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SCIENCE FOR A SUSTAINABLE DEVELOPMENT

"Biodiversity of three representative groups of the Antarctic Zoobenthos - Coping with Change"

«BIANZO II»

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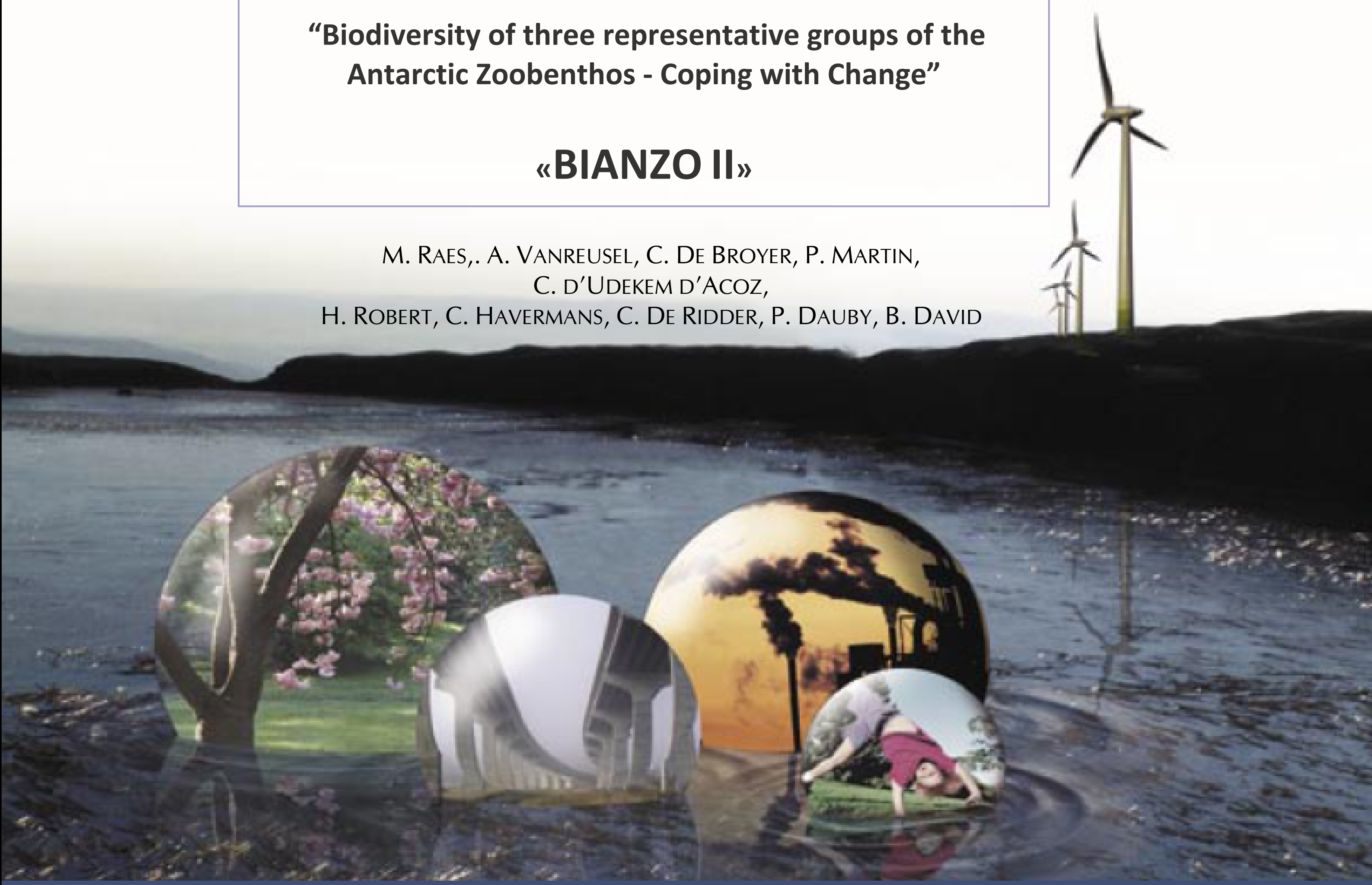

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SCIENCE FOR A SUSTAINABLE DEVELOPMENT
(SSD)

Antarctic Biodiversity

FINAL REPORT PHASE 1

Biodiversity of three representative groups of the Antarctic Zoobenthos - Coping with Change

"BIANZO II"

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BIODIVERSITY OF THREE REPRESENTATIVE GROUPS OF THE ANTARCTIC ZOOBENTHOS COPING WITH CHANGE

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Scientific context

Polar regions experience greater rates of climate change than any other region in the world. Their biota are highly adapted to the extreme environment they are living in and appear vulnerable to shifts in climate conditions. Antarctic marine species are especially sensitive to temperature variation as their physiology is set to a narrow range of temperatures. Because of the key-role of the Southern Ocean in the global system and the growing impact of global environmental change, it is crucial to establish comprehensive baseline information on Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. It is equally important to better understand the ecological role of biodiversity in the functioning of the Southern Ocean ecosystem and to assess how its structural and functional characteristics might be affected by a changing climate. These aspects are addressed in the BIANZO II project, by focusing on benthic organisms and communities, specifically representatives from three different size classes of the zoobenthos: Nematoda (meiobenthos), Amphipoda (macrobenthos) and Echinoidea (megabenthos).

BIANZO II has been accepted as an IPY activity (# 391) linked to CAML (IPY core activity). Its aims fully contribute to the objectives of the SCAR EBA programme. The BIANZO II consortium is also involved in the development of SCAR-MarBIN, which was initiated by the BIANZO I project, and is currently implemented by the Belgian Biodiversity Platform. All partners are contributing to the IPY ANDEEP-SYSTCO project, which is the continuation of the very successful ANDEEP collaboration. Additionally, UGent is involved in ClicOpen, also an IPY project (# 34).

Project aims

The BIANZO II project is built on three complementary work packages: NOWBIO, DYNABIO and FOREBIO. The first two work packages include core activities of phase 1, whereas the FOREBIO work package will be targeted specifically during phase 2.

The aim of NOWBIO is to characterize the biodiversity of the Antarctic zoobenthos and its distribution along bathymetric and geographical gradients, and to explain their underlying processes. Current knowledge of the Antarctic benthic biodiversity remains highly patchy in terms of coverage of geographical areas, bathymetric zones, habitats, taxonomic groups, ecofunctional groups, or size spectrum, and further exploration is required, focusing on unknown Antarctic areas and habitats (within the CAML framework). The investigation of deep-sea communities initiated during BIANZO I (SPSD II project) is sustained, while the benthic communities under the recently collapsed Larsen ice-shelves are studied for the first time.

The DYNABIO work package is focusing on the ecofunctional role of benthic biodiversity and the ability of the benthos to cope with change. The trophic position of the three benthic groups, their trophic diversity and plasticity is studied through complementary analyses (stomach contents, morphology, stable isotopes, and fatty acids) and experiments using ^{13}C labeled food sources. Impact of temperature-related change, including direct temperature impact, changes in food availability and composition, increased sedimentation and seawater acidification, on functional and structural aspects of the benthic communities are investigated mainly by an experimental approach. Additional data on the effects of warming, sedimentation, food quality and quantity change, and acidification (either carried out in the Antarctic or in the lab) are collected from ongoing or finished experiments.

Information collected in previous studies (ANTAR3, ANTAR4, BIANZO I) and in the first two workpackages of this project will also be used to develop a model on the possible changes in benthic communities due to global environmental change (FOREBIO WP).

The detailed objectives of the BIANZO II project (both phase 1 and phase 2) are:

1. to study benthic life under permanent ice shelves (former Larsen A & B);
2. to study benthic life in abyssal basins;
3. to assemble and map biogeographical and phylogeographical information for the selected taxa;
4. to provide basic biological and environmental data in order to forecast changes in biodiversity;
5. to continue the study of selected nematode genera at species level, in order to allow further evaluation of the level of endemism and local and regional species diversity patterns;
6. to continue a taxonomic revision of the Antarctic amphipod fauna;
7. to continue the synthesis of distribution and ecological data related to Antarctic amphipods;
8. to develop electronical interactive identification keys for Antarctic amphipods;
9. to analyse the biogeographic distributions of echinoids in the light of past and present environmental constraints;
10. to assess the ecological, evolutionary and functional significance of ectosymbiosis in cidaroid echinoids;
11. to assess evolutionary relationships with the surrounding oceans and world biodiversity on the basis of molecular phylogeny and phylogeography of key taxa (mainly amphipods);
12. to develop and consolidate the existing BIANZO databases and to contribute to the development of SCAR-MarBIN;
13. to study the trophic position of meiobenthos from the shallow subtidal to the deep sea;
14. to predict potential food-web effects of global change;
15. to assess the impact of temperature and temperature-related (*e.g.* food quality and quantity, sedimentation) changes on structural and functional aspects of meiobenthic communities;
16. to analyse the dependence of amphipod crustaceans on food availability;
17. to characterise food preferences of selected amphipod species, as well as trophic plasticity in communities along a latitudinal gradient;
18. to evaluate the ecological significance of the Antarctic shelf benthic scavenger assemblages of amphipods by combining feeding ecology and physiology of representative species;

19. to characterise the trophic categories of Antarctic and subantarctic echinoids;
20. to investigate the influence of food resources on the distribution of Antarctic and subantarctic echinoids, in order to determine their potential response to current and future environmental change in relation to their trophic categories;
21. to study the impact of seawater acidification on skeletal growth in larval and adult echinoids;
22. to integrate the collected results on potentially climate-related effects on the Antarctic zoobenthos;
23. to develop biological hypotheses and/or models simulating changes in marine benthic biodiversity in response to climatic scenarios that could occur in the XXIst century.

Expected results and products

1. an improved knowledge of the biogeography and community composition of the Antarctic benthic target groups (including ectosymbionts on cidaroid echinoids) **(phase 1)**;
2. an assessment of similarities/dissimilarities with oceans worldwide **(phase 1)**;
3. a better understanding of the trophic position of the three benthic groups in the food web from shelf to slope **(phase 1)**;
4. a better understanding of the trophic position of the three benthic groups in a chemo-autotrophic food web under a recently collapsed ice shelf **(phase 1)**;
5. an evaluation of the share of prokaryotes in benthic energy flows through detritivorous and necrophagous amphipods **(phase 1)**;
6. a first estimation of metabolic rates of scavenger amphipods based on respiration and excretion measurements **(phase 1)**;
7. the characterisation of the trophic categories of Antarctic echinoids and preliminary data on the feeding plasticity of selected taxa **(phase 1)**;
8. measures of the effects of seawater acidification on the skeletogenesis of selected cold temperate echinoid taxa **(phase 1 and 2)**;
9. measures of the effect of warming on Antarctic micro-, meio- and macrobenthos **(phase 2)**;
10. a review paper on the impacts of climate change on the Antarctic zoobenthos **(phase 2)**;
11. a model concerning macro-ecology of the three benthic groups **(phase 2)**;
12. a model concerning impacts of climate-related changes on the three benthic groups **(phase 2)**;
13. a model forecasting future changes in benthic biology **(phase 2)**.

Methodology

Collection of material

Collection of samples from previously unknown Antarctic areas and habitats has been carried out (1) in the deep Weddell and Scotia Sea (ANDEEP I-III campaigns: 2002, 2005; IPY ANDEEP-SYSTCO campaign: 2008), (2) in the formerly ice-covered Larsen A and B areas (IPY *Polarstern* ANT XXIII-8 expedition: 2006-07) (3) in the Bellingshausen Sea (BENTART'06 campaign 2005-5006) and (4) in Potter cove, a shallow bay near King Georges Island.

Meiobenthic samples were collected by means of a multicorer (shelf and deep sea) or by divers (shallow subtidal). Material was fixed with 4% buffered formalin. Vertical distribution of the meiofauna was investigated by slicing up the sediment core intended for community analysis in sediment slices of 1 cm (0-1; 1-2; 2-3; 3-4; 4-5 cm). Parallel sediment slices were kept frozen for later analysis of sediment granulometry and pigment content. Nematodes (200 per sediment core) were identified up to genus level. At shallow stations, samples were taken by scuba divers, at a depth of approx. 15 meter. Plastic cores with an internal diameter of 53mm were pushed into the sediment and closed with stoppers. These cores were brought up with 10cm of relatively undisturbed sediment, covered with ambient water. Other cores were filled only with water from close to the bottom, taken with a Niskin-bottle. The sampling strategy used for the meiobenthos allows assessing spatial variation in subtidal communities in relation to environmental parameters. In combination with data available at Ghent University (from the Atlantic part of the Southern Ocean and the Ross Sea), conclusions on the distribution patterns of the nematofauna and their possible origin and evolution can be drawn.

Samples of macro- and megafauna were collected with diverse sampling gear such as Agassiz trawls and Rauschert dredges. Various collections of amphipods are available for study, including the rich USARP material provided by the Smithsonian Institution, Washington.

Additional echinoid data will be provided by the network of collaborators to the Echinoid Database (**David *et al.*, 2005**), through examination of museum collections and new literature (this task will take advantage of the existing collaborations between Dijon, Santiago and San Francisco).

Biogeography (related to joint paper)

Nematode distribution data were compiled by Raes (unpubl.), amphipod geographic and bathymetric records as well as taxonomical information were taken from **De Broyer *et al.* (2007)**, and echinoid data were taken from **David *et al.* (2005)** and updated. These datasets are hosted in the BIANZO databases (Nemys.be, Ant'phipoda, Antarctic Echinids), accessible through the SCAR-MarBIN portal (www.scarmarbin.be/).

