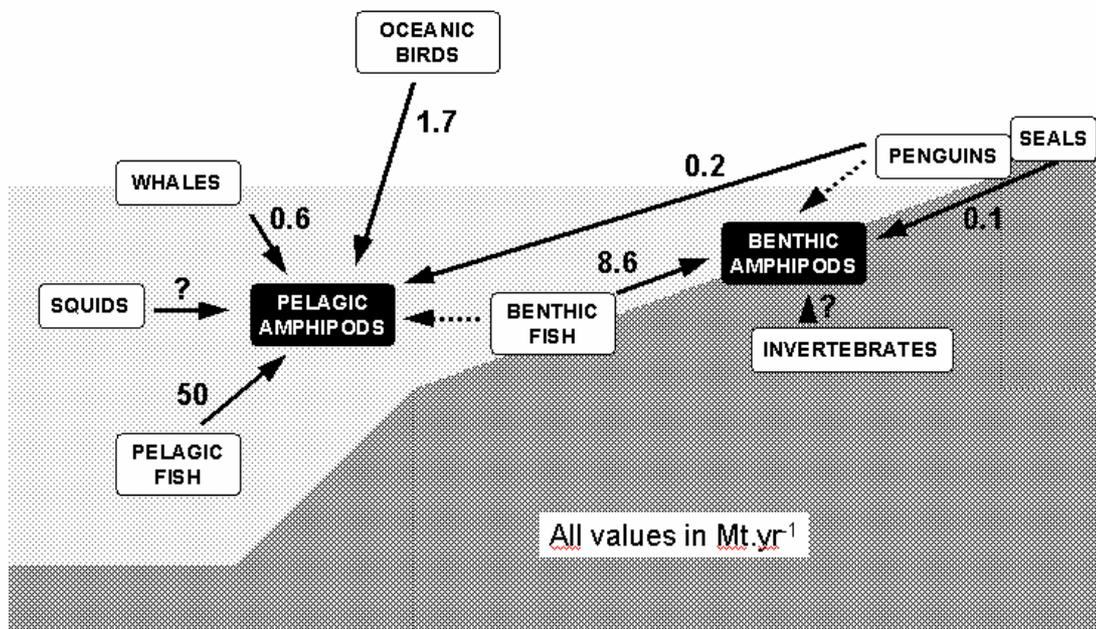


Fig. 27. Scheme of the different predation fluxes on benthic and pelagic amphipod crustaceans (in MT.yr^{-1}) by the main Southern Ocean predator groups.

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

3.3.3. ECHINOIDEA TROPHODIVERSITY AND SYMBIOSES

Two topics have been investigated in the project: the trophodiversity of echinoids and the ecological significance of ectosymbioses developed by the cidaroids, the most diverse and abundant group of Antarctic echinoids.

3.3.3.1. Echinoid trophodiversity

On the basis of the nature of the gut contents, 4 trophic categories were recognized among the Antarctic echinoids: (1) the deposit-feeders (sediment swallowing), (2) the carnivorous opportunistic browsers, (3) the vegetarian opportunistic browsers and (4) the strict vegetarian browsers (Table 16). The deposit-feeders (sediment swallowing) are the irregular echinoids; in the Antarctic they count 4 families (Plexechinidae, Pourtalesiidae, Urechinidae, Schizasteridae), 19 genera and 46 species. The carnivorous opportunistic browsers feed mostly on benthic sessile animals (*e.g.*, foraminiferans, bryozoans, annelids, sponges), but also on dead animals (*e.g.* fishes) and on bottom material (*e.g.* mud); in the Antarctic they count 2 families (Cidaridae, Echinothuriidae), 6 genera and 22 species. The vegetarian opportunistic browsers feed on algae when available, but animal material (sponges, bryozoans, seal feces, dead animals) as well as bottom material (mud) are also found in their gut; in the Antarctic they count one family (Echinidae), 3 genera and 7 species. The strict vegetarian browsers feed mostly on algae and occasionally on bottom material or dead animals; in the Antarctic they count 2 families (Arbaciidae, Temnopleuridae), 2 genera and 4 species. These results clearly indicate that there are two predominant trophic categories in the Antarctic, the deposit-feeders (58% of the Antarctic species) and the carnivores (30% of the species).

Table 16. Biodiversity of echinoid trophic groups.

Trophic groups	N of families	N of genera (N & % of endemic genera)	N of species (N & % of endemic species)
Deposit-feeders	4	19 (4) (21%)	46 (29) (63%)
Carnivorous	2	6 (3) (50%)	22 (17) (77%)
Vegetarian (opportunistic)	1	3 (0)	7 (4) (57%)
Strict vegetarian	2	2 (0)	4 (0)

3.3.3.2. The cidaroid ectosymbioses as a source of ecological niches

Ectosymbionts biodiversity

In total, 130 species of ectosymbionts were recorded on the 13 investigated cidaroid species. They were 36 bryozoans, 34 sponges, 27 cnidarians (6 anthozoans and 21 hydrozoans), 12 annelids (polychaetes), 10 echinoderms (5 holothurids, 5 ophiurids), 5 arthropods (4 crustaceans and 1 pycnogonid), 5 molluscs and 1 foraminiferan. Ectosymbionts biodiversity is detailed in Hétérier (2007). Comparisons of two morphologically contrasted hosts (*Ctenocidaris spinosa* and *Rhynchocidaris triplopora*) have indicated that ectosymbionts biodiversity is related to the spines features (Hétérier *et al.*, 2005). These results are summarized here. The spines of *C. spinosa* are coarsely thorny or spinulated (aboral and oral spines, respectively) while those of *R. triplopora* are smoother, bearing only fine thorns (Fig. 28).

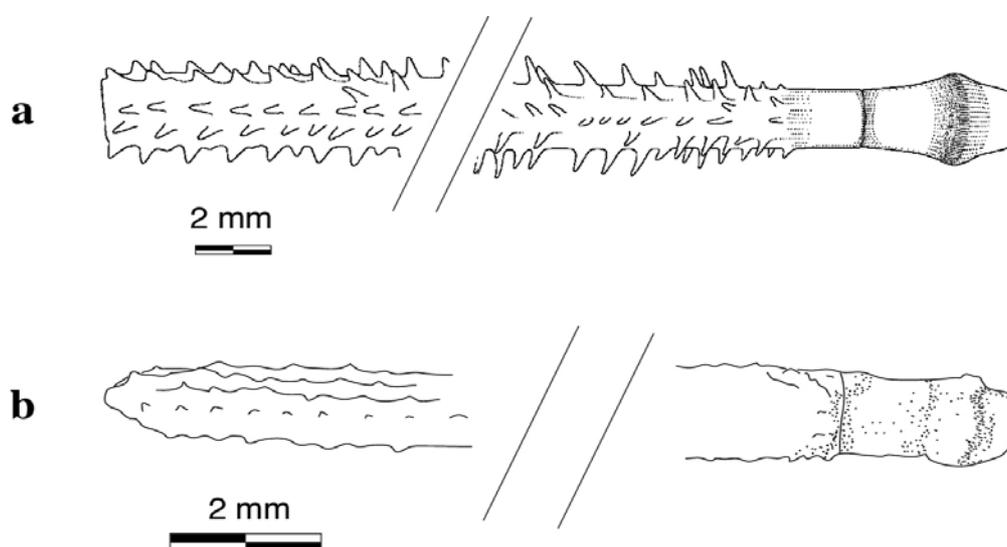


Fig. 28. Aboral primary spines. (a, from David *et al.*, 2005). *Ctenocidaris spinosa* (a); *Rhynchocidaris triplopora* (b).