The whole Southern Ocean (*sensu lato*), extending from the Antarctic continent up to the Subtropical Convergence, and including sub-Antarctic islands and part of Patagonia (up to 41°S on the Southern Chile side), was considered. The area was partitioned in 30 (operational) geographic regions, more or less following the limits of the geographical entities used by **Linse *et al.* (2006)**, **Clarke *et al.* (2007a)**, **Barnes & Griffiths (2008)** and **Griffiths *et al.* (2009)** to allow a better comparison with previous biogeographical studies. Only the species occurring between 0 m to 1000 m depth were taken into account, except for the bathymetrical analysis, where all depth records were considered.

The bathymetric distribution analysis was performed with species occurring around the continent (incl. Antarctic Peninsula), excluding Scotia Arc and sub-Antarctic records. Bathymetric zones include (1) the shelf zone (0-1000 m), divided in three sub-zones: 0 to 100 m (phytal zone), 100 to 500 m and 500 to 1000 m depth; (2) the bathyal zone (1000-3000 m), divided into two sub-zones: 1000 to 2000 m and 2000 to 3000 m depth; and (3) the abyssal zone: >3000 m.

The PRIMER v6 software was used to perform multivariate analyses and determine faunal similarities between the different areas and depth zones. Non-transformed presence/absence data were used to build a similarity matrix based on Bray-Curtis similarities, which was then applied for a non-metric multidimensional scaling (nMDS) and cluster analysis, in order to display faunal similarities. A preliminary analysis of echinoid distribution was also performed with the Jaccard Index.

Morphological taxonomy

Nematodes. Identification of the nematodes occured under light microscopy, relying on the on-line identification key (NeMysKey©) developed within Nemys and the pictorial key of **Warwick *et al.* (1998)**. Transmission and scanning electron microscopy could be applied for detailed investigations.

Amphipods. New and poorly known species were described, selected families of the Antarctic fauna revised and all results synthesised as family monographs to contribute to the "Synopses of Antarctic Amphipoda", with the contribution of the Antarctic Amphipodologist Network (16 specialists; 12 countries). Electronic interactive keys for selected families were built using the Delta/Intkey software (delta-intkey.com/). Drawings of *Liljeborgia* were electronically inked with ADOBE Illustrator and a WACOM drawing board. During this process, the methods described in the literature were improved (e.g. the conception of art brushes for the illustration of spines and thick setae). Such innovations considerably speeded up the creation of taxonomic illustrations.

Echinoids. The recently published "Synopses of Antarctic Echinoids" and an interactive database (on CD-ROM) are the basic references to identify echinoid species. Any new records were added to the database, which in turn is interfaced with SCAR-Marbin.

Molecular taxonomy and phylogeny

Nematodes. Our collaboration within CEMOFE (Center for molecular phylogeny and evolution, UGent) allowed us to perform molecular analyses where needed.

Amphipods. Genetic characterization of selected deep-sea and shelf taxa was conducted by sequencing COI, 28S and 18S rDNA. The respective performance of COI and 28S rDNA as taxonomic markers for amphipods was evaluated to contribute to "Barcode of Life" (**Hebert *et al*., 2003**). Sequence analysis was performed by using classical and complementary methods for the reconstruction of phylogenetic trees (*e.g.* Maximum Parsimony, Maximum Likelihood, Bayesian Method). Molecular analyses aimed at assessing the importance of hidden biodiversity in the Antarctic amphipod fauna, by revealing the existence of cryptic species in generally assumed "circum-Antarctic" distributed species.

Echinoids. Molecular analyses were realized on selected taxa in order to detect cryptic species or to gather formerly separated geographic morphotypes.

Trophic position

Nematodes. Stable isotopes ($\delta^{13}C$; $\delta^{15}N$: different C-sources) and fatty acids (PUFAs: selective take-up of organic matter) analysis and enrichment experiments with labeled food sources have been conducted in shallow water and the deep sea. In shallow water systems, cores were collected by scuba divers and incubated under controlled conditions in the lab. For the shelf and deep sea, cores were sampled with a multicorer. Comparison of stable isotope ratios with potential food sources (sedimentary material, phytoplankton, bacteria, phytodetritus, other benthic components...), collected in bulk, could also be carried out. Material from the deep sea (ANDEEP-SYSTCO), shelf (Larsen) and shallow subtidal (King George Island) is available. All samples were frozen (-20°C) for further analysis.

Amphipods. The promising results obtained during BIANZO I on the trophic position of amphipods, were refined by studying new selected species, with emphasis on scavengers. Investigations included gut content analyses, morphological observations and tracing techniques such as stable isotope or fatty acid analyses to identify the origin of food. The importance of prokaryotes in the digestive tract of amphipods was assessed by epifluorescence or SE microscopy, and by immunological or DNA techniques. Laboratory experiments were performed with labeled bacteria in order to quantify ingestion rates.

Echinoids. In literature, regular echinoids are considered as opportunistic browsers. Although they feed on what is available in their habitat, they usually display some food preferences. Various taxa belong to particular trophic groups: carnivores (Cidaroidea) versus opportunists (many Euechinoidea). Compared to specialized echinoids, the generalists are, at first sight, good candidates to acclimatize to new trophic resources. The objectives are to identify tolerance ranges of Antarctic echinoids in order to propose potential responses to environmental changes (biological filters for FOREBIO, see workpackage 3). Therefore, the feeding behaviours of generalists (Echinidae) and of specialists (Cidaridae) were characterized through three series of analyses: (1) a qualitative inventory of gut content through microscopic observations, (2) a stable isotope analysis (gut content, gonads, muscles) and (3) the investigation of genetic features of the digestive microflora by molecular tools (DGGE and 16S rRNA cloning). Echinoids were dissected on board. For microscopic and genetic observations, gut content samples were isolated and fixed in ethanol 100%. For isotopic analyses, gut contents, gonads and muscles (Aristotle's lantern musculature) were isolated and kept in liquid nitrogen (at -27°C).

Experiments on the ability of the Antarctic zoobenthos to cope with change

Nematodes. The ability of the Antarctic meiobenthos to cope with warming was tested in shallow water systems. Cores collected by scuba divers were incubated under different temperature conditions for a period of 14 days. Benthic respiration rates were investigated. The samples are analysed for several structural and functional, community-related parameters, such as densities, vertical distribution, individual and total biomass, nematode community composition, diversity and nutrient fluxes.

Amphipods. Changes in food supply from the water column to the benthos (seasonal or long-term) could force amphipods into a "trophic shift". Feeding experiments were set-up in aquaria, mainly with scavenging species, using different labeled substrates. In parallel, measurements of the energy demand by scavengers (metabolic activity, respiration and body composition) were performed to evaluate the influence of trophic stress (*e.g.* climatic, human-induced…) on the general energy budget of individuals. These results, together with literature information, will be integrated in a balanced model of scavenger assemblage trophic links and energy flows, showing the significance of the scavengers' share in overall benthic energy flow and the potential sensitivity of the system to changes in food supply.

Echinoids. The impact of acidification on skeletal growth of adults and larvae was assessed firstly on easy-to-obtain temperate and boreal species, and secondly on Antarctic and Magellanic species, under altered sea-water chemistry. Larvae were grown following standard procedures under normal and altered sea-water composition, covering a range from pre-industrial CO_2 levels (280 ppm) to approximately triple pre-industrial values (750 ppm), (**Riebesell *et al.*, 2000**). Larval development was characterized using embryotoxicity protocols (**Warnau *et al.*, 1996**), to distinguish between normal and altered general morphologies. Spicule development was quantified using image analysis of micrographs. Morphology of spicules was monitored by SEM. Growth of adult urchins was measured in fast-growing young specimens reared in closed-circuit aquaria with normal and altered sea water chemistry. Test growth (4 months) and spine regeneration (2 weeks) was determined, the former by measuring the immerged weight, the latter by measuring regenerates under the microscope. Possible alterations of mechanical properties (Young modulus and fracture force) of the skeleton were assessed by bending tests of spines grown during the experiment (**Schinner *et al.*, 1995**). For both larvae and adults, dose-response relationships were established for the different dependent variables under study, related to carbonate and dissolved CO_2 concentrations.

Building the model for FOREBIO

Different steps:

1. Build the frame for the GIS:
- georeference data (latitude, longitude, depth)
- a template for the other data (build the layers)
2. Add shared data:
- edaphic data (sediments)
- oceanographic (currents, saturation horizon for aragonite and calcite, O_2 concentration…)
- climatic data (SST at different months, SbottomT, predictions according to different scenarios)
3. Add taxon-specific biological data for the selected taxa (taxonomy, ecology, phylogeny,

physiology)
4. Run the GIS:
- produce macro-ecological outputs: what are the present large-scale patterns of distribution, and how are they related to climatic and edaphic parameters?
- forecast future changes on the basis of different climatic scenarios

This process implies:

1. Gathering biological, abiotic and climatic information: existing data from literature and databases (*e.g.* those developed during BIANZO I), data collected during the first phase of BIANZO II and new data: species inventory, patterns of current and past distributions, saturation horizon for aragonite and calcite, O_2 concentration. Climatic and abiotic data include SST, bottom temperature, currents, sediment distribution…
2. Defining potential influencing factors related to climate change (*filters*). This includes the main parameters driving ecosystem alteration (climatic variables such as the increase in atmospheric CO_2, warming and acidification of the sea...) and biological variables indicative of the sensitivity of organisms to change (diet ranges, dispersion mode...).
3. Generating hypotheses based on the present day situation and expected climatic changes. We will propose scenarios of distribution based on the *filters* applied. We aim to predict (1) whether 10%, 50% or 80% of the fauna will be affected, (2) the extent of migrations than extinctions, (3) whether the different clades are affected the same way, (4) overall changes in diversity, densities and biomass.
4. Build a biogeographic model. Various biogeographic models allow to predict how organisms may respond to climatic changes are already available (**Cheddadi *et al.*, 2001**; **Cramer, 2002**). They rely on mechanistic approaches linking biological processes to environmental conditions, and are based on georeferenced distribution ranges, and on functional attributes.

Scientific results

The scientific results of all research groups in our consortium are brought together here in a few paragraphs, related to our 3 work packages. All results within each paragraph are integrated and connected to each other. At the end of this chapter, the project's results are briefly summarized across the three work packages.

LIFE ON THE SOUTHERN OCEAN FLOOR

Biology, biogeography and taxonomy of the Antarctic zoobenthos

Structural and functional aspects of Antarctic deep-sea meiobenthic communities

In order to unravel the role of meiofauna in the C-flow through benthic deep-sea sediments of the Antarctic in relation to their biodiversity, and the link between meiobenthic diversity and function, it is essential to reveal interactions in the benthic food web and the trophic position of different meiobenthic taxa and functional groups at locations with contrasting food input. It remains unclear what drives the high local biodiversity of small benthic taxa in the deep-sea, but a relation in productivity is possible. A repeated sampling near the Southern Polar Front and more southward allows to estimate the variation in local biodiversity in relation to changing productivity levels. In total, 6 deep-sea stations were sampled in the Southern Ocean along a N-S transect from 52°S 0°W to 70°S 03°W during the ANT XXIV-2 expedition on board of RV *Polarstern* (11/2007-02/2008). Multiple core samples were collected to study meiobenthic community structure, stable isotope and lipid signatures and environmental variables in the sediment (granulometry, total organic carbon and chloroplastic pigments). This study contributes to the generalised energy-flux model and food web study, an objective of the ANDEEP-SYSTCO project.

Little is known about nematode trophic status and functioning in deep-sea sediments. Previous studies showed that nematode standing stock in deep-sea sediments is closely linked to organic matter input. Their response to seasonally varying phytodetritus deposition seems often delayed in time. There is growing evidence that nematodes feed on bacteria rather than using fresh phytodetritus as a food source. In order to test the uptake rate and potential preference for microbial- related food sources, an *ex situ* enrichment experiment was performed during the ANT XXIV-2 expedition on board of RV *Polarstern* (11/2007-02/2008). Samples were obtained from Maud Rise (2120 m depth) and injected with several ^{13}C labeled substrates to label the natural microbiota. When grazing on bacteria took place, the ^{13}C label can be traced in the nematodes. Together with a natural biomarker analysis of selected genera, an integrated view on the degree of selectivity and food preferences of nematodes for particular components of the deep-sea ecosystem will be obtained. A parallel experiment at 1200 m depth in the Hausgarten site (Arctic Ocean) revealed little or no uptake of bacteria by nematodes (Ingels et al, submitted).

Feeding experiments with nematodes

In November 2007, a laboratory feeding experiment was carried out at the Dallmann laboratory, Jubany station, located near the coast of Potter Cove on King George Island, close to the Antarctic Peninsula.

In this experiment, the uptake of two labelled food sources was investigated, in order to identify food selectivity and preferences.

The sediment cores used for this experiment were taken on 19/11/2007. ^{13}C-labelled diatoms (food source 1) and bacteria (food source 2) were freeze-dried in the laboratory in Ghent beforehand. Six sediment cores received a fixed amount of 30mg of labelled diatoms and six other cores received 30mg of labelled bacteria. All cores were incubated at 0°C for 10 days, and aerated. After 5 and 10 days, the cores were sampled and sliced as follows: 0-1cm, 1-2cm, 2-5cm, 5-10cm. From these sediment samples, meiofauna (esp. nematodes) will be picked out later this year for stable isotopes analysis.

More data will become available when the sediment of the incubated cores is analysed in more detail. This sediment was sampled at the beginning and the end of the incubation period.

First results on the natural community indicate high total abundances of meiofauna when compared to other temperate shallow water systems (**Vanhove *et al.*, 1998**). Three replicates (from 15 m depth) were analyzed as a preliminary survey of the sampled area in Potter Cove. The most abundant taxa were nematodes (92.52%), nauplii (4.56%) and copepods (1.83%) (**Table 1**). Nematode abundances were highly variable between replicates, ranging from 3287 to 10042 ind./10 cm^2, with a mean value of 6315 ind./10 cm^2. Similar densities have been recorded by **Vanhove *et al.* (2000)** in Factory Cove (Signy Island), where they fluctuated between 700 and 18800 ind./10 cm^2 (average 6200 ind./10 cm^2). Copepod abundances were similar to those reported under summer conditions in Potter Cove by **Veit-Köhler & Fuentes (2007)** (100-200 ind./10 cm^2). In our samples, Cumacea were also relatively abundant (0.46%), which is consistent with data from **Kowalke & Abele (1998)**, who found a soft-bottom macro-infaunal community where Cumacea comprised about 60% of the total community in the inner cove area of Potter Cove. Cumacea are known as deposit feeders, consuming sedimentary organic matter and bacteria. Fresh-water melt flow due to glacier action, and consequent sediment run-off, may be the reason of the relative high abundance of this taxon (**Kowalke & Abele, 1998**).

Taxon	Rel ab. (%)
Nematoda	92,52
Nauplii+Copepodites	4,57
Copepodes	1,83
Cumacea	0,46
Polychaeta	0,26
Holothuroidea	0,09
Hydrozoa	0,05
Amphipoda	0,05
Isopoda	0,05
Ostracoda	0,04
OTHER	0,03
Turbellaria	0,02
Bivalvia	0,01
Sipunculida	0,01
Gastropoda	0,01
Tanaidacea	0,01

Table 1. Meiofauna taxa, relative abundances.

Genus	Trophic guild	Rel. ab. (%)
Aponema	2A	31,06
Daptonema	1B	13,82
Amphimonhystrella	1B	12,67
Halalaimus	1A	12,02
Desmolaimus	1B	4,37
Dichromadora	2A	3,31
Metasphaerolaimus	2B	2,68
Trichotheristus	1B	2,66
Metalinhomoeus	1B	2,66
Chromadorita	2A	1,79
Retrotheristus	1B	1,76
Acantholaimus	2A	1,43
Anticoma	1B	1,33
Prochromadorella	2A	1,01
Sabatieria	1B	0,87
Linhomoeus	1B	0,70
Oxystomina	1A	0,65
Paramonhystera	1B	0,59
Aegialoalaimus	1A	0,54
Neochromadora	2A	0,51

Table 2. Nematode genera, relative abundances.

The nematode assemblage comprises a total of 44 genera. A list with the most abundant genera is reported in **Table 2**. *Aponema*, *Daptonema, Amphimonhystrella* and *Halalaimus* were dominant, constituting more than 60% of the total nematode community. *Daptonema* and *Aponema* were also reported by **Vanhove *et al.* (1998, 2000)** to represent more than 60% of the whole nematode assemblage of Factory Cove, followed by *Neochromadora* and *Sabatieria*. The dominance of *Aponema* in our samples can be related to the high abundance of benthic diatoms (personal observation) and, probably, to the summer phytoplankton bloom in November/December (early summer). *Daptonema* is known as an *epistrate feeder* and is in some way an “opportunistic genus*”*, with a particular preference for diatoms as a food source, although it can easily switch to bacteria. Its densities have been positively correlated with the pico- and nano-fraction of the water pigment by **Vanhove *et al.* (2000)**, and it was the dominant genus at Factory Cove throughout the year. Food appears not to be a limiting factor in Antarctic shallow water systems (**Vanhove *et al.*, 2000**; **Smith *et al.*, 2006**), and some hypotheses stress the importance of the microbial loop during winter times. In general, the assemblage found in this preliminary investigation appears to be similar to assemblages found in other shallow subtidal environments with fine sands (**Heip *et al.*, 1985**; **Juario, 1975**; **Vanreusel, 1990**), with a dominance of Xyalidae (*e.g. Daptonema*), Microlaimidae (*e.g. Aponema*), Chromadoridae (*e.g. Neochromadora*), and Comesomatide (*e.g. Sabatieria*).

In order to test the set-up of the experiment, and to enable a bipolar comparison, analogous experiments were carried out at Koldewey station, Spitsbergen (78°55'N; 11°56'E).

Systematics and phylogeography of Southern Ocean amphipods

A thorough descriptive study of *Liljeborgia* species of the Southern Ocean was carried out. It should become the foundation for biogeographical and phylogenetic studies of this genus, and a model for phylogeographic studies of Southern Ocean amphipods in general. *Liljeborgia* is an ideal test group because it is present both in shallow and deep water and because the number of species is neither too small nor too large. Such a monograph will also be of key importance for ecological studies requiring precise species identification.

During the ANTXXIII-8 (November 2007-January 2008) and ANDEEP-SYSTCO (November 2008-January 2009) campaigns, new samples of *Liljeborgia* were collected for morphological and molecular studies. Extensive *Liljeborgia* material from various museums, collected between 10 and 4000 m depth, was brought together for morphological studies. Part of the material of the Museum of Verona was also examined. The twelve valid species previously recorded in the Southern Ocean were redescribed as their previous descriptions were outdated and/or very poor. Based on material from different museums, thirteen new species were described and named, two new species were described but not named (the material was in a bad condition), one species proved to be invalid and the records of two species in the Southern Ocean were considered as resulting from erroneous identifications.

Antarctic and sub-Antarctic species could be divided into two morphological groups. Species from the continental shelf were often closely related with abyssal species, suggesting recent faunal exchanges between depth layers. The Antarctic, sub-Antarctic archipelagos and Magellanic region were populated by different species of *Liljeborgia*. In Antarctica, some species were only known from the Scotia Arc and islands of the Antarctic Peninsula, while others were only found in the eastern Weddell Sea. However, due to the limited amount of material available for some species, it was not possible to definitively confirm that such species are local endemics within true Antarctic waters. All these data were included in two large monographs (**d'Udekem d'Acoz, 2008**; **d'Udekem d'Acoz, *submitted***). A number of further putative new species were only superficially examined at this stage; they have not yet been described and were not treated in the first two monographs.

All Antarctic and sub-Antarctic shelf species of the *georgiana* group had eyes, in contrast to Arctic and sub-Arctic shelf species, that have no eyes. This suggests an origin of the group on the Southern Ocean shelf, a northwards migration through the abysses (with a complete loss of eyes) and a recolonization of the northern seas' shelf, without recovery of the visual organs (**d'Udekem d'Acoz & Vader, *in press***).

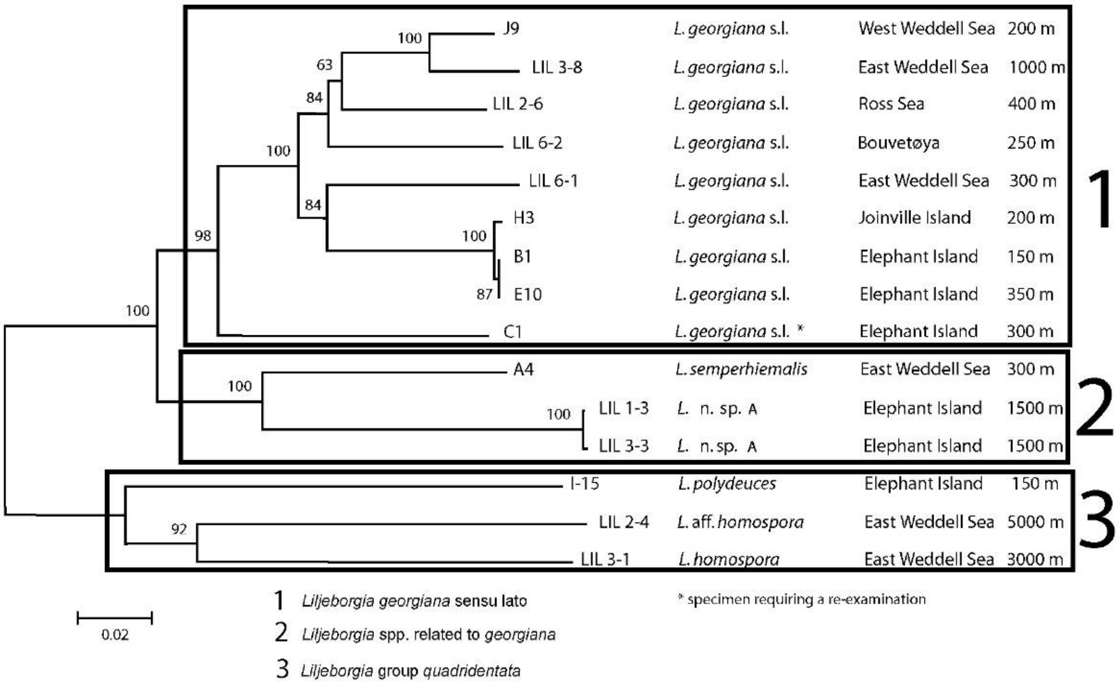

Fig. 1. Neighbour-Joining tree for the Antarctic *Liljeborgia*.

Recent molecular analyses revealed that a number of so-called "circum-Antarctic" benthic crustacean species are a complex of cryptic species with a restricted geographic distribution. In order to investigate these issues for the genus *Liljeborgia*, fragments of the cytochrome c oxidase subunit I gene were sequenced and used as DNA barcode. Twenty-five specimens were successfully sequenced so far and were clustered in a Neighbour-Joining tree (**Fig. 1**; Kimura two-parameter model), which focuses on the georgiana species group.

In the morphospecies *L. georgiana*, specimens from the same area (e.g. the Ross Sea or Bouvet Island) have the same haplotype. In contrast, distant populations are genetically distinct, as a probable result of the low dispersal capacity of *Liljeborgia* species. This result sharply contrasts with orchomenid lysianassoids, in which some highly mobile species exhibit a remarkable genetic homogeneity throughout the Southern Ocean. Interestingly, the specimens initially identified as *'L. georgiana'* from the continental slope (1,500 m) are genetically very distinct from other shelf samples; a related but clearly distinct morphospecies *(L. semperhiemalis)* is positioned in between. A second examination of the deep *'L. georgiana'* has revealed small but significant differences with *L. georgiana* and it will be described as a new species by **d'Udekem d'Acoz (*submitted*)**. The different taxonomic units in the genus *Liljeborgia* (morphospecies and different haplotypes of the same species) seem to have a regional rather than a global distribution.

In the framework of the ongoing revision of the Southern Ocean amphipod fauna, undertaken with the collaboration of the "Antarctic Amphipodologists Network", two new families, the Alicellidae fam. nov. and the Valettiopsidae fam. nov., are described based on genera traditionally considered as lysianassoid amphipods. The Alicellidae fam. nov. are deep-sea scavengers often associated with thermal vents. The family contains 6 genera: *Alicella* Chevreux, 1899; *Apotectonia* Barnard & Ingram, 1990; *Diatectonia* Barnard & Ingram, 1990; *Paralicella* Chevreux, 1908; *Tectovalopsis* Barnard & Ingram, 1990; *Transtectonia* Barnard & Ingram, 1990. The Valettiopsidae fam. nov. are deep-sea scavenging amphipods that contain two genera, *Valettiopsis* Holmes, 1908 and *Valettietta* Lincoln & Thurston, 1983 (**Lowry & De Broyer, *in press***).

An up-to-date catalogue of Antarctic and sub-Antarctic Phoxocephalidae has been established, including 35 species. An extensive list of bibliographical references with synonymy, detailed information on geographic and bathymetric distribution, ecological data, museum locations of type-material, remarks on taxonomic and biogeographical status, are provided for each species. The catalogue is based on taxonomic and ecological literature until 31 December 2006. Additional unpublished records of species from the Antarctic and sub-Antarctic collections at the Alfred Wegener Institut für Polar- und Meeresforschung, Bremerhaven, and at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, have been included. The taxonomic status of all Southern Ocean species has been checked. Species allocated to the genera *Paraphoxus* and *Parharpinia*, and *Fuegiphoxus uncinatus* require further study to clarify genus allocation. Most of the Southern Ocean phoxocephalids have a wide bathymetric distribution, equally present in the Antarctic and sub-Antarctic regions. The highest species richness is found above 200 meters depth in the sub-Antarctic region. Of 35 phoxocephalid species reported, 25 are endemic to the Southern Ocean s. lat., 15 are endemic to the Antarctic region and 6 are endemic to the sub-Antarctic region, the latter distributed only in the Magellan province. Endemicity at genus level attains 22% for the whole Southern Ocean, with 3 genera restricted to the Magellan province and one genus to the West Antarctic, Magellan and sub-Antarctic island provinces. Habitat and substrate preferences, dietary and burrowing behaviour are scarcely known for most of the phoxocephalid species from the Southern Ocean (**Alonso de Pina *et al.*, 2008**).

Another study focuses on the evolutionary relationships between shelf and deep-sea taxa. For this aim, a combined morphological and molecular phylogeny of Lysianassid taxa will be constructed, using both nuclear (28S and 18S rDNA) and mitochondrial markers (COI, 12S rRNA) in order to test the "emergence" (emergence of eurybathic species originating from adjacent deep-sea basins) or "submergence" (migration from the continental shelf followed by radiation in the deep-sea) hypotheses. The target taxon of this study is an orchomenid complex of genera (Lysianassoidea) that comprises the genera *Orchomene* Boeck, 1871, *Orchomenyx* De Broyer, 1984, *Orchomenella* Sars 1895 *Abyssorchomene* De Broyer, 1984, *Falklandia* De Broyer, 1985, and *Pseudorchomene* Schellenberg, 1926. Until now, DNA was extracted from 240 specimens. Amplification of the mitochondrial COI gene was carried out with the polymerase chain reaction using the universal primers LCO1490 and HCO2198 (**Folmer *et al.*, 1994**). For the 28S, primers 28F and 28R designed by **Hou *et al.* (2007)** were used for amplification. PCR products were sequenced bidirectionally with ABI BigDye terminator sequencing protocols. The sequencing of COI was successful for 127 of the 240 extracted specimens. For 28S rDNA, the sequencing was successful for 42 of the 45 samples. Alignments and phylogenetic analyses are still in progress for these sequences. For the COI gene, sequences were obtained for at least 24 different taxa within the orchomenid complex. Sequence divergences were calculated using the Kimura 2-Parameter distance model (**Kimura, 1980**) and a Neighbour-Joining tree of distances (**Saitou & Nei, 1987**) was created using MEGA version 4 (**Tamura *et al.*, 2007**).