Sixty-three and thirty-one morphological types of ectosymbionts were found respectively on *C. spinosa* and *R. triplopora*. These morphological types belong to the same eight phyla in both hosts and correspond preferentially to sponges, bryozoans, annelids, echinoderms, cnidarians, molluscs, arthropods (crustaceans), and foraminiferans. Interestingly, the ectosymbiont morphological types are twice as numerous in *C. spinosa* than in *R. triplopora*, but their proportions inside each phylum (*i.e.* number of types in a given phylum / total number of types) are identical (Fig. 29, $\chi^2 = 1.36$; $p = 0.99$). Within each echinoid species, there is no relationship between the number of ectosymbiont morphological types per spine and the test diameter. To analyze the distribution of the ectosymbionts on the spines, an ANOVA was made, following a stepwise procedure. This allowed removing the non significant effects from an original model including: the host species (*C. spinosa* vs. *R. triplopora*), the spine location on the test (oral, ambital or apical), the zone of the spines (distal vs. proximal), the spine length and their interactions. The average number of ectosymbiont morphological types per spine is higher in *C. spinosa* than in *R. triplopora* (Table 17). Whatever the host species, the proximal zone of the

spines harbors slightly but significantly more ectosymbiont types than the distal zone (Fig. 30). The number of ectosymbiont morphological types is also positively related to the spine length, and changes with the spine location on the test. For equivalent length, the apical and ambital spines bear more ectosymbiont types than the oral spines. The proportion of spine surface coated with ectosymbionts varies. This variation is mainly related to the host species and to the location of the spines on the test. It appears that ectosymbionts occupy a larger spine surface in *C. spinosa* than in *R. triplora*. Moreover, whatever the host species, the apical spines are more coated than the ambital ones, which are in turn more coated than the oral ones.

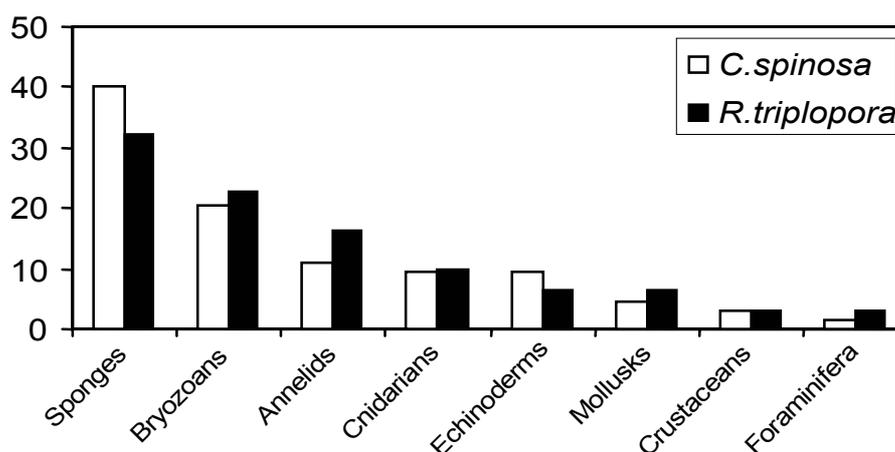


Fig. 29. Proportions of ectosymbionts morphological types in *C. spinosa* and *R. triplora*. (H  tier et al., 2005).

Table 17. Analysis of variance following a stepwise procedure, analyzing factors influencing the average ectosymbionts morphological types on spines. Analysis made on Log-transformed data for spine length.

Source of variation	Sum of Squares	d. f.	F	p
Species	74.95	1	41.05	< 0.001
Spine location (a)	89.58	2	24.53	< 0.001
Zone on the spine	9.46	1	5.18	0.02
Spine length (b)	24.09	1	13.19	0.0003
Interaction a*b	23.37	2	6.40	0.002

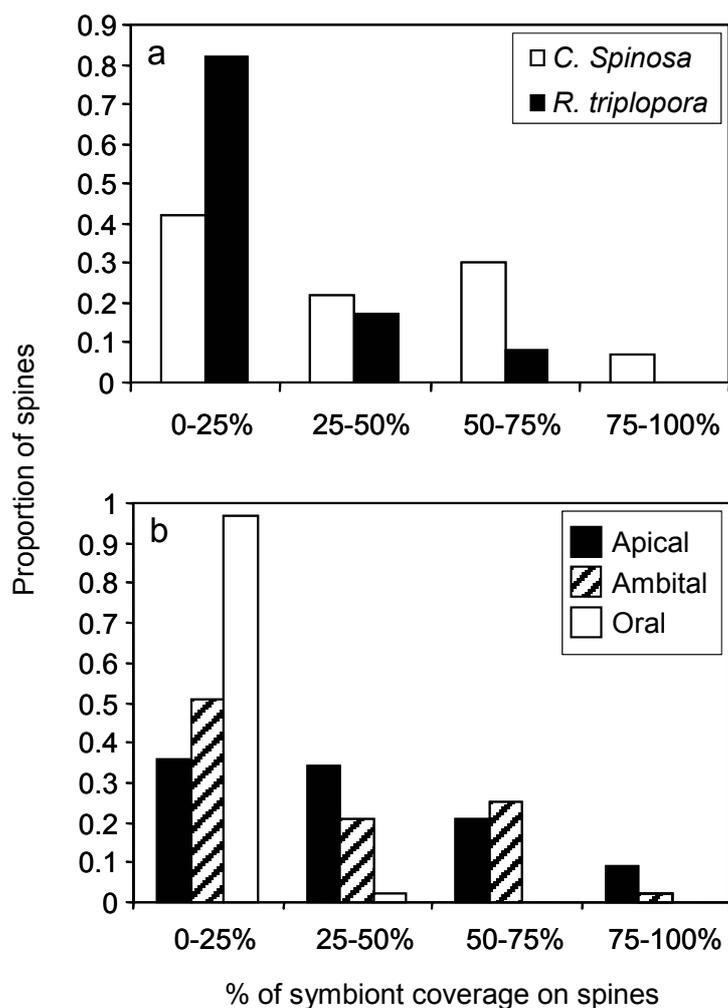


Fig. 30. Percentage of spine surface covered by ectosymbionts, according to the host species (a) and to the spines location on the test, the two host species being grouped (b).

Spines morphology and related ectosymbionts colonization

In study #1, we demonstrated that two species with rather distinct spine morphologies housed different symbiotic communities. Such a difference in symbiosis could be at least partly related to the physical aspect of the spine (size and shape). Owing to that, the objective of this study (#2) was to describe quantitatively the spine morphology in different cidaroid species in order to explore the relationships between the morphological features of the spines and the settlements of symbionts. For this purpose, two sets of parameters were considered in thirteen species: (i) raw dimensional variables, and (ii) proportion-based variables. Morphological differences were found between the three considered types of spines (oral, ambital and apical), suggesting the existence of a morphological gradient between the spine types. Discriminant analyses attested that strong differences separate oral from apical spines, while ambital spines are more closely related to apical ones. Inter-species morphological differences were also found, for each spine type (Fig. 31). These differences are not related to the geography and can be attributed to the systematics.

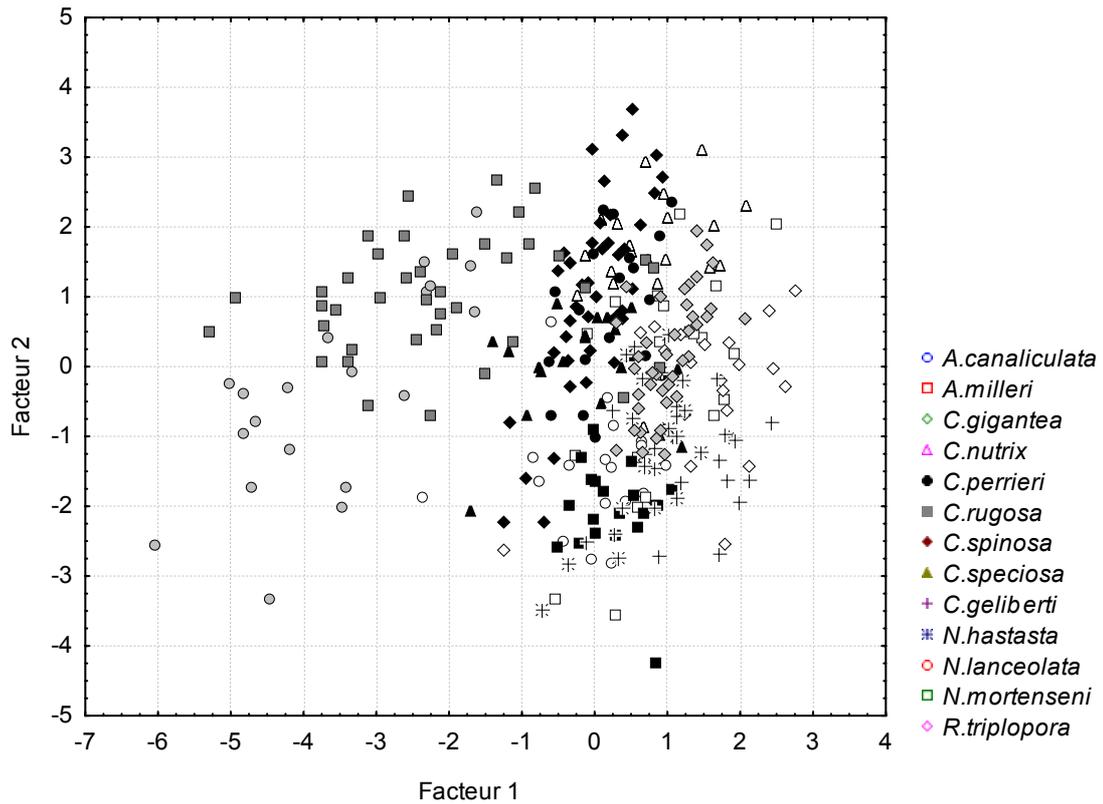


Fig. 31. Morphological space of apical spines (Factors 1 and 2 of a PCA on proportion-based variables).

However, the discriminant analysis does not allow an unambiguous attribution of spines to the different species: the global percentage of correct attribution is about 75% (proportion-based variables were more discriminant, and apical spines were found to be more discriminant than oral spines). This means that the same kind of support can be offered by different species. CAH combining apical and oral spines have allowed clustering spines, independently of taxonomy, in nine main categories representing each a type of “offer” for symbionts.

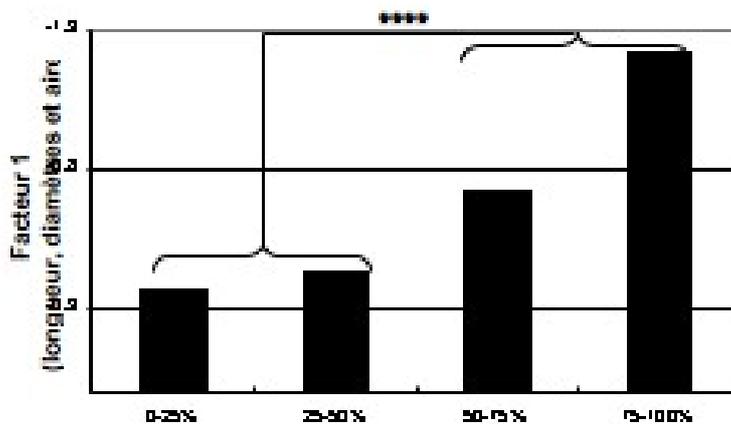


Fig.32. Importance of the symbiotic coverage (ranked in 4 classes) according to the size parameters of the spines (F1 scores of the PCA).

Results also suggest that the importance of colonization by symbionts is more strongly related to dimensional parameters of the spines (i.e. length, area, diameter and spinosity) than to shape parameters (Fig. 32). In addition, and surprisingly, the success of symbionts settlement does not seem related to the disparity, i.e. the range of spine morphologies presented by a given species.

Impact of ectosymbioses on local biodiversity

In the two compared stations (Sta. 142 and 151), the species richness of the sessile fauna fixed on hard substrates is about the same on the tillites, but not on the sea urchins. The *Ctenocidaris speciosa* of Sta. 151 bear more symbionts than the *Aporocidaris milleri* from Sta. 142 (Fig. 33). This may corroborate, on another pair of species, the results of study #1 (see above). Moreover, the specific diversity – which also takes into account the abundances – is higher on the tillites than on sea urchins at Sta. 142, but not at Sta. 151 where sea urchins and pebbles bear about the same diversity of sessile organisms.

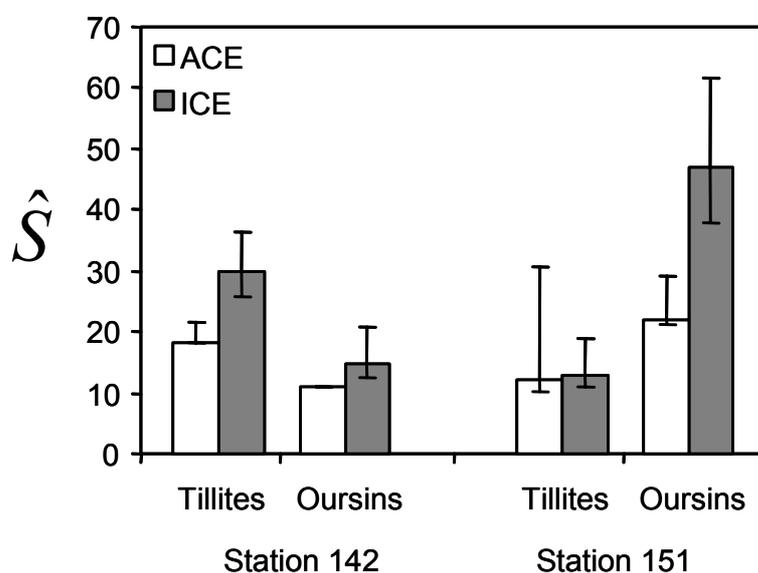


Fig. 33. Specific richness as estimated by two indexes (ACE and ICE) on tillites and sea urchins in two stations of the Weddell Sea. Error bars represent 95% confident intervals.

However, when the similarity between tillites and sea urchins is estimated, it clearly appears that species shared by tillites and sea urchins are relatively few: between 2 and 10% at Sta. 142 and between 20 and 50% at Sta. 151 (Fig. 34).

These results mean that the presence of sea urchins leads to increase the number of sessile species present on a given spot. In other words, cidaroid sea urchins have an impact on the biodiversity of Antarctic soft bottoms. Their impact is all the more important than only 8 to 11% of the tillites are colonized by sessile organisms while 78 to 100% of the cidaroids are: even if sea urchins are few, they may have a significant impact. Such a result must yet be considered exploratory as only two stations have been studied so far, but it is very encouraging and further explorations would allow collecting more data allowing a reliable appraisal of the impact of sea urchins on the diversity of the benthic Antarctic ecosystem.

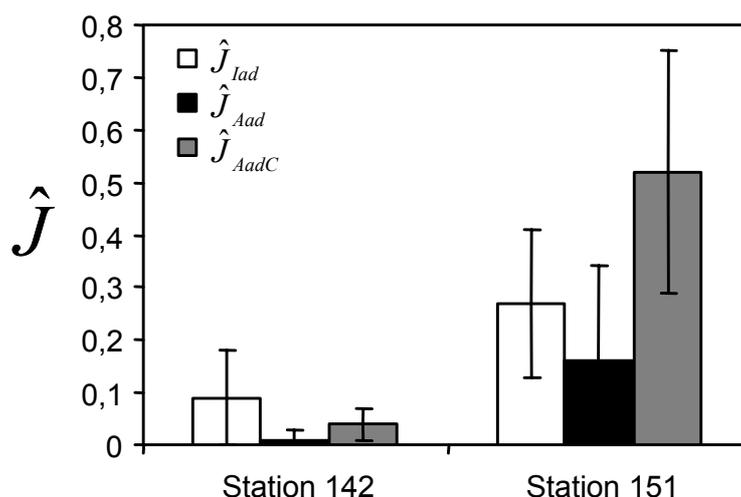


Fig. 34. Similarity of sessile fauna bear by tillites and cidaroid echinoids in two stations of the Weddell Sea. Error bars represent standard errors. Three indexes have been used based on incidence or abundance data.