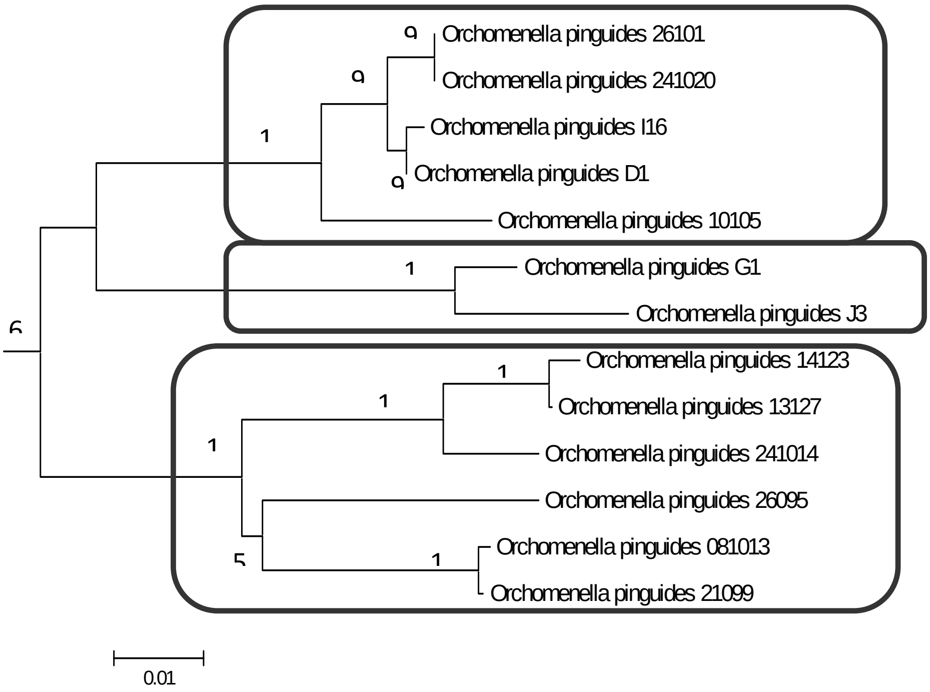

Fig. 2. Part of Neighbour-Joining tree showing three clusters of *O. (O.) pinguides* (in red). Bootstrap values (%) at each node indicate the support for the different clades.

The average intraspecific distance between specimens of known species was 0.003 or 0.3% and the average interspecific distance was 0.116 or 11.6%. The Neighbour-Joining analysis permitted to detect and confirm new species, e.g. *Abyssorchomene* sp.2 and *Pseudorchomene* “corrugated”, which were already morphologically suggested as putative new species. Moreover, in *Orchomenella (Orchomenella) pinguides* at least three different clusters were detected (**Fig. 2**), separated by high intraspecific distances (9.4-11.5%), in the same range as observed interspecific distances. Moreover, bootstrap values gave a high support to the three clusters with values of 100% for each node. When considering the sample locations, we noticed that some specimens of different clusters occurred at the same sample site. The sympatry of the three distinct lineages of *O. (O.) pinguides*, together with the high genetic distances, may indicate reproductive isolation. We conclude that *O.(O.) pinguides* is probably a complex of cryptic, sympatric species, which merits a detailed morphological analysis.
The Neighbour-Joining method could also detect a similar pattern in *Orchomenella (Orchomenopsis) cavimanus*. Morphological analyses already showed interspecific rather than intraspecific morphological variations between populations. On the contrary, in other species, such as *Abyssorchomene plebs*, an extremely low genetic diversity (0.2%) could be observed between different specimens from remote sample locations and from shelf and abyssal depths. In conclusion, the COI barcoding permitted us to distinguish between possible cryptic species complexes and possible circum-Antarctic species. The detection of cryptic species may have some influence of the current views on species richness and distributions of species belonging to the most abundant group of amphipods in the Southern Ocean. Moreover, a more accurate investigation of the geographical and bathymetric distributions might be very useful for the examination of their response to future climate change. Finally, the DNA barcoding permitted to detect some new species, which contributed to a more accurate estimation of the species diversity within the orchomenid complex.

Trophic and metabolic aspects of amphipods

Eight species of peracarids have been analysed to determine their fatty acid composition. Hierarchical clustering and multi-dimensional scaling (MDS) were performed based on Bray-Curtis similarity, applied to untransforned percentage composition data (PRIMER v5; **Clarke & Warwick, 1994**). Because pelagic species were available, they were included to be compared with their benthic homologues. Statistical analysis separated 8 species into 3 distinct groups at the 80% similarity level (**Table 3**). As expected, the first cluster combines the pelagic species *Cyllopus lucasi* and *Hyperiella dilatata*. Both species share the highest proportion of docosahexaenoic acid (DHA) which is consistent with a carnivorous or omnivorous diet on flagellates. The PUFA 18 :4 (n-3), which dominates in the species *Ampelisca richardsoni* (24%), is a major FA in the prymnesiophyte *Isochrisis* sp and the cryptomonad *Chroosomas salina* (**Phleger *et al.*, 2002** and references therein). As already demonstrated in **Nyssen *et al.* (2005)**, scavengers in the third cluster are typically characterised by a very high proportion of MUFAs composed of 18C. Various hypotheses might explain the scavenger's particular fatty acid composition as a very intensive *de novo* biosynthesis. However, a detailed analysis of the underlying mechanism will be an important task to be developed in the near future.

	CLUSTER 1 (89,4%)	CLUSTER 2 (92,3%)	CLUSTER 3 (80,4 %)
CLUSTER 1	-	**33%** 18:4n-3 / 22 :6n-3	**45,7%** 18 :1n-9+7 / 22 :6n-3
CLUSTER 2		-	**49,2%** 18:1n-9+7 / 18 :4n-3
CLUSTER 3			-

Table 3. Results of SIMPER analysis : within group similarity (% in parenthesis), average dissimilarity (%) and separating fatty acids (FA) (most discriminant).

An experiment on trophic level change in three Antarctic scavengers indicates that the speed of adjustment in body tissue stable isotope ratio as a reaction to a new food source differs between species and depends on lifestyle. This hasn't been revealed before. Fourteen amphipod species, belonging to two families drastically different in trophic habit (Lysiannassidae: mainly opportunistic with a great trend to scavenging; Iphimediidae: specialists consuming particular prey such as hydrozoans and bryozoans), and one isopod species were analysed for stable isotope ratios. Results will be presented at the July 2009 SCAR International Polar Biology Symposium (Sapporo, Japan).

Metabolic rate is a proxy of overall energy expenditure (production + respiration + excretion) of an organism, and hence it is one possible way of estimating energy flow through the individual organism. Oxygen consumption rates of unfed (deprived of food for at least three days), unstressed and inactive animals were used as a proxy of standard metabolic rate. Oxygen content was assessed using a modified intermitted flow system and oxygen microoptodes connected to a Microx TX 3–array (® PreSens GmbH, Neuweiler, Germany. During the last cruise, certain expected amphipod species were surprisingly not found. So, owing to the fact that mainly isopod species have been sampled in adequate supply, nearly all experiments have been focused on those. One amphipod (*Eurythenes gryllus*) and two isopods (*Glyptonotus antarcticus* and *Natatolana oculata*) have been used in experiments.

The Specific Dynamic Activity (SDA) experiment was designed to provide a detailed picture of the post-prandial metabolism increase. We encountered many problems with the physiological experiments. First, only experiments implying isopods lead to valid results. Data for *E. gryllus* have been discarded because of total absence of feeding. So, we changed the protocol and extended starvation as well as feeding periods. Even after all changes made, non-feeding events repeated several times in all species. Secondly, we did encounter technical problems with the water circulating system. During some experimental runs, the diminution of oxygen was more pronounced in the reference chamber than in chambers with animals. This response, probably due to bacteria in the system, was dealt with by cleaning and renewal of the water. Nevertheless, the problem persisted, so all components (tubes, optodes, chambers) had been replaced and the system was rebuilt. The experiments provided the first metabolic data available for those Antarctic amphipods. The first striking feature we registered with scavengers was their ability to cope with long periods of starvation. For the experiments with *N. oculata*, we let the animals starve for six weeks (the maximum observed is in the order of several months), and some specimens did not feed even after such a long period without food. Our specific dynamic action (SDA) results for *G. antarcticus* are in good agreement with the scarce existing literature. A publication of those results is in preparation and will be submitted to a peer-reviewed journal in the near future.

The digestive tract of 7 species was dissected and prepared for SEM observation. Results are underway.

Trophic studies on echinoids

Preliminary results have been obtained by Marquet (Master Thesis, 2007) through the comparison of three series of echinoid samples (all from the family Echinidae): (1) *Paracentrotus lividus* from Brittany, (2) *Paracentrotus lividus* from the Mediterranean Sea and (3) *Sterechinus antarcticus* from the Antarctic Peninsula (BENTART-06; Margarita Bay). Results based on the nature of the gut content and on isotope analyses indicate that *Sterechinus antarcticus* from the Antarctic Peninsula is a carnivore and deposit feeder, feeding mainly on animals and sediments. In contrast, the European species *Paracentrotus lividus* feeds mainly on vegetal material. Interestingly, *P. lividus* displays some flexibility in its feeding behaviour along the latitudinal gradient (Brittany versus Mediterranean Sea): the Mediterranean individuals are strictly vegetarian while those from Brittany display a wider spectrum of food sources, feeding both on animals and plants/algae.

Pierre Becker (Post-doctoral fellow supported by the BIANZOII contract) investigated a larger set of samples collected along the Antarctic Peninsula (depth ranges: from 100 to 350 meters) during the campaigns BENTART 06 (R.V. Hesperides) and ANT XXIII/8 (2007; R.V. Polarstern). He focused on one species of Echinidae *Sterechinus antarcticus* (from 8 stations; **Table 4**) and three species of Cidaridae (*Ctenocidaris gigantea, Ctenocidaris perrieri* and *Notocidaris mortenseni*) (**Table 5**). The gut content, gut microflora and stable isotopes analyses of *S. antarcticus* (4-5 individuals/station) were characterized. For the Cidaridae species, the gut content was observed for 3 individuals/station. Molecular techniques were applied on *N. mortenseni* (3 individuals from PS69/702-9) and *C. perrieri* (2 individuals from PA39-1), but no bacterial DNA could be amplified from the gut content.

	Station	Locality	Position (start)	Mean depth (m)	Trawl	Sample
Ant XXIII/8	PS69/654-6	Elephant Island	61°22.80’S/ 56°03.84’W	342.5	Small Agassiz trawl	61228-10
	PS69/685-1	Joinville Island	62°34.61’S/ 55°39.38’W	162.8	Bottom trawl	70104-1
	PS69/702-9	Larsen B South	65°57.85’S/ 60°28.42’W	218.2	Large Agassiz trawl	70112-3
	PS69/703-2	Larsen B West	65°30.81’S/ 61°40.06’W	339.0	Bottom trawl	70113-1
	PS69/725-6	Larsen A	64°54.80’S/ 60°37.46’W	180.6	Large Agassiz trawl	70122-2
Bentart	PA39-2	Margarita Bay		160	Large Agassiz trawl	070206-10 to 14
	PA43	Adelaide Island		250	Large Agassiz trawl	110206-3 to 4
	LOW47	Bransfield Strait		115	Large Agassiz trawl	120206-2 to 6

Table 4. List of stations analysed for *Sterechinus antarcticus*.

	Species	Station	Locality	Position (start)	Mean depth (m)	Trawl	Sample
Ant XXIII/8	*Ctenocidaris gigantea*	PS69/689-3	Joinville Island	62°27.28'S/ 55°20.74'W	216.9	Small Agassiz trawl	70104-3
	Notocidaris mortenseni	PS69/702-9	Larsen B South	65°57.85'S/ 60°28.42'W	218.2	Large Agassiz trawl	70112-3
		PS69/721-2	Larsen B North	65°55.41'S/ 60°34.01'W	296.6	Large Agassiz trawl	70121-2
Bentart	*Ctenocidaris perrieri*	PA39-1	Margarita Bay		160	Large Agassiz trawl	070206-26 and 28

Table 5. List of the stations analysed for Cidaridae.

Becker's results show that all sampled *S. antarcticus* individuals had sediment pellets in their digestive tube but additional fragments of animals (crustaceans, bryozoans, hydrozoans and skeletal parts of other invertebrates) may also occur. In Cidaridae (*C. gigantea*, *C. perrieri* and *N. mortenseni*), the digestive contents always consist of animal remains (hydrozoans and bryozoans). Stable isotope analyses (*S. antarcticus*) show that delta ^{13}C values of the gut contents (-24.12 ± 0.92) are in the range of various marine animals including crustaceans, cnidarians and polychaetes but far from macroalgae (-30 to -31). Interestingly, there is a marked enrichment of ^{13}C in the gonads (-19.43 ± 0.67) that could be indicative of a broader source of nutriments (i.e. sediments). Stable-nitrogen isotope ratio (delta ^{15}N) of the muscles (6.47 ± 0.53) corresponds to scavenging marine animals such as ophiuroids and isopods. These results stress the importance of sediments and its associated organic matter in the diet of *S. antarcticus*. Bacterial communities associated with the gut of *S. antarcticus* were characterized by DGGE (Denaturing Gradient Gel Electrophoresis) and 16S rRNA gene cloning analyses. DGGE was used to compare bacterial diversity of the microflora of sea urchins from different stations (bacterial DNA from the gut of three individuals was pooled for each station). **Fig. 3** illustrates a DGGE gel obtained from the gut microflora of *S. antarcticus* at seven stations near the Antarctic Peninsula: Elephant Island (654-6), Joinville Island (685-1), Larsen B South (702-9), Larsen B West (703-2), Larsen A (725-6), Margarita Bay (PA39-2) and Bransfield Strait (LOW47). No bacterial DNA was amplified from samples of Adelaide Island (station PA43). A replicate gel was performed, with an identical pattern. Ten phylotypes were revealed on the gels. Only one phylotype (band 1) was present in gut contents from all stations. Other phylotypes were detected in one to five stations. The bacterial microflora thus varies according to sites and is consequently not specific.