Discussion. Cidaroids are the most abundant “regular” echinoids in the Antarctic. They correspond to a primitive clade of echinoids, characterized by the absence of epithelium on the spines. This characteristics provides a potential substrate for various sessile organisms, which attach to cidaroid spines. In the Antarctic deep sea in particular, hard substrates are scarce, and cidaroids could therefore play an important role in the life cycle of some of their epizoic symbionts. Although spines morphology is heterogeneous in the 13 studied species of cidaroids, the aboral, ambital and oral categories of spines respectively belong to a particular morphological type. Our results have indicated that the spine morphologies have a determinant effect in the occurrence (diversity) and abundance of ectosymbionts. In general, the size of the substrate rather than its micromorphology has a predominant impact on the abundance and diversity of ectosymbionts as also observed by Key & Barnes (1999) for the ectosymbiotic bryozoans attached to isopods. However, one cannot reject the fact that the settlement of particular species of ectosymbionts could rely on particular micromorphologies of the spines. These observations are supported by the fact that large spines are more likely to be encountered by planktonic larvae and subsequently colonized by post-metamorphic individuals. Sponges, bryozoans and annelids are the most frequent phyla of ectosymbionts. Together these three phyla account for 71.7% and 70.9% of the ectosymbiont morphological types encountered on *Ctenocidaris spinosa* and *R. triplopورا*, respectively. Interestingly, these predominant phyla are sessile and suspension-feeding organisms, which presumably gain a better access to the water column via the erected spines. This is supported by their preferential installation on the apical and, at a lesser degree, ambital spines, *i.e.*, the more exposed spines to the water column. In apparent contradiction with this latter point, the proximal zone of the spines, close to the test, harbors slightly but significantly more ectosymbionts types than the distal zone, whatever the host species, a phenomenon yet to be explained clearly. The most frequent ectosymbiont phyla correspond to the most common phyla found in the Weddell Sea (Gutt *et al.*, 2001). This could indicate that ectosymbionts are opportunistic, using the sea-urchin spines as a hard substrate easy to access. However, the small proportion of symbionts shared by *C. spinosa* and *R. triplopورا* indicates that the symbionts have reached some degree of host preference. This can be drawn from comparison of

hosts from distinct populations of the same species, and through the comparison of hosts of different species from the same collecting site. Such specificity could be related to particular microhabitats provided by the echinoids and more particularly by their spines, a possibility reinforced by observations made on the ectosymbiotic fauna associated with *Ctenocidaris gigantea*, *C. spinosa* and *Notocidaris mortenseni* (Jacob, 2001). Could cidaroids influence - at least at local scale - the biodiversity of the deep-sea benthos? This hypothesis has been investigated through the comparison of sessile species occurring on hard substrates of about the same size (tillites) and on cidaroid spines. 6 to 10% of the tillites against 87.5% of the cidaroids were colonized by sessile epifauna. This clearly indicates that the cidaroids provide adequate microhabitats to benthic organisms. This is further supported by three series of observations: (1) epifaunal individuals are more abundant on cidaroids than on tillites, (2) the specific composition of the epifauna differs between cidaroids and tillites and, (3) tillites and cidaroids have only a low number of epifaunal species in common. The results also indicate that cidaroids are preferentially chosen as substrate by the epifauna and that particular host species are not preferred. A preference for an "elevated" position, *i.e.* for a substrate giving access to the water column, is commonly observed for suspension-feeders in the Antarctic (Cacchione *et al.*, 1978; Gutt & Schickan, 1998). This could also be the case, meaning that most of the ectosymbionts of cidaroids are primarily "attracted" by the erected position of the spines rather by the echinoid species itself. Interspecific competition for space presumably occurs on cidaroid spines; this could influence the epifaunal composition of the surroundings: tillites could for instance be colonized by less competitive/successful species than those colonizing the spines. In conclusion, further observations are still needed to clarify the host-symbiont interactions and specificity. Such future studies are crucial to ascertain the significance of sea urchin symbioses, and more generally to get an accurate picture of Antarctic biodiversity as the abundance and distribution of cidaroids may influence the distribution of biodiversity of some other Antarctic invertebrates. Cidaroids could be local "hot spots" for biodiversity and could play a role in ecosystem engineering, such as other invertebrates (*e.g.* Thomas *et al.*, 1998).

4. BIODIVERSITY INFORMATION SYSTEM FOR THE ANTARCTIC BENTHOS

4.1. INTRODUCTION

The third objective of the BIANZO project aimed at contributing to develop an information system for the Antarctic benthic biodiversity.

Biodiversity information systems are becoming essential tools in taxonomical, ecological and biogeographic research as well as in biodiversity conservation and sustainable management. Biodiversity data (species taxonomy and nomenclature, geographic and bathymetric distribution, habitat, ecology, etc,...) are usually widely scattered, highly patchy, not easily nor fully accessible, and sometimes vanishing.

There is a strong need for building informative and comprehensive databases for the Antarctic biodiversity to meet the Antarctic Treaty System's requirements in terms of biodiversity information, in particular for assessing the Global Change effects, establishing the "State of the Antarctic Environment Report", or facilitating the "bioregionalisation" process of the Southern Ocean. In addition, as the Rio Convention on Biological Diversity does not directly apply to the Antarctic region south of 60°S (as its provisions are only applicable to sovereign territories), there is an obvious interest to develop a "clearing house mechanism" for biodiversity information within the Antarctic Treaty System.

On the other hand, accurate species identification is fundamental in biodiversity studies and relies on efficient identification tools, which are still lacking for some highly diverse and taxonomically difficult groups of the Southern Ocean, such as nematodes, amphipods, polychaetes or copepods. A revolution is taking place in the way taxonomic tools are designed and biodiversity information is packaged and presented to various groups of users. Systematists are now increasingly developing interactive identification keys available on-line or on CD-ROMS. These interactive keys largely rely on abundant illustrations (sometimes difficult to offer in conventional guides) and allow a more flexible and efficient use of diagnostic characters (multi-entry keys) than the rigid dichotomous keys of traditional handbooks. The role of interactive databases in modern taxonomy is growing rapidly.

4.2. THE BIANZO DATABASES

The **Nemys** database (www.NeMys.UGent.be) has been initiated in the Marine Biology Section (Ghent University) under ANTAR4 as an information system for improving identification, classification and description of Antarctic nematode species (NemasLan; Deprez et al., 2001) and was further developed during the BIANZO project. It gathered all published taxonomical knowledge of the 331 species of free-living marine nematodes from the Antarctic and the Subantarctic. Nematode information from other oceans has been included and at present Nemys contains data on almost 7000 nematode taxa worldwide. The database holds over 6000 distribution records and 3000 bibliographical records (of which almost 2000 are available in pdf).

An interactive, polytomous, well-illustrated identification key for free-living nematodes (NeMysKey©) was developed and can be accessed online. On the other hand, well developed mapping tools allow detailed biogeographical analysis of nematode distribution patterns in Antarctica and on a global scale. Information at nematode species level in Antarctic environments is still preliminary and large areas of

the Southern Ocean remain uninvestigated. Therefore further efforts are needed to gain more taxonomical and geographical data.

The “**Ant’Phipoda**” database was also initiated under the ANTAR4 programme at the Royal Belgian Institute of Natural Sciences (De Broyer et al., 2001b) and developed under BIANZO. It holds exhaustive information on taxonomy, geographic and bathymetric distribution, and bio-ecology of all Antarctic and sub-Antarctic amphipod species. It contains in particular an authoritative species catalogue with up-to-date systematic classification, complete citation records and synonymy (885 spp, 300 synonyms, 1052 taxa), information on expeditions, stations and sampling gears (114 expeditions, 1124 collecting stations), 8000 georeferenced distribution records with ecological data, as well as an integrated and hierarchized gazetteer of Southern Ocean geographical features (5940 place-names). The linked bibliographic section holds 13500 references searchable by taxonomic, geographic and thematic keywords. In addition, the Ant’Phipoda database holds sample data on the extensive reference collections of Antarctic crustaceans (> 400 000 specimens) kept at RBINS.

The “Ant’Phipoda” database operates with the collaboration of a network of 17 contributing specialists (the “Antarctic Amphipodologist Network”), involved in the revision of the Antarctic fauna, the synthesis of its distribution and bio-ecological traits, and the preparation of new identification tools. It also cooperates actively to the development of ABBED, the Admiralty Bay Benthos Diversity Database, a Polish-Belgian-Brazilian initiative.

The “**Antarctic Echinoids**” database was developed in cooperation between the University of Bourgogne in Dijon (B. David, T. Choné and A. Festeau) and the Marine Biology Laboratory of University of Brussels (C. De Ridder). This long lasting survey reached its end during the BIANZO project. The database was built as a complement to the volume «Antarctic Echinoids» in the series “Synopsis of the Antarctic Benthos” (David *et al.* 2001) and it was designed to provide a tool for scientists interested in Antarctic benthos. “Antarctic Echinoids” is an interactive database synthesizing the results of more than 100 years of Antarctic expeditions. It comprises information on the 78 echinoid species present south to the Polar Front (Antarctic Convergence). It includes illustrated keys for the identification of the species, and information about their morphology and ecology (with text, illustrations, and glossary), their distribution (maps and histograms of bathymetrical distribution); detailed sources of the information (bibliography, collections and expeditions) are also provided. All those data (taxonomic, morphologic, geographic, bathymetric...) can be interactively queried in two main ways: (i) A static way displaying listings of taxa, geographic records, cruises, literature and collections, with possibility of sorting and printing. In this part, a system of illustrated keys allows progressing step by step in the identification of families, genus and species, (ii) An interactive way allowing links and joined queries between taxonomy, geography, bathymetry, cruises and data sources. A glossary of echinoid terminology is available to help reading the diagnoses. It includes 139 terms with precise illustrated definitions. Localities are divided into quadrats of 5° latitude and 10° longitude in conjunction with depth. Only the localities situated south to the Polar Front have been considered. Two maps are available, one with cells corresponding to the quadrats and another one with several sets of larger cells (including the four classical Antarctic quadrants, and rings of latitudinal range). The database works on Apple Macintosh and Windows systems; it is constantly updated with fresh data from new expeditions, which

helps to complete the knowledge of this key representative of the Antarctic benthos. It is freely available on CD-ROM format and now accessible through the SCAR-MarBIN portal (www.scarmarbin.be).

The Antarctic biodiversity data from the three BIANZO databases have been made fully accessible and disseminated through individual websites or through federating initiatives, such as the SCAR-MarBIN portal (see 4.3). Through SCAR-MarBIN, BIANZO results are disseminated widely by contributing original data to worldwide biodiversity information initiatives, such as OBIS (Ocean Biogeographic Information System) and GBIF (Global Biodiversity Information Facility).

4.3. THE STEP FORWARD: THE “SCAR-MarBIN” PROJECT

The BIANZO project played the key-role in the elaboration of the SCAR-MarBIN - Antarctic Marine Biodiversity Information Network project - initiated by De Broyer & Danis and implemented within the Belgian Biodiversity Platform.

SCAR-MarBIN (www.scarmarbin.be) is a cooperative initiative aiming at establishing and supporting a distributed system of interoperable databases, established under the aegis of the SCAR (Scientific Committee on Antarctic Research).

SCAR-MarBIN compiles and manages existing and new information on Antarctic marine biodiversity by coordinating, supporting, completing and optimizing database networking. The project contributes to larger biodiversity initiatives such as OBIS - the information component of the Census of Marine Life (CoML) - and GBIF (Global Biodiversity Information Facility). SCAR-MarBIN gives a single and easy access to relevant Antarctic marine biodiversity information and maximizes the exploitation of these resources.

SCAR-MarBIN is the companion-project of the Census of Antarctic Marine Life (CAML), an ambitious 5-year project which will investigate the nature, distribution and abundance of Antarctica's marine biodiversity, from viruses to whales (www.caml.aq). SCAR-MarBIN will leave a valuable legacy for future generations, in the form of an information tool that will provide a baseline reference for establishing a State of Antarctic Environment, and predicting the future for marine communities around Antarctica, which are currently facing global change.

5. SUMMARY AND CONCLUSIONS

5.1. NATURE AND DISTRIBUTION OF BENTHIC BIODIVERSITY

BIANZO efforts first concentrated on the **exploration of unknown habitats**, in particular the continental slope, abyssal plains and trenches of the Atlantic sector of the Southern Ocean, in the framework of the ANDEEP programme. On the other hand, **comprehensive syntheses** of the biodiversity and distribution knowledge of the nematodes (meiobenthos), amphipods (macrobenthos) and echinoids (megabenthos) groups were developed and completed, and new identification tools designed. These two approaches allowed describing and analyzing the biodiversity of the three target groups and discussing their large-scale biogeographic and macroecological patterns and driving processes.

Meiobenthos and Nematodes. Meiobenthic life in the Antarctic deep sea beyond 2000 m water depth was completely unknown before the project. Moreover, nematode communities – which form the bulk of the meiobenthos - were until recently only studied at genus level and no indication of the existence of an Antarctic endemic fauna at shallow, shelf and deep-sea depths was available. During the ANDEEP cruises, emphasis was put on meiobenthic communities along bathymetric gradients from the lower continental slope down to hadal depths (6300 m) in the South Sandwich trench and on spatial variability in the Weddell Abyssal Plain. Species diversity and distribution – in relation with biogeography, bathymetry and environmental characteristics – were investigated in selected genera and compared with communities in marine sediments in other oceans.

In terms of **composition**, the dominant nematodes of the Antarctic deep-sea communities generally belonged to typical cosmopolitan deep-sea genera. Particular attention was paid to the species level, not commonly investigated in deep-sea nematodes community studies. This approach revealed a high number of new species: more than 85 % of species recognized in 5 selected genera were new to science. A first assessment was made on genus diversity and community composition of nematodes in the Weddell Abyssal Plain. All nematode communities were dominated by typical deep-sea genera, suggesting a high connectivity between the Weddell Sea and the Atlantic Ocean in the past. The nematode assemblages along the bathymetric gradient of the South Sandwich Trench generally contained the same genera, however their relative abundance differed considerably between the “shallow” (750-1100 m) and “deep” (4000-6300 m). The intermediate stations (especially at 3000 m) form a transition with changing overlap with both extremes. The “shallow” communities resemble those from the Weddell Sea continental margin. The sediments at 2300-6300 m show a composition similar to abyssal nematode communities worldwide. The wide distribution of families and genera suggests that radiation of nematodes in abyssal depths occurred relatively long ago, or modern-day dispersal of nematodes over vast distances has been quite efficient.