Cloning results are summarized in **Table 6**. Three clone libraries were obtained from the gut microflora of *S. antarcticus* collected at Elephant Island (72 clones, 43% of coverage value), Larsen B West (40 clones, 65% of coverage value) and Margarita Bay (40 clones, 20% of coverage value). Two samples were pooled for construction of each library. Sequences with at least 97% of similarity were gathered, giving 78 operational taxonomic units (OTU). All OTUs were assigned to one or two of the three stations but never to all stations. The most numerous sequences from all libraries belonged to the *Proteobacteria* and particularly *Gamma*- and *Alphaproteobacteria*. *Planctomycetes* was the second most represented group but accounted only for 9% of the total clones and was absent from Larsen B West. Interestingly, about two thirds of the OTUs were related to bacteria from marine sediments. These sediments were of various origins including Wadden Sea, Yellow Sea, Baltic Sea, Bering Sea and Arctic Ocean. OTU 20, accounting for 10 clones from Elephant Island and Larsen B West, was close (96-98% similarity) to *Psychromonas profunda*, a psychropiezophilic bacterium isolated from deep Atlantic sediments (**Xu *et al.*, 2003a**). Some OTUs belonging to various bacterial groups were related to cold-seep sediments, most from the Japan Trench. In addition to bacteria from sediments, OTU 37, representing 12 clones had 97-99% of sequence identity with *Colwellia psychroerythrus*, a psychrophilic bacterium associated with sea ice from Antarctic coastal areas (**Bowman *et al.*, 1997**). Most of the remaining OTUs were related to bacteria associated with marine invertebrates such as corals, sponges and crabs or to *Moritella* sp. Members of this genus such as *M.*

marina (**Urakawa *et al.*, 1998**), *M. profunda* (**Xu *et al.*, 2003a**), *M. abyssi* (**Xu *et al.*, 2003b**), *M. dasanensis* (**Kim *et al.*, 2008**) and *M. japonica* (**Nogi *et al.*, 1998**) are generally psychrophilic bacteria from deep-sea water or sediments. Our data indicate that the gut microflora of *S. antarcticus* are bacteria occurring in the environment.

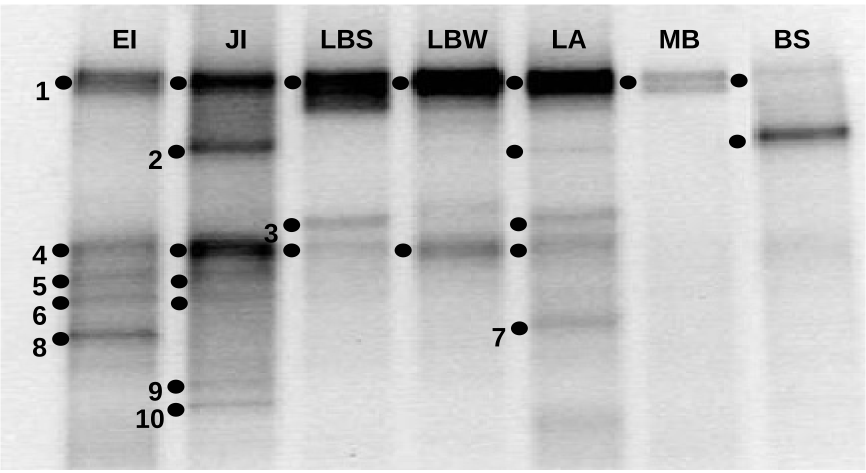

Fig. 3. DGGE gel profile of the 16S rRNA gene fragments from the gut microflora of S. *antarcticus*. BS: Bransfield Strait, EI: Elephant Island, JI: Joinville Island, LA: Larsen A, LBS: Larsen B South, LBW: Larsen B West, MB: Margarita Bay.

OTUs (no. of clones)	No. of bases	Related organism (GenBank accession no.)	Source	ID%	Division	Location of the clone[b]		
						EI	LB	MB
1 (3)	464-524	Uncultured bacterium clone S26-28 (EU287328)	Arctic sediments	90-93	α-proteobacteria	X		
2	477	Uncultured bacterium clone B78-110 (EU287074)	Arctic sediments	96	α-proteobacteria			X
3	417	Uncultured alpha proteobacterium clone ss1_B_03_28 (EU050759)	Arctic sediments	93	α-proteobacteria			X
4 (6)	423-535	Uncultured alpha proteobacterium clone NKB7 (AB013259)	Deep-sea sediments	93-96	α-proteobacteria	X	X	
5 (2)	511-546	Uncultured bacterium clone D64 (AY375148)	Deep-sea sediments	96	α-proteobacteria			X
6 (3)	507-575	Uncultured bacterium clone D8S-121 (EU652591)	Yellow Sea sediments	99	α-proteobacteria	X		
7 (2)	453-501	Uncultured bacterium clone 10bav_E9_ARB (EU181484)	Marine sediments	95-99	α-proteobacteria	X		
8	457	Uncultured bacterium clone 308c2 (EF459996)	Baltic Sea sediments	97	α-proteobacteria	X		
9	532	Uncultured alpha proteobacterium clone GoM161_Bac79 (AM745160)	Cold-seep sediments	96	α-proteobacteria		X	
10	505	Uncultured bacterium clone TfC20H58 (EU362214)	Tidal flat sediments	97	α-proteobacteria			X
11 (4)	421-602	Uncultured organism clone ctg_CGOAA08 (DQ395424)	Deep-sea octacoral	99	α-proteobacteria	X		
12	421	Uncultured alpha proteobacterium clone 1m04AMLD11R (EF630051)	Sponge tissue	93	α-proteobacteria	X		
13	474	Uncultured bacterium clone Hg5a1A10 (EU236323)	Sponge tissue	98	α-proteobacteria		X	
14 (2)	504-505	Uncultured alpha proteobacterium clone S2-27 (EF491346)	Surface submerged in sea water	94-95	α-proteobacteria	X		
15	455	Uncultured bacterium clone S1-21(EF491282)	Surface submerged in sea water	98	α-proteobacteria	X		
16	464	*Thalassobacter oligotrophus* strain CECT 5294T (AJ631302)	Sea water	98	α-proteobacteria	X		
17 (2)	424-531	Uncultured bacterium ARCTIC39_F_11	Arctic	97	α-proteobacteria			X

		(EU795102)						
18 (2)	459-476	Uncultured bacterium clone S26-9 (EU287309)	Arctic sediments	97-98	β-proteobacteria	X		
19	481	Uncultured bacterium clone Sd-NB03 (AB193935)	Hydrothermal vent water	99	β-proteobacteria			X
20 (10)	415-605	*Psychromonas profunda* (AJ416756)	Atlantic sediments	96-98	γ-proteobacteria	X	X	
21 (6)	424-592	Uncultured bacterium clone P13-20 (EU287113)	Arctic sediments	96-99	γ-proteobacteria	X		X
22 (5)	451-510	Uncultured bacterium clone S11-68 (EU287251)	Arctic sediments	96-98	γ-proteobacteria	X		
23 (2)	496-580	Uncultured bacterium clone P13-57 (EU287150)	Arctic sediments	98	γ-proteobacteria	X		
24	420	Uncultured bacterium clone P13-72 (EU287165)	Arctic sediments	98	γ-proteobacteria	X		
25	431	Uncultured bacterium clone S11-63 (EU287246)	Arctic sediments	99	γ-proteobacteria	X		
26	417	Uncultured bacterium clone S11-64 (EU287247)	Arctic sediments	99	γ-proteobacteria	X		
27 (6)	438-564	Uncultured gamma proteobacterium clone BNT06-03 (AB240686)	Cold-seep sediments	91-95	γ-proteobacteria	X		X
28	415	Uncultured *Pseudomonas* sp. clone BJS81-001 (AB238993)	Cold-seep sediments	98	γ-proteobacteria	X		
29	542	Uncultured proteobacterium isolate C1_B009 (AF420361)	Hydrothermal vent sediments	98	γ-proteobacteria	X		
30	434	Uncultured bacterium clone F36 (AY375119)	Deep-sea sediments	96	γ-proteobacteria	X		
31 (4)	430-489	Uncultured bacterium clone B107 (AY375080)	Deep-sea sediments	98-99	γ-proteobacteria		X	
32	534	Uncultured bacterium clone h34 (DQ462301)	Deep-sea sediments	98	γ-proteobacteria		X	
33	415	Uncultured bacterium DS21 (EU707312)	Wadden Sea sediments	98	γ-proteobacteria		X	
34	510	Uncultured bacterium JS9_43 (EU707310)	Wadden Sea sediments	97	γ-proteobacteria			X
35	513	Uncultured bacterium JSS S04 clone 422 (EU707322)	Wadden Sea sediments	99	γ-proteobacteria			X
36	507	Uncultured bacterium clone TfC20L41 (EU362305)	Tidal flat sediments	98	γ-proteobacteria			X
37 (12)	405-566	*Colwellia psychroerythrus* IC064 (U85842)	Antarctic sea ice	97-99	γ-proteobacteria	X	X	
38 (5)	419-515	*Moritella* sp. ODA02 (AB011353)	Pacific Ocean	98-99	γ-proteobacteria	X		
39	483	Uncultured gamma proteobacterium clone TAA-10-78 (AM259846)	Sponge tissue	95	γ-proteobacteria	X		
40 (2)	461-538	Uncultured gamma proteobacterium clone Cobs2TisB5 (EU246800)	Crab tissue	94-96	γ-proteobacteria			X
41 (4)	400-497	Uncultured gamma proteobacterium clone G1-45 (EU005288)	Surface submerged in sea water	95-98	γ-proteobacteria	X		X
42	513	Uncultured *Photobacterium* sp. clone BECC1447a-36 (EF067913)	Marine basalts	100	γ-proteobacteria	X		
43	478	*Pseudoalteromonas* sp. BSw20075 (EU365560)	Arctic sea water	96	γ-proteobacteria		X	
44	517	Uncultured bacterium clone P9X2b7A05 (EU491163)	Seafloor lava	98	γ-proteobacteria			X
45	543	Uncultured bacterium clone P0X3b5E05 (EU491390)	Seafloor lava	97	γ-proteobacteria			X
46	513	Uncultured marine bacterium clone AntCL2A1 (DQ906741)	Antarctic seawater	97	γ-proteobacteria			X
47	525	Uncultured gamma proteobacterium clone pItb-vmat-7 (AB294927)	Hydrothermal system	96	γ-proteobacteria			X
48 (5)	488-587	Uncultured delta proteobacterium clone JTB20 (AB015241)	Cold-seep sediments	98-99	δ-proteobacteria		X	
49	459	Uncultured delta proteobacterium clone HCM3MC78_7C_FF (EU373901)	Slope sediments	91	δ-proteobacteria	X		
50	442	Uncultured delta proteobacterium clone HCM3MC91_7B_FF (EU373912)	Slope sediments	94	δ-proteobacteria			X

51	461	Uncultured bacterium clone TfP20L16 (EU362255)	Tidal flat sediments	97	δ-proteobacteria	X		
52	508	Uncultured bacterium clone 246b2 (EF459921)	Baltic Sea sediments	91	δ-proteobacteria			X
53	454	Uncultured bacterium clone FS266-91B-03 (AY869686)	Ridge flank crustal fluids	96	δ-proteobacteria	X		
54	537	Uncultured bacterium clone EPR3967-O2-Bc57 (EU491803)	Seafloor lava	97	δ-proteobacteria	X		
55	503	Uncultured bacterium clone ANTLV2_G05 (DQ521526)	Antarctic lake	90	δ-proteobacteria			X
56 (2)	420-442	Uncultured epsilon proteobacterium clone NKB12 (AB013264)	Deep-sea sediments	96	ε-proteobacteria		X	
57	557	Uncultured epsilon proteobacterium clone NKB9 (AB013261)	Deep-sea sediments	96	ε-proteobacteria		X	
58	437	Uncultured bacterium clone S11-52 (EU287235)	Arctic sediments	96	ε-proteobacteria		X	
59	487	Uncultured bacterium clone C11-D11 (AY355302)	Hydrothermal vent gastropod	97	ε-proteobacteria		X	
60 (2)	426-523	Uncultured planctomycete clone Belgica2005/10-ZG-18 (DQ351810)	Marine sediments	96-97	Planctomycetes	X		X
61	485	Uncultured planctomycete clone Sylt 14 (AM040110)	Wadden Sea sediments	95	Planctomycetes	X		
62	438	Uncultured bacterium clone 220b2 (EF459947)	Baltic Sea sediments	92	Planctomycetes	X		
63 (2)	524-536	Uncultured bacterium clone 039C42 (EU734947)	Bering Sea sediments	98	Planctomycetes			X
64	486	Uncultured bacterium clone EP1-29 (EF491463)	Deep-sea sediments	94	Planctomycetes			X
65	554	Uncultured *Planctomyces* sp. clone B30 (EU360295)	Deep-sea sediments	97	Planctomycetes			X
66	523	Uncultured bacterium clone ES0505-S28 (EU675827)	Deep-sea sediments	99	Planctomycetes			X
67	404	Uncultured planctomycete clone 6mML1B01 (EF630283)	Sponge tissue	98	Planctomycetes	X		
68	518	Uncultured bacterium clone BME12 (DQ917817)	Coral tissue	92	Planctomycetes			X
69 (2)	507-561	Uncultured planctomycete isolate ikaite un-c21 (AJ431347)	Ikaite column	97-98	Planctomycetes	X		X
70	532	Uncultured bacterium clone EPR4059-B2-Bc54 (EU491556)	Seafloor lava	98	Planctomycetes			X
71 (2)	514-531	Uncultured bacterium clone BJS960-36 (AB426417)	Deep-sea sediments	97-98	Cyanobacteria			X
72	408	Cyanobacterium clone 16B_215 (AM501410)	Lagoon sediments	98	Cyanobacteria			X
73	505	Uncultured bacterium clone 102B39 (EF687202)	Mud volcano	92	CFB	X		
74	424	Uncultured bacterium clone BT60DS1BH1 (AF365715)	Coral tissue	89	CFB			X
75 (2)	577	Uncultured *Fusobacterium* sp. clone JT75-113 (AB189363)	Cold-seep sediments	99	Fusobacteria	X		
76 (2)	442-482	Uncultured bacterium clone P13-63 (EU287156)	Arctic sediments	96	Nitrospirae	X		X
77	511	Uncultured bacterium clone P13-85 68 (EU287178)	Arctic sediments	93	Acidobacteria	X		
78	507	Uncultured bacterium clone GoM161_Bac49 (AM745150)	Marine sediments	99	Chloroflexi	X		

[a] Listed are the numbers of clones with >97% similarity (in brackets), the numbers of bases sequenced, the best-matched organisms in GenBank followed by their accession numbers, sources, percent identities and divisions.