Different patterns in **densities** were detected among the different genera investigated. In contrast to previous studies, no link was observed between depth and relative and absolute densities at shelf and slope depths in *Acantholaimus*, a typical deep-sea genus comprising 55 morpho-species in the Antarctic. However in the Weddell Sea, this genus showed a significant link with chlorophyll a

concentrations, with highest absolute and relative densities at lowest chlorophyll a concentrations. Although mostly confined to deep slope and abyssal depths in other parts of the world, where it often occurs in high densities, *Acantholaimus* species regularly occurred on the continental shelf and slope of the Weddell Sea (182- 2008 m). Most (39) species were recorded in less than 500 m water depth and about half of them extend their distribution to the lower slope, exhibiting an **eurybathic distribution** pattern already described for the macrofauna.

High total meiobenthos densities were observed near the South Sandwich Trench, in an upwelling area characterized by high primary production. However, micro-algae availability in the sediment was extremely low and, therefore, a highly depauperate fauna was expected. On the contrary, densities from the South Sandwich Trench were above the world ocean average and also abundance on the Trench floor was higher than at similar depths in other trench regions of the world ocean.

If no Antarctic **endemism** was recorded at genus level, species-level investigations in selected genera revealed high apparent nematode endemism in the deep sea, similar to the macrofauna observations (Brandt et al. 2007a). Many nematode species from the deep Southern Ocean are undescribed and apparently confined to particular parts of the Weddell Sea; Less than 10 % of the identified species also showed wider distributions.

Biogeographical analysis based on morphological and molecular data also indicated that the Scotia Arc may well have served as a **migration** path for particular Antarctic nematode species. Although nematodes are assumed to be permanent sediment inhabitants, their occurrence in the water column is not exceptional in high-energy areas and their dispersal by passive transport in the bedload or water column may be driven by hydrodynamics. Considering the complex current system and movement of vast water masses of the Southern Ocean, the dispersion of benthic meiofauna by hydrodynamics cannot be excluded since turbulent water masses are encountered at considerable depth and have enough energy to transport small animals.

Amphipods. The investigations of the amphipod taxocoenoses of the Antarctic deep-sea revealed the presence of over 200 different species from >38 families, including a great majority of **new taxa**. By comparison, only 72 benthic species were previously known in the Antarctic below 1000 m and 502 benthic species were described from Antarctic shallow and shelf depths.

The deep-sea crustacean **scavenger guild**, which was studied in details for the first time in the Antarctic, comprises 51 species. Both at slope and abyssal depths the bulk of the catches consisted of amphipod crustaceans (46 spp), in particular lysianassoids (39 spp from 18 genera and 8 families). New species were discovered in 10 different lysianassoid genera. No significant reduction in species richness was observed from shelf down-slope to the abyssal zone. These first results on the Antarctic deep sea scavengers show that the Antarctic slope (1000–3000 m) appears to be richer in scavenger species than elsewhere in the world at similar depth range. The higher slope richness seems to be due to the extension of the rich deep-shelf fauna on the upper slope favoured by the isothermic continuum of the water column. In the Antarctic abyssal waters (> 3000 m), the species richness of the scavenger guild appears also higher than in the abyssal trap collections elsewhere in the world and may be related to the higher regional productivity.

A comprehensive **census** of the whole gammaridean and corophiidean amphipod fauna of the Southern Ocean pointed out its remarkable species richness, with 536 species occurring in Antarctic waters south of the Polar Front and 407 spp in sub-Antarctic waters between the Polar Front and the sub-Tropical Front zone. Both regions share 128 species, *i.e.* 24% of the Antarctic fauna or 31% of the sub-Antarctic fauna. In terms of composition, the Antarctic and sub-Antarctic amphipod fauna is mostly dominated by representatives of Lysianassoidea (158 spp in 57 genera and 18 families), Eusiroidea (108 spp in 27 genera and 4 families), Stenothoidae (66 spp in 16 genera), Ischyroceridae (49 spp in 7 genera), Iphimediidae (46 spp in 13 genera), Phoxocephalidae (34 spp in 18 genera) and Epimeriidae (26 species in 5 genera). The **high species richness** of some macrozoobenthic groups of the Antarctic shelf has been attributed to different evolutionary and ecological factors: the long evolution in isolation of the southern polar ecosystem, the glaciological history and the oscillations of the ice sheet (the “climatic pump of biodiversity”; Clarke & Crame, 1997) and at smaller time scales, the regular seasonality or predictability of the system, the role of disturbance (by ice in particular), the energy input and the high spatial heterogeneity. The diversity of habitats in particular is enhanced in the Southern Ocean by the biogenic sediments such as the sponge spicule mats and bryozoan debris, the ubiquitous dropstones providing hard substrates even in the deep sea, and the abundant and diverse sessile epibenthos which provide tri-dimensional substrates, food resources and opportunities for symbioses. In addition, some particular determinants of the high species diversity in Antarctic amphipods and isopods can be put forward: the *brooding habit*, which implies limited dispersal of juveniles and enhanced reproductive isolation; the rather *low mobility* exhibited by many benthic species, and the *emergence of new adaptive zones* due to the faunal extinction events during the Tertiary cooling of the Southern Ocean.

A clear distinction both in species richness and composition can be made between the different **bathymetric** zones. The Antarctic shelf fauna (0-1000 m) comprises 474 benthic and benthopelagic species, with 427 species restricted to shelf depths. On the other hand, 164 benthic and benthopelagic species occur between 500 m (average depth of the continental shelf break) and 3000 m, but only 56 spp between 1000 and 3000 m. This clearly indicates that part of the shelf fauna extends its distribution to the upper slope. The deep-sea fauna (found below 1000 m) amounts 96 benthic and benthopelagic species in the whole Southern Ocean, 91 species in the Antarctic and 21 species in the sub-Antarctic region. The presently known abyssal fauna, below 3000 m, counts 19 benthic and benthopelagic species in the Antarctic and only 4 species in the sub-Antarctic region. These numbers do not include the preliminary results from the recent *Polarstern* ANDEEP cruises. When included, the number of Antarctic deep-sea species may surpass 200 species. The few cases of very wide eurybathic distribution of benthic species possibly indicate the presence of cryptic species and require molecular analysis for confirmation.

In terms of **endemism**, the Antarctic fauna show a level of 72,3% of endemic species (all components) or 66,6% if only benthic species are considered. The newly discovered Antarctic abyssal fauna also shows high apparent endemism and has more affinities with peripheral abyssal basins than with the Antarctic shelf fauna.

Echinoids. In terms of **composition**, the Antarctic echinoid fauna comprises 78 species, most of which belong to only 2 families: Cidaridae (21 spp) and Schizasteridae (30 spp). This represents about 10 % of the World echinoid fauna. An outstanding feature of the Cidaridae and the Schizasteridae is the **brooding behavior** displayed by most of their species: 70% of the Cidaridae and more than 83% of the Schizasteridae are brooders. The remarkable predominance of brooders in Antarctic echinoids has been explained by the glacial conditions that have counter-selected indirect developers and therefore have limited their diversification. This could have resulted in the extinction of taxa with planktonic larvae during glacial extremes and in the diversification of taxa with lecithotrophic eggs. As brooding habit reduces dispersal and gene flow, it must have increase speciation and endemism rates. Interestingly, the Cidaridae and Schizasteridae are also the oldest families to occur in the Antarctic, with respectively Mesozoic and Cenozoic fossils records, giving ample time for speciation in these two groups.

The comparison of the observed **distribution** of echinoid regional biodiversity in the four (classic) **longitudinal** sectors of the Southern Ocean (Atlantic, Indian, Australia-New Zealand and Pacific) resulted in expected patterns (with highest similarity between contiguous sectors), which can be explained, on one hand, by historical factors (the opening chronology of the straits isolating Antarctica), and, on the other hand, by geographical and hydrological factors (the land masses distribution, and the direction of main currents). The analysis of the **latitudinal patterns** of echinoid regional biodiversity revealed an interesting feature: the apparent boundary role of the Divergence zone. In comparison with the southernmost faunule, a drop of 18 % of species richness was recorded north to the Divergence. More than half of the echinoid species (55%) are affected by the Divergence boundary. Among the 13 species restricted to the south, 10 spp (77%) are brooders; among the 18 species reported exclusively north to the Divergence 9 spp (50%) are brooders; 19 (73%) of the trans-latitudinal species are brooders. In terms of **bathymetric patterns**, the shelf fauna (0-1000 m) appears homogenous (with 73% of the species occurring in this depth range). In contrast, only ca. 30% of the deep water species (occurring below 1000 m) are also present on the lower shelf. The shelf and the deep-sea echinoid fauna are consequently distinct (The new ANDEEP collections are still under study but should not modify this general pattern). This pattern is observed all around Antarctica, in the four longitudinal sectors. The echinoid **endemism** is high as 64% of the species and 27% of the genera are endemic to the Southern Ocean s.s.

5.2. ECOFUNCTIONAL BIODIVERSITY

To contribute to understand the role of biodiversity in the functioning of the Southern Ocean benthic ecosystems the BIANZO project focused on the identification and description of the functional niches occupied by representatives of the three target groups, in particular their trophic niches and their integration in the benthic food web, as well as other functional aspects such as the role of size and biomass, habitat component, mode of life or mobility.

5.2.1. TROPHODIVERSITY AND TROPHODYNAMICS

Meiobenthos and Nematodes. Nematodes along the South Sandwich Trench transect were mainly selective deposit-feeders (36%), epistratum grazers (33%) and non-selective deposit feeders (27%).

Predators/omnivores were well below 10%. There was no significant change in this composition with depth. The selective deposit-feeders with minute buccal cavity, presumably feeding on bacteria, were observed in highest proportions in the two shallowest stations with moderately sorted silts with thin fluff layer on top. Non-selective deposit (with big mouth cavity) and predatory/scavenging (with big teeth) feeding modes appear more at the shallow (750 and 1100 m) and burrow-rich (2300 m) sites. Both feeding types are, generally, related to high energy labile organic matter levels: non-selectivity prevails over selectivity in circumstances of labile detritus excess and higher trophic complexity is to be expected where food is trapped.

First attempts have been made to analyse stable isotope ratios in nematodes from deep-sea environments. The natural ^{13}C signals in the bulk sediment were much more depleted in the Southern Ocean than in other world oceans. The nematodes did show a vertical profile in the 2 sediment layers: larger $\Delta\delta^{13}\text{C}$ values were observed in the upper cm than in the cm below. This could indicate different dietary preference, with the deeper layer nematodes feeding more on bulk organic matter available in the sediment, while in the upper layer selectivity might occur. These stable-isotopes data were complemented with feeding experiments in which ^{13}C labeled food items – bacteria and diatoms – were added to sediment cores. Only bacteria were consumed by the nematodes. No response was measured for the ^{13}C -enriched diatoms over the whole sediment profile. It seems that nematodes in the Antarctic deep sea do not react directly on the input of microphytoplankton. Our data suggest that settled phytoplankton enters the food chain via a bacterial link. Bacteria might be a more reliable food source in the Antarctic deep-sea than diatoms, which have a highly seasonal input.

Macrobenthos and Amphipoda. To compare with the eastern Weddell Sea food web previously studied, the trophic structure of the shelf macrobenthic community of the Antarctic Peninsula region was investigated by relying on stable isotopes as trophic biomarkers. The most striking features of the **Antarctic Peninsula benthic trophic web** were, on the one hand, a general impoverishment in ^{13}C compared to other ecosystems (e.g. tropical), probably originating from a depleted food source but transferred throughout the food web. The SPOM isotopic ratios are considerably lower than values previously recorded for other regions but within the range of Antarctic as well as Arctic values. Low temperature (below 2°C), low light intensity and high water $[\text{CO}_2(\text{aq})]$ values lead to very low ^{13}C content in the phytoplankton and, in addition, a substantial role of irradiance in the process of ^{13}C incorporation in marine diatoms may also account for these low values. On the other hand, a considerable overlap of the $\delta^{13}\text{C}$ values was observed between the different macrobenthic groups. Isotopic investigations – in particular the similarity in $\delta^{13}\text{C}$ values between pelagic POM-based feeders and benthic filter feeders – also indicated that a major part of the benthic community is supported primarily by phytoplanktonic POM reaching the benthos.

Within the macrobenthic food web, the **trophodiversity of the amphipod taxocoenosis** was analysed in detail by a multi-proxy approach (stomach content analysis, morphology of feeding appendages, feeding experiments, stable isotopes and lipids as trophic biomarkers). The large amphipod trophodiversity encountered in the Weddell Sea was also found in the Peninsula region.

The multiproxy approach of the amphipod trophodiversity revealed that: (1) Natural history observations of living animals remain a rarely used but invaluable source of information; (2) The morphology-based approach of the feeding appendages is of limited value and restricted to few

characteristic families or genera; (3) Gut content analyses are essential to obtain a rough pre-classification of species in different trophic types, which were usually confirmed afterwards by the analytical methods. The revealed trophic categories were numerous and diverse, from typical suspension feeders to presumed obligate scavengers, with a lot of amphipods that can be considered opportunistic feeders; (4) Both fatty acid composition and stable isotope ratios are suitable tools for trophic ecosystem analysis in their own right. Fatty acids point towards food web links and stable isotopes identify trophic positions. However, the use of only one of the two tools can sometimes lead to misinterpretations with serious implications. It was clearly demonstrated that the combination of both approaches creates a 2-dimensional biomarker assay with higher accuracy and better trophic resolution.

The significance of amphipods in Antarctic trophodynamics has been approached in terms of potential food resources for higher trophic levels. As a result of a vast literature survey, 192 different predators were identified. The most numerous records concern fishes (101 predator species from 19 families, especially from notothenioids) and seabirds (48 species from 12 families, mainly procellariids and spheniscids). Amongst invertebrates, the more important amphipod predators were polychaetes and echinoderms (starfishes, sea-urchins and brittle stars) in the benthos, and several species of squids in the water column. To synthesize the dataset, a tentative 'box-model' was built up, which shows the relative importance of both pelagic and benthic amphipods in the diet of the Southern Ocean top predators. The total amphipod mass ingested per year was estimated at roughly 60 Mt, *i.e.* about 1.6 t.km⁻².yr⁻¹. Despite several biases in the calculation, this preliminary estimation can be considered a rather realistic working hypothesis about the importance of pelagic and benthic amphipods for Southern Ocean top predators.

Echinoids. On the basis of gut contents analyses, 4 trophic categories were recognized among Antarctic echinoids: (1) deposit-feeders (swallowing sediment), (2) carnivorous opportunistic browsers, (3) vegetarian opportunistic browsers and (4) strict vegetarian browsers. Most Antarctic echinoid are deposit feeders (58% of species; spatangoids, holasteroids) or carnivorous (30 % of species; cidaroids). Vegetarian species are rare and belong to Echinidae, Arbaciidae, and Temnopleuridae: they usually display an opportunistic feeding behaviour, being able to feed on bottom materials with its load of organic particles and on algae when accessible.

5.2.2. SIZE AND BIOMASS

Nematoda. Biomass spectra are useful tools in assessing functional changes in nematode communities as a result of a changing environment. A striking characteristic of the Antarctic nematode communities is the shift towards higher sizes in deeper water along the continental slope, in contrast to other parts of the world. Body width vs. length measurements were performed along stations of the South Sandwich Trench transect and showed two distinct morphological groups, the "plump" and "slender" types, and one less distinct third group combining very big and very slender types. L:W morphometrics were negatively correlated with sand and positively with silt. Plump nematodes belong to selective deposit-feeding genera of the order Desmoscolecida. Slender nematodes mainly mixed among selective and epistratum feeding modes.