[b] X signs indicate the location of the clones. EI: Elephant Island, LB: Larsen B, MB: Margarita Bay.

Table 6. 16S rRNA gene sequence identities of clones associated with *Sterechinus antarcticus* microflora[a].

In conclusion, the diet of *S. antarcticus* (Echinidae) differs from that of *Ctenocidaris gigantea, C. perrieri* and *Notocidaris mortenseni* (Cidaridae). In both families, all the investigated species are carnivores/scavengers. However, *S. antarcticus* ingests a wider set of animals and is also a deposit–feeder. Its diet is clearly not restricted to food of animal origin. Noteworthy, no macroalgae were found in its gut, probably due to low availability or absence of this resource in the investigated stations, especially at their depth range (100-350 meters). Interestingly, the digestive bacterial microflora of *S. antarcticus* is not symbiotic, varies with station (as only one of the ten phylotypes detected by DGGE was found in all stations) and presumably fluctuates with the nature of the ingested food. Moreover, cloning analyses did not reveal clones common to all libraries. Consequently, the digestive microflora is neither specific nor symbiotic but rather consists of transient bacteria. These bacteria seemingly originate from the pellets of sediments ingested by the echinoid as a majority of the clones were related to bacteria from marine sediments. The presence of bacteria related to cold-seep sediments has to be stressed as a recent survey at the Larsen Ice Shelf reports the presence of a chemosynthetic-based ecosystem in this area (**Domack *et al.*, 2005**). No bacterial amplification was obtained for the gut contents of Cidaridae, which could indicate that their bacterial microflora is poorly developed. These echinoids could rely on intrinsic digestive enzymes; these enzymes could degrade bacteria, preventing their proliferation in the gut. However, further morphological analyses of the digestive tube of these sea urchins are needed to confirm this hypothesis. Regarding its feeding behaviour, *S. antarcticus* might be well-adapted to cope with changes in food resources resulting from global warming. Cidaridae would most presumably be more sensitive to changes although one cannot exclude their acclimatization to a new set of preys.

Ectosymbiosis on echinoids

To test the contribution of cidaroid ectosymbiosis to local benthic communities, their abundance, distribution, richness, diversity and similarity indexes were compared to those of sessile epibionts occurring on drop stones. For this purpose, several cidaroid species and stones were collected at six contrasted areas: Weddell Sea, South Shetlands, Antarctic Peninsula (including Larsen embayments where ice shelves collapsed very recently), Bellingshausen Sea and Dumont d'Urville Sea. Our results demonstrate the importance of cidaroids for local epibiont diversity. However, contrasting patterns of diversity were found in the different sampling areas, likely due to contrasting environmental conditions (latitude, depth and currents). In contrast with other areas, the symbiotic communities in the Larsen embayments show low diversity values and a strong similarity with epibionts present on stones. We therefore propose that, in this newly colonized habitat, symbiotic communities are not at the origin of sessile organism recolonization and have not reached their climax yet.

Comparative biogeography of Antarctic meio-, macro- and megabenthos

Based on new and complete datasets with distribution records of the three target taxa, a common biogeographical analysis was undertaken, aiming to compare geographical and bathymetrical distribution patterns, focusing on the differences between meio-, macro- and megabenthos. The analysis aimed to match these patterns with the biogeographical schemes of other benthic taxa, in particular with the recent comprehensive biogeographical analyses performed on molluscs (**Linse *et al.*, 2006**; **Clarke *et al.*, 2007b**), bryozoans (**Barnes & Griffiths, 2008**) and general macrobenthos (**Griffiths *et al.*, 2009**). Another goal was to identify potential causal factors of the observed patterns.
The classic Southern Ocean biogeographical scheme designed by **Hedgpeth (1969, 1970)** and **Dell (1972)**, mostly based on benthic distribution patterns, was to a large extent confirmed by biogeographical studies on e.g. Demospongia (352 spp.: **Sara *et al.*, 1992**), Hexacorallia (122 spp.: **Rodriguez *et al.*, 2007**), Sipunculida (16 spp.: **Saiz-Salinas & Pagola-Carte, 1999**), Polychaeta (558 spp.: **Knox & Lowry, 1977**; **Glasby & Alvarez, 1999**; **Sicinski & Gillet, 2002**), Pycnogonida (264 spp.: **Munilla & Soler Membrives, 2009**), Amphipoda (445 spp.: **Knox & Lowry, 1977**; 815 spp.: **De Broyer & Jazdzewski, 1993**; **1996**; **De Broyer *et al.*, 2007**), Echinoidea (79 spp.: **David *et al.*, 2005**), and Ascidiacea (237 spp.: **Primo & Vasquez, 2007**). Recent extensive databases on Gastropoda (895 spp.) and Bivalvia (379 spp.) (**Linse *et al.*, 2006**; **Clarke *et al.*, 2007b**), Bryozoa (1681 spp.; **Barnes &**

Griffiths, 2008) allowed for new in-depth multivariate biogeographical analyses and provided new insights into the biogeography of the Southern Ocean benthos. Moreover, **Griffiths *et al.* (2009)** attempted to generalize Southern Ocean (s.l.) benthos biogeographical traits, partly challenging the Hedgpeth-Dell classic scheme. No biogeographical analysis of the nematode species of the Southern Ocean has been performed so far. The biogeography of Southern Ocean amphipod species was investigated by **Knox & Lowry (1977)**, **Watling & Thurston (1989)** and **De Broyer & Jazdzewski (1993, 1996)**. The amphipod, echinoid (**David *et al.*, 2005**) and asteroid (**McKnight, 1976**) distribution patterns detected mostly fit into the Southern Ocean biogeographical scheme established by **Hedgpeth (1970)** and **Dell (1972)**.

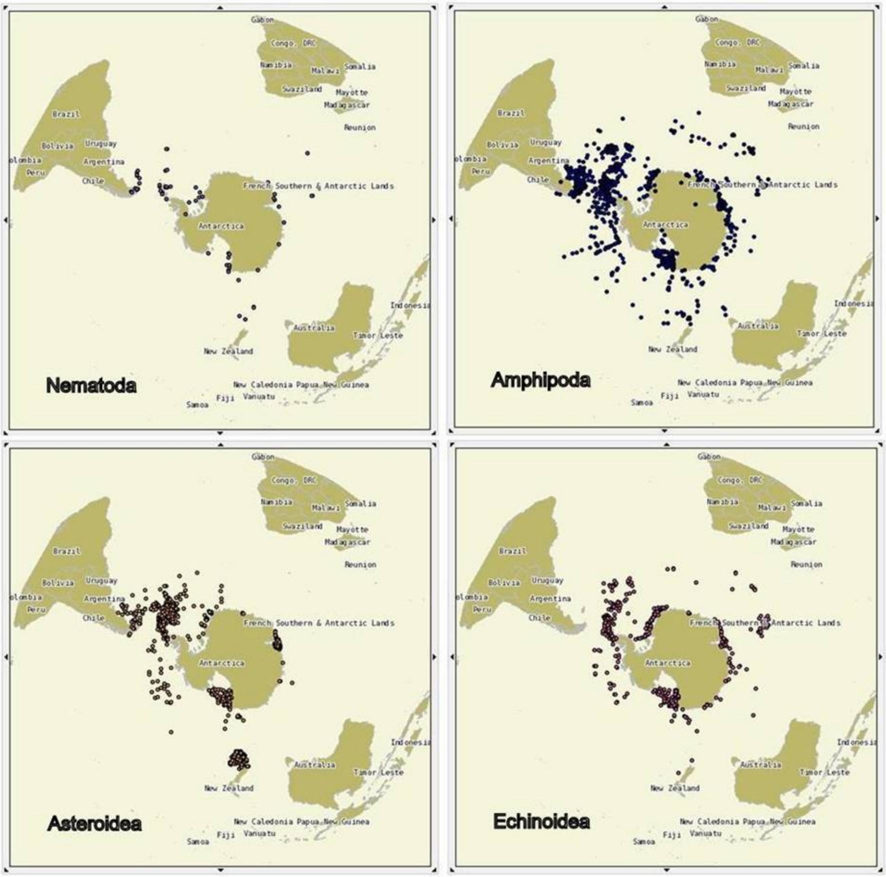

Fig. 4. Distribution records of Nematoda, Amphipoda, Asteroidea and Echinoidea.

Distribution data on the Antarctic benthos in general increased enormously during the last two decades. Moreover, extensive biogeographical databases are now being built for some species-rich groups and new insights are progressively provided by molecular analyses. In particular, a number of potential cryptic species has been detected in Antarctic isopods and molluscs (*e.g.* **Page & Linse, 2002**; **Held, 2003**; **Held & Wägele, 2005**; **Raupach & Wägele, 2006**) and these results may question our current estimation of species richness and our widely accepted view of circum-Antarctic distribution patterns for benthic species (**De Broyer *et al.*, 2003**).

New complete distribution datasets for Southern Ocean species of the four model taxa were built within the framework of the BIANZO II project (**Fig. 4**), including Nematoda (meiobenthos: 341 spp.; 1367 records; **Raes & Vanreusel, *unpubl.***); Amphipoda (macrobenthos: 859 spp.; 8046 records; **De Broyer *et al.*, 2007**); Asteroidea (megabenthos: 209 spp.; 3689 records; **Danis & Jangoux, *unpubl.***) and Echinoidea (megabenthos: 79 spp.; 1895 records; **David *et al.*, 2005**).

Nematode biogeography is currently being investigated, and first data are not yet available. Species level diversity information at such a broad scale has never been reported in literature before. However, on the genus level, nematode diversity is comparable to that in the Atlantic and Mediterranean, and much higher than in the Arctic Ocean (**Vanhove *et al.*, 1999**). Amphipod species richness recorded in the geographic regions considered here is shown in **Table 7**. When comparing respective areas per region, some regions appear as biodiversity hotspots: Weddell Sea, Peninsula + South Shetland Islands, Ross Sea, South Georgia, Kerguelen Islands and Bouvet Island. However, except for Bouvet Island, all of these regions are obviously also the most intensively sampled. There are about 900 species of echinoids in the World Ocean, and 79 of them occur south of the Antarctic Polar Front. These Antarctic species belong to 7 of the 19 Post–Paleozoic echinoid orders and are represented by 9 families (**Table 8**).

	area (km²)	N. recs.	N. genera	N. spp.	N. endemic spp.	% endemic spp. per region
Weddell sea	639681	658	102	195	12	6.1
Dronning Maud + Enderby Ld	407434	93	19	28	1	3.5
Dronning Maud Ld		58				
Enderby Land		35	19	25	0	0
Prydz Bay region		614	54	75	8	10.6
Davis S. and Wilkes Ld		79	35	47	7	14.9
Adelie Coast + Oates Ld		279	57	93	7	7.5
Ross Sea	679693	749	60	104	11	10.6
Amundsen Sea		31	1	1	0	0
Bellingshausen Sea & Peter I I.	336011	59	16	22	6	27.3
Antarctic Peninsula and South Shetland Is.	457953	495	141	321	70	21.8
South Orkney Is.	91170	10	61	85	5	5.9
South Sandwich Is.	80294	36	19	21	3	14.3
South Georgia	122672	324	97	172	25	14.5
Shag Rocks		26	18	19	1	5.3
Bouvet I.	2626	5	31	31	1	3.2
Heard & McDonald Is.	27332	20	13	14	3	21.4
Magellan area	660552	1104	120	210		
Southern Chile	147186	63	29	31	4	12.9
Southern Argentina	488073	126	47	65	14	21.5
Tierra del Fuego + Estrecho de Magallanes	96920	606	87	134	24	7.9
Falkland Is.	158879	309	71	107	22	20.6
Prince Edward & Marion Is.	3894	194	49	62	13	21.0
Crozet Is.	68455	64	16	18	0	0
Kerguelen Is.	252265	361	71	97	23	23.7
Macquarie I.		96	25	31	4	12.9
Auckland I.		88	37	45	7	15.5
Campbell Is.		93	30	41	4	9.7
Antipodes Is.		7	7	7	0	0
Bounty I.		1	1	1	0	0
Tristan da Cunha and Gough Is.	2293	45	27	32	8	25.0
Antarctic	34800000	5183	205	536	388	72.3
Southern Ocean s.l.		8046	301	859	651	79.8

Table 7. Rate of Amphipod endemism for each sub-region of the SO (*s.l.*).

orders	families	N. genera	N. spp.	% endemic genera	% endemic spp.
Cidaroida	Cidaridae	5 (3)	21 (17)	60 %	81 %
Echinothurioida	Echinothuriidae	1	1	0	0
Arbacioida	Arbaciidae	1	1	0	0
Temnopleuroida	Temnopleuridae	1	3	0	0
Echinoida	Echinoidae	3	7 (4)	0	57 %
Holasteroida	Plexechinidae	1	2 (1)	0	50 %
	Pourtalesiidae	6 (1)	8 (5)	17 %	62 %
	Urechinidae	4 (1)	6 (3)	25 %	50 %
Spatangoida	Schizasteridae	8 (3)	30 (20)	37 %	67 %
7 orders	9 families	30 (8)	79 (50)	27 %	63 %

Table 8. Echinoid biodiversity in the Southern Ocean (*s.s.*).