Length and width based biomass was calculated per station and large biomass differences were observed between stations, thus showing a highly different morphological nematode structure with

depth. Total nematode biomass per m² was considerably higher in the Southern Ocean (Weddell Abyssal Plain) than in the North Atlantic. These differences are due to a combination of higher densities and higher individual biomass of the nematodes. This observation points to higher food availability for the meiofauna in Antarctica.

Amphipoda. A comprehensive and systematic analysis of the amphipod size spectra revealed that the Antarctic contains the greatest percentage of giant species. Comparison with other marine and freshwater ecosystems of the world showed that oxygen availability rather than temperature was responsible for this tendency towards gigantism. This "oxygen hypothesis" was validated by the analysis of new datasets showing that reduced oxygen at high altitude also limits maximum size in amphipods.

5.2.3. SYMBIOSES

During the last decades, symbiosis has been described as a pervasive and evolutionary significant biological phenomenon, as it widens the set of available niches in the environment and thus may increase biodiversity. It has been well documented that in benthic communities, substratum space is often limited and competition may be intense. Within the BIANZO project, we explored the importance of echinoids in the Antarctic benthic ecosystems as substrate providers for sessile and vagile ectosymbionts and as a source of ecological niches.

Ectosymbionts diversity. Detailed analysis of Weddell Sea shelf and deep-sea samples of 13 cidaroid species revealed that cidaroids provide microhabitats for a wide variety of ectosymbionts. In total, 130 ectosymbiont species were recorded: 36 bryozoans, 34 sponges, 27 cnidarians (6 anthozoans and 21 hydrozoans), 12 annelids (polychaetes), 10 echinoderms (5 holothurids, 5 ophiurids), 5 arthropods (4 crustaceans and 1 pycnogonid), 5 molluscs and 1 foraminiferan. Most ectosymbionts are suspension – feeders; they presumably get a better access to the water column by colonizing the sea urchin spines. When comparing the epifauna occurring on tillites (pebbles) from the same stations, cidaroids seems to be preferentially chosen as substrate. In that context, interspecific competition for space presumably occurs on cidaroid spines that could influence the epifaunal composition of the surroundings: tillites could for instance be colonized by less competitive/successful species than those colonizing the cidaroid spines.

Comparisons of two morphologically contrasted hosts (*Ctenocidaris spinosa* and *Rhynchocidaris triplopora*) showed that ectosymbionts biodiversity is related to the spines features. The spines of *C. spinosa* are coarsely thorny or spinulated (aboral and oral spines, respectively) while those of *R. triplopora* are smoother, bearing only fine thorns. Sixty-three and 31 morphological types of ectosymbionts were found respectively on *C. spinosa* and *R. triplopora*. These morphological types belong to the same eight phyla (enumerated above) in both hosts.

Ectosymbionts colonization. Such a difference in symbiotic assemblage composition could be at least partly related to the spine physical aspect (size and shape). In a second step, the spine morphology of the different cidaroid species was described quantitatively in order to explore the relationships between the morphological features of the spines and the symbiont settlements. Morphological differences were found between the three considered types of spines (oral, ambital and apical), suggesting the existence of a morphological gradient between the spine types. Discriminant analyses attested that strong differences separate oral from apical spines, while ambital spines are more

closely related to apical ones. Inter-specific morphological differences were also found, for each spine type. The results suggested that the importance of colonization by symbionts is more strongly related to the dimensional parameters of the spines (i.e. length, area, diameter and spinosity) than to the shape parameters. In addition, and surprisingly, the success of symbiont settlement does not seem related to the disparity, *i.e.* the range of spine morphologies presented by a given species.

To assess the **impact of ectosymbioses on the local biodiversity**, the ectosymbiont specific diversity – which also takes into account the abundances – was compared respectively on tillites (pebbles) and cidaroids in two stations. Specific diversity was higher on the tillites than on sea urchins at one station, but not at the other where sea urchins and pebbles bear about the same diversity of sessile organisms. However, when the similarity between tillites and sea urchins was estimated, it clearly appears that species shared by tillites and sea urchins are relatively few. These first results mean that the presence of sea urchins leads to increase the number of sessile species present on a given spot. Their impact is all the more important than only 8 to 11% of the tillites are colonized by sessile organisms while 78 to 100% of the cidaroids are. Even if cidaroid sea urchins are few, they may have a significant impact on the biodiversity of Antarctic soft bottoms.

5.3. BENTHIC BIODIVERSITY INFORMATION SYSTEM

The third objective of the BIANZO project aimed at contributing to develop an information system for the Antarctic benthic biodiversity. Biodiversity information systems are becoming essential tools in taxonomical, ecological and biogeographic research as well as in biodiversity conservation and sustainable management. Biodiversity data are usually widely scattered, highly patchy, not easily or fully accessible, and sometimes vanishing.

Three comprehensive biodiversity databases have been developed in the BIANZO framework. The **Nemys** database (U Gent) was developed as an information system for improving identification, classification and description of Antarctic nematode species (abt 350 spp), and further extended to world species. Besides taxonomic information, it holds extensive distribution records and bibliographical references (with pdfs) as well as an interactive, polytomous, well-illustrated identification key for free-living nematodes (NeMysKey©) accessible online.

The “**Ant’Phipoda**” database (IRScNB-KBIN) holds exhaustive information on taxonomy, geographic and bathymetric distribution, and bio-ecology of all Antarctic and sub-Antarctic amphipod species (abt 900 spp). It contains an authoritative species catalogue with complete citation records and synonymy, information on expeditions, stations and sampling gears, abt 8000 georeferenced distribution records with ecological data, a hierarchized gazetteer of Southern Ocean geographical features, IRScNB-KBIN reference collection data, as well as an extensive and searchable bibliographic section.

All Antarctic biodiversity data from the three BIANZO databases have been made fully accessible and disseminated through individual websites or through the SCAR-MarBIN portal (www.scarmarbin.be).

The expertise gained by the BIANZO partners - pioneers in Antarctic biodiversity databases - resulted in the elaboration of the **SCAR-MarBIN project** – the SCAR Information Network for Antarctic Marine Biodiversity - and its submission to Belspo, SCAR and the Census of Marine Life (Sloan

Foundation, N.Y.). SCAR-MarBIN is a cooperative initiative under the aegis of SCAR aiming at establishing and supporting a distributed system of interoperable databases holding information on Antarctic marine biodiversity. SCAR-MarBIN integrates these efforts, giving a single and easy access to relevant marine biodiversity information and maximizing the exploitation of these resources. SCAR-MarBIN forms the Antarctic Regional Node of OBIS (Ocean Biogeographic Information System) and, through OBIS, contributes original data to GBIF (Global Biodiversity Information Facility).

5.4. CONCLUDING REMARKS

In the course of the project, the BIANZO consortium has delivered 56 papers (33 peer-reviewed), 3 books, 3 CD-ROMs (2 with interactive database), 2 Ph.D. Theses, and 9 Master Theses. Forty-six oral and poster communications have been presented in international meetings and symposia.

Relying on an unprecedented systematic exploration of the Antarctic deep sea and on new comprehensive biodiversity and biogeography syntheses, the BIANZO project substantially increased the knowledge of the nature and distribution of Antarctic benthic biodiversity.

The project contributed to the understanding of the role of biodiversity in the functioning of the Southern Ocean benthic ecosystems by focusing on the functional niches occupied by representatives of the three target groups, in particular their trophic niches and their integration in the benthic food web, as well as other functional aspects such as the role of size and biomass, habitat component, mode of life or mobility.

Comprehensive biodiversity databases have been developed by the BIANZO partners to compile, integrate and disseminate biodiversity information on the three target benthic groups and facilitate accurate species identification. The expertise gained by the partners allowed elaborating and proposing the SCAR-MarBIN initiative for managing and developing the Antarctic Marine Biodiversity Information at world level.

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