Several studies recorded the distribution of nematode species within a number of selected, dominant genera over the Atlantic sector of the Southern Ocean (**Vermeeren *et al.*, 2004**; **Fonseca *et al.*, 2006**; **De Mesel *et al.*, 2006**, **Ingels *et al.*, 2006**). Within the Southern Ocean (*s.s.),* many nematode species are rare and only found once or twice. In *Acantholaimus*, 34 of the 55 species were found at only a single station, and 36 species in only one of the four studied regions (*i.e.* Drake Passage, Bransfield Strait, Kapp Norvegica or Vestkapp; **De Mesel *et al.*, 2006**). In contrast, some species are found in a very broad area: 25 of the 89 species of *Molgolaimus*, *Dichromadora* and *Acantholaimus* described above were found in more than 3 Antarctic regions: South Sandwich Trench, Weddell Sea, Drake Passage or Peninsula (Bransfield Strait). Most of the species found in Antarctic sediments were new to science, which might indicate a high degree of Antarctic endemism at species level. *Molgolaimus* communities in the Southern Ocean and the Indian Ocean have only one species, *Molgolaimus sabakii*, in common (**Fonseca *et al.*, 2007**), and *Dichromadora* communities at similar depths in the Arctic and Atlantic Ocean were completely different in composition compared to the Southern Ocean (**Vermeeren *et al.*, 2004**). However, faunal exchange with lower latitudes might be possible via the deep sea (**Brandt *et al.*, 2007a**) and via shallow-water migration routes (**Ingels *et al.*, 2006**). Whether some nematode species have a true circumpolar distribution is unknown at present. *Desmodorella* aff *balteata*, which was found at many of our study sites in Antarctica, is very similar to *D. balteata* found at hydrothermal vents in the East Pacific Rise at a depth of 2000m. *Desmodora campelli*, originally described from the sub-Antarctic Campbell Islands south of New Zealand, has also been found in Chile and Argentina and recently at both sides of the Scotia Arc. Although this information is very fragmented and these species have often only been reported from a restricted number of sites, it does suggest a very wide distribution over the southern hemisphere. According to **Fonseca *et al.* (2006)**, morphologically similar species occur in the same geographical region. This does not support the idea of a common origin of deep-sea nematodes, or of Antarctica as a source or sink for benthic biodiversity, but it rather implements that speciation could be driven locally.

More than 20% of the amphipod species occurring in the regions of Bellingshausen Sea, Peninsula and South Shetland Is, Heard I., Falkland Is., Prince Edward and Marion I. and Kerguelen Is. are endemic (**Table 7**). The endemic species from the Peninsula and South Shetland Is., South Georgia, Kerguelen Is. and Falkland Is. represent respectively 8.15, 2.91, 2.68, 2.56% of the total Southern Ocean (*s.l.*) endemics. The whole fauna of gammaridean and corophiidean amphipods presents an endemism rate of 72.3% in the Antarctic zone and 79.8% in the Southern Ocean (*s.l.*). Strong faunal similarities of amphipods (more than 50 % of shared species) were found respectively between Peninsula+South Shetlands and the Weddell Sea, the Ross Sea and Adélie+Oates Coasts, Tierra del Fuego and Southern Argentina. There is a less marked similarity between the Falkland Islands and Southern Chile, and between Auckland and Campbell Islands. Around 40% faunal similarity was detected respectively between the South Orkney Islands and South Georgia, between the clusters Adélie+Oates Coasts / Ross Sea and Peninsula+South Shetlands / Weddell Sea, and between Davis

Sea+Wilkes Land and Dronning Maud Land. The Antarctic and sub-Antarctic regions *sensu* **Hedgpeth (1969)** remain clearly distinct (**Fig. 5**).

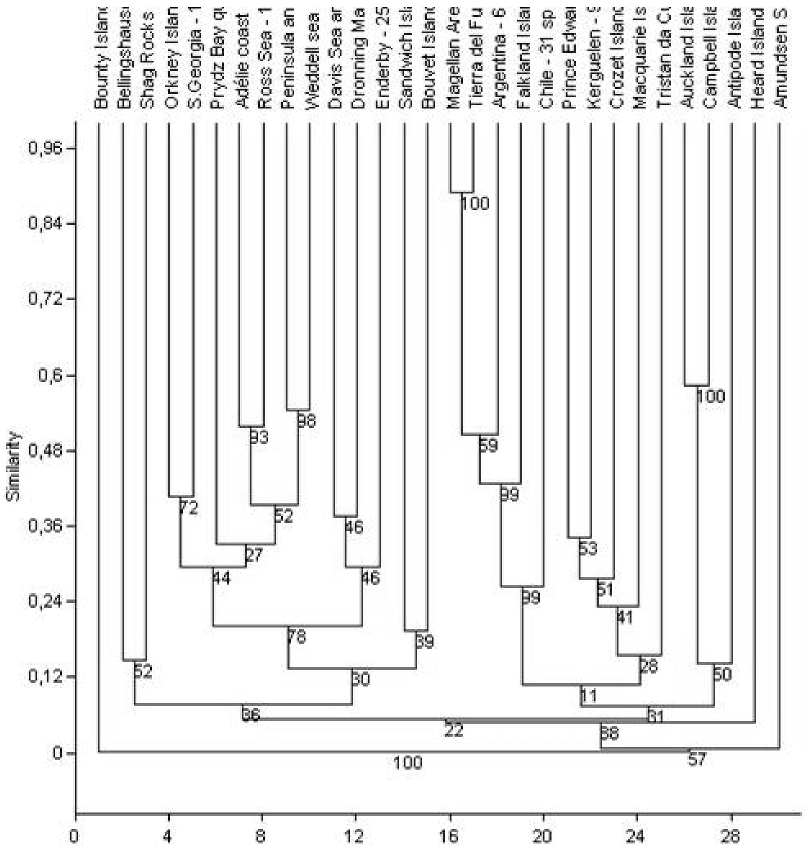

Fig. 5. Amphipod faunal similarity of shelf regions (based on Bray-Curtis similarity index).

Endemism in Antarctic echinoid species is particularly high: 68% of the species are endemic to the Southern Ocean (*s.s.*). The dominant Cidaridae and Schizasteridae are remarkable as most of their species (80% of the Cidaridae species and 83% of the Schizasteridae species) are endemic. High level of endemism is also observed for Pourtalesiidae and Urechinidae, although these families are less diversified at the species level. Eight Antarctic echinoid species display a circumpolar distribution. Six occur along the coast and 2 off the coastal zone. The coastal species belong to the Cidaridae (*Ctenocidaris rugosa*, *Notocidaris platyacantha*), to the Echinidae (*Sterechinus neumayeri*) and to the Schizasteridae (*Abatus cavernosus*, *Abatus philippi*, *Abatus shackletoni*). These species are either carnivorous or opportunistic carnivorous browsers or deposit/bottom feeders; none of them are strict vegetarian browsers. A brooding behaviour has been reported for 4 of them. Longitudinal distribution of species richness (partly based on Jaccard index and 4 longitudinal sectors) is presented in **Table 9**.

	Total species	Atlantic Ocean	Indian Ocean	Australia + New Zealand	Pacific Ocean
Species richness of echinoid species according to longitudinal sectors					
Atlantic Ocean	54		32	14	21
Indian Ocean	50			20	20
Australia + NZ	20				13
Pacific Ocean	27				
Similarity coefficients (Jaccard index = C/N_1+N_2-C) between the echinoid fauna					
Atlantic Ocean	54		0.44	0.23	0.35
Indian Ocean	50			0.40	0.35
Australia + NZ	20				0.38
Pacific Ocean	27				
Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna (depths < 500 m)					
Atlantic Ocean	43		0.39	0.07	0.29
Indian Ocean	28			0.21	0.26
Australia + NZ	6				0.24
Pacific Ocean	20				
Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna (depths: 500 – 1000 m)					
Atlantic Ocean	38		0.18	0.10	0.16
Indian Ocean	22			0.12	0.21
Australia + NZ	7				0.12
Pacific Ocean	12				
Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna (depths: > 1000 m)					
Atlantic Ocean	29		0.21	0.16	0.12
Indian Ocean	17			0.39	0.08
Australia + NZ	8				0.21
Pacific Ocean	9				

Table 9. Species richness and similarity coefficients for Antarctic echinoids, related to longitudinal distribution.

Distribution patterns of the Antarctic zoobenthos are also influenced by bathymetry.
A shift in nematode genus composition is obvious from shelf to lower slope (**Vanhove *et al.*, 1995**). For instance, the typical deep-sea genus *Acantholaimus* occurred quite abundantly on the Antarctic shelf (**De Mesel *et al.*, 2006**). Eurybathic distribution patterns in Antarctica are well-described for macrofauna but are less known for meiofauna. Our findings indicate that nematode genera might also have a wider depth range in Antarctica compared to other parts of the world. A wide depth range was found in several *Acantholaimus* species: between 200 m and 2000 m. **Muthumbi & Vincx (1997)** found some *Acantholaimus* species to occur between 500 m and 2000 m water depth. More information both from Antarctica and from other parts of the world is needed to confirm eurybathic species distribution.

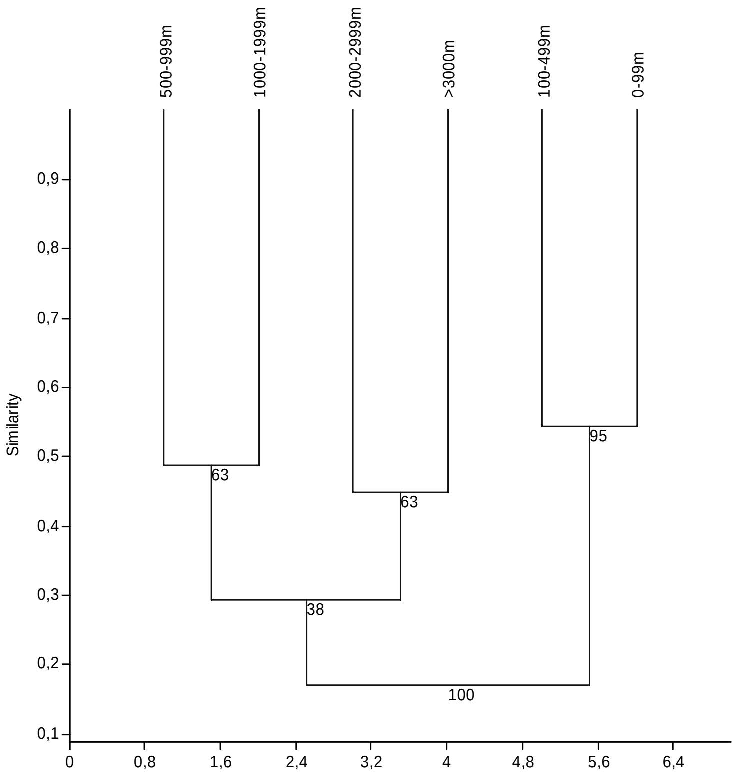

Fig. 6. Cluster analysis of Southern Ocean bathymetric zones (Amphipod data, Bray-Curtis similarity index).

The bathymetric distribution of Antarctic amphipod species (Scotia Arc excluded) reveals three distinct groups: a shelf cluster (0-99 m and 100-499 m), a deep shelf-upper slope cluster (500-999 m and 1000-1999 m) and a deep slope-abyssal cluster (2000-2999 m and >3000 m) (**Fig. 6**). Half of the 72 Antarctic amphipod species occurring below 1000 m are shelf species that extend their distribution: from a few tens of metres depth up to the upper slope at a maximum depth of 1500–2000 m (in one case even 2894 m). Eighteen species (15 Antarctic endemics) are restricted to the bathyal zone (1000–3000 m) and 13 species (nine endemics) to the abyssal zone (>3000 m depth). A number of scavenger species occur on both shelf and slope, showing in some cases an extended level of bathymetry (**De Broyer *et al.*, 2004**). *Eurythenes gryllus* is the only scavenger species found on shelf, slope and in the abyssal zone. It is known as a deep-sea, pan-oceanic stenothermal species, with a benthopelagic life style, that can occur far above the seafloor (**Thurston, 1990**). Two other species with a widely eurybathic range are *Orchomenopsis cavimanus* (6-3070 m) and *Abyssorchomene scotianensis* (385-3070 m), but small morphological differences have been observed between shelf and deep-sea populations, and a molecular analysis is required to detect potential cryptic species before confirming such very wide eurybathy.

In echinoids, there are stronger similarities between the shelf (from 0 to 500 m depth) and the deeper shelf or upper slope (from 500 to 1000 m) than between the slope and the deep-sea (below 1000 m) (**Table 10**). The same distribution pattern is observed in the four main retained longitudinal regions.

	Total species	0 – 500 m	500 – 1000 m	> 1000 m
Echinoid species richness according to depth ranges				
0 – 500 m	52		43	21
500 – 1000 m	50			24
> 1000 m	41			
Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna according to depth ranges				
0 – 500 m	52		0.73	0.29
500 – 1000 m	50			0.36
> 1000 m	41			

Table 10. Species richness and similarity coefficients for Antarctic echinoids, related to bathymetrical distribution.

This detailed comparative analysis, which is still ongoing, provides new insights into geographical and bathymetrical distribution patterns, hotspots of species richness and endemism, center(s) of radiation, circumpolarity and cryptic species, eurybathy, and potential causal factors of the observed patterns.

COPING WITH CHANGE...

Effects of warming, temperature-related changes and acidification on the Antarctic zoobenthos

Response to ice-shelf collapse events

Direct warming effects can already be seen all over the world, but the Antarctic Peninsula is considered one of the fastest warming areas in the world (**King *et al.*, 2003**; **Chapman & Walsh, 2007**). Extreme warming near the peninsula was manifestly expressed in 2002, when 500 billion tons or 3250 km² of ice from the Larsen B ice shelf collapsed at the eastern side of the Antarctic Peninsula, and this in only one month's time (31/01-07/03/2002) (**Fig. 7**). A few years before, in 1995, the ice shelf of the nearby Larsen A region had already disintegrated completely. The collapse of these ice shelves has indeed been attributed to extreme warming, and the Larsen B collapse happened during the warmest summer on record for the area (**Scambos *et al.*, 2000**). Ice-shelf collapse initially leads to increased iceberg disturbance and may have detrimental effects on surface primary productivity (**Arrigo *et al.*, 2002**). Later, the formerly ice-covered area opens up, leading to increased primary production and the opportunity to enter the area for scientific investigations.

Between 11/01/2007 and 22/01/2007, the Larsen area was investigated by a team of researchers with the German research vessel Polarstern (campaign ANT-XXIII/8). A synoptic approach was applied, including different spatial scales, different groups of organisms (from pelagic to benthic, from primary producers to apex predators) and different environmental characteristics at a limited number of sampling stations (**Gutt *et al.*, *submitted***). Representatives of the BIANZO II consortium sampled and investigated the continental shelf benthic fauna in the area. The Antarctic shelf is notoriously rich at local as well as regional scales (**Arntz *et al.*, 1994**), and effects of large-scale ice-shelf collapse events were still visible after 5 years. The investigations of the BIANZO II group were meant to provide information on the following topics:

1. Current status of the Larsen benthic shelf fauna;
2. Biogeography and taxonomy of certain benthic taxa;
3. Response of the Larsen benthic fauna to large-scale ice-shelf disintegration events/ability of this fauna to cope with a changing environment;
4. Recolonization speed of the Larsen benthic fauna after large-scale ice-shelf disintegration events.

Meiofauna (Raes et al, Submitted)

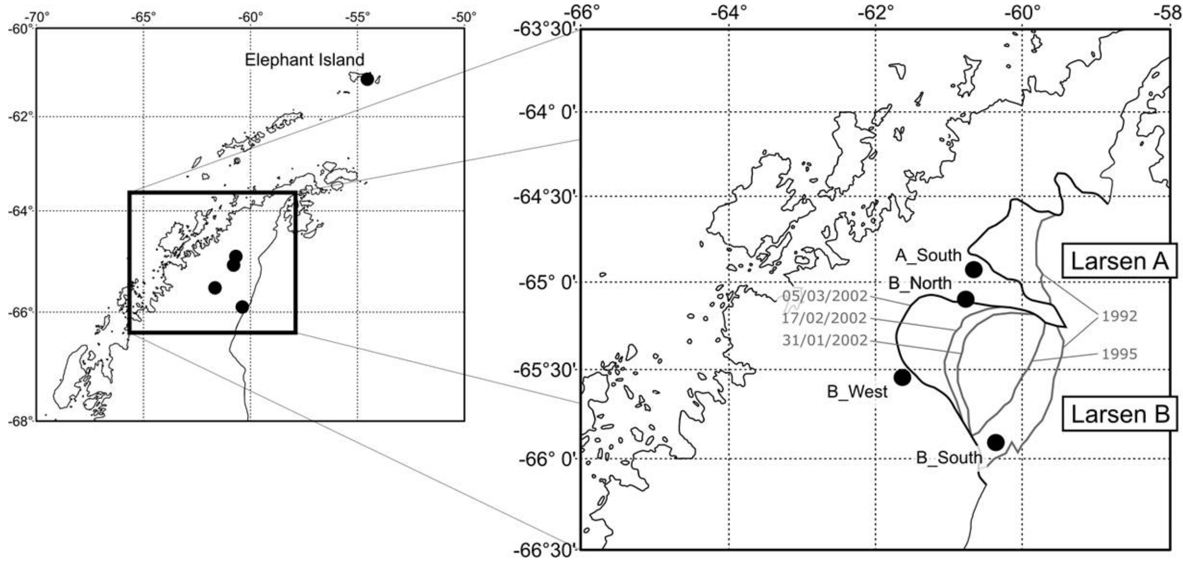

Fig. 7. Map of the study area, with indication of all sampling stations and the maximum ice extent at Larsen A and B between 1992 and March 2002 (Based on BAS, AMM and ESA ERS imagery). The world map is shown in Mollweide projection.

Meiofauna and nematodes were collected at three stations in Larsen B and one station in Larsen A (**Fig. 7**), all at comparable depths: between 229 and 427 m. Five replicate drops were attempted at each station, although only four were successful at station A_South. Three replicate samples of meiofauna were collected near Elephant Island, *i.e.* at the northern tip of the Antarctic Peninsula, at a similar depth.

The sampling stations at Larsen have been free of ice cover for different periods of time (**Fig. 7**): the area of station B_South has been ice-free at least since 1995 (Larsen A collapse), the area of station B_North probably became ice-free in 2002 (Larsen B collapse) and the other two stations became free of ice cover somewhere between 2002 and 2007 (time of sampling). Note that, judging from this figure, stations B_West and A_South were still completely ice-covered after 05/03/2002, whereas station B_North was situated near the shelf edge at that time. The 'outer' station B_South, situated at the eastern border of the Larsen B area, is regarded here as a reference site.

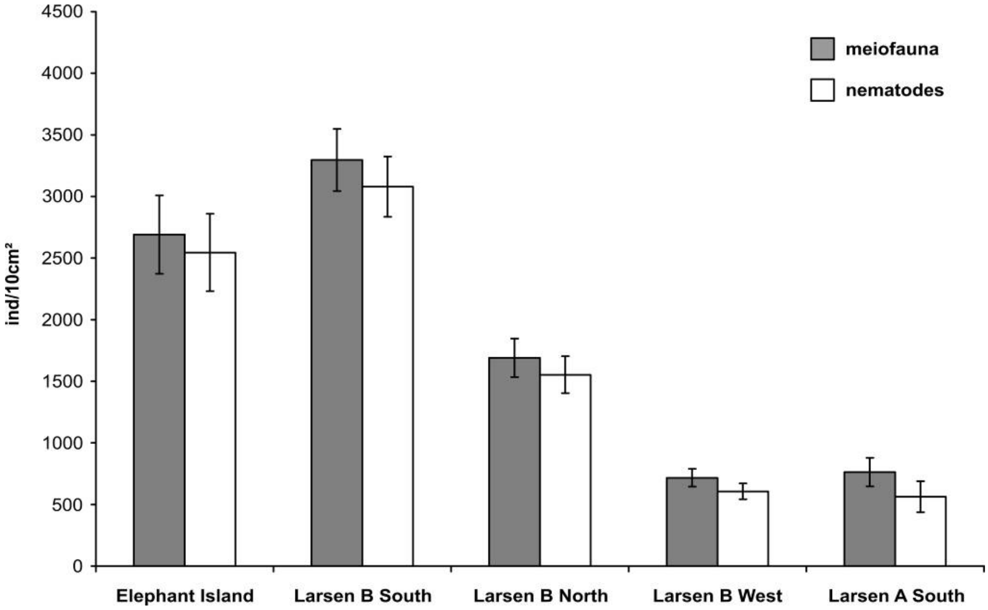

Fig 8. Abundances (+ standard deviation) of meiofauna and nematodes in the Larsen area and Elephant Island station.

An overview of meiofauna and nematode densities is provided in **Fig. 8**. Average density of meiofauna over all Larsen stations was 1661.40±1129.98 ind/10cm². Meiofauna densities at Larsen B_South (3296.32±548.85 ind/10 cm²) were much higher than at the other stations, including the Elephant Island station (2691.22±308.96 ind/10cm²). Larsen B_North was characterised by intermediate values (1690.20±340.35 ind/10 cm²), whereas the other two stations yielded very low densities of meiofauna: 762.44±227.62 ind/10 cm² (A_South) and 716.85±156.07 ind/10 cm² (B_West). Average nematode densities followed the same trend and differed greatly between stations; they were significantly lower at stations A_South (563.38 ± 244.04 ind/10 cm²) and B_West (606.00 ± 141.48 ind/10 cm²) (Kruskal-Wallis ANOVA; df =1; $p \leq 0.001$), intermediate at Larsen B_North (1552.51 ± 327.45 ind/10 cm²) and significantly higher at Larsen B_South (3079.86 ± 531.80 ind/10 cm²) (Kruskal-Wallis ANOVA; df =1; $p = 0.0012$).

The most abundant meiobenthic taxa were nematodes (90.11%), harpacticoid copepods (3.56%) and their nauplii (4.78%). The relative abundance of nematodes followed a trend similar to that of meiobenthic densities: highest at Larsen B_South (93.3±1.0%) and B_North (91.7±1.9%), and considerably (and significantly) lower at Larsen B_West (84.2±4.2%) and A_South (72.0±12.6%) (Kruskal-Wallis ANOVA by ranks; df = 1; $p < 0.001$). Highest nematode relative abundance was found at the Elephant Island station (94.55±1.0%).

Microlaimus was the dominant genus at B_South, whereas the other stations were dominated by the closely related genera *Halomonhystera* and *Thalassomonhystera* (**Table 11**). In contrast to stations B_North and A_South, which were dominated by *Thalassomonhystera*, B_West was dominated by *Halomonhystera*. The communities at B_North and A_South were dominated by the same four genera: besides the aforementioned genera also *Neochromadora* and *Prochromadorella*. Nevertheless, the dominance of *Thalassomonhystera* was much higher at Larsen B_North (57.28 % vs. 27.82 % at A_South).

Larsen B_South		Larsen B_North		Larsen B_West		Larsen A_South	
Genus	%	Genus	%	Genus	%	Genus	%
Microlaimus	32.20	*Thalassomonhystera*	57.28	*Halomonhystera*	57.88	*Thalassomonhystera*	27.82
Metadesmolaimus	10.98	*Halomonhystera*	23.34	*Thalassomonhystera*	21.00	*Halomonhystera*	21.94
Paracanthonchus	9.90	*Neochromadora*	6.08	*Theristus*	3.83	*Neochromadora*	9.76
Halomonhystera	9.09	*Prochromadorella*	3.09	*Acantholaimus*	3.17	*Prochromadorella*	6.18
Monhystrella	4.23	*Metadesmolaimus*	2.51	*Daptonema*	2.28	*Procamacolaimus*	4.19
Neochromadora	3.11	*Elzalia*	1.77	*Monhystrella*	1.97	*Paracanthonchus*	3.76
Prochromadorella	3.09	*Acantholaimus*	1.13	*Desmodorella*	1.83	*Theristus*	3.76
Araeolaimus	3.07	*Theristus*	1.04	*Halalaimus*	1.19	*Acantholaimus*	2.66
Acantholaimus	2.78					*Araeolaimus*	2.23
Thalassomonhystera	2.35					*Microlaimus*	2.01
Theristus	2.00					*Innocuonema*	1.97
Leptolaimus	1.87					*Monhystrella*	1.56
Elzalia	1.42						
Daptonema	1.33						
Desmodorella	1.30						
Halichoanolaimus	1.27						
Dichromadora	1.18						
Desmodora	1.10						

Table 11. Relative abundance of dominant genera per station (relative abundance > 1%).

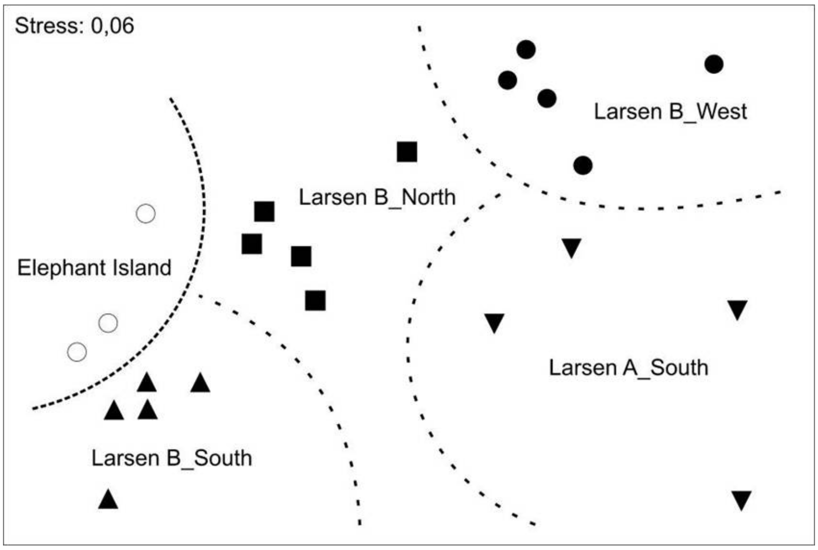

Fig 9. Non-metric multidimensional scaling biplot of meiofauna data.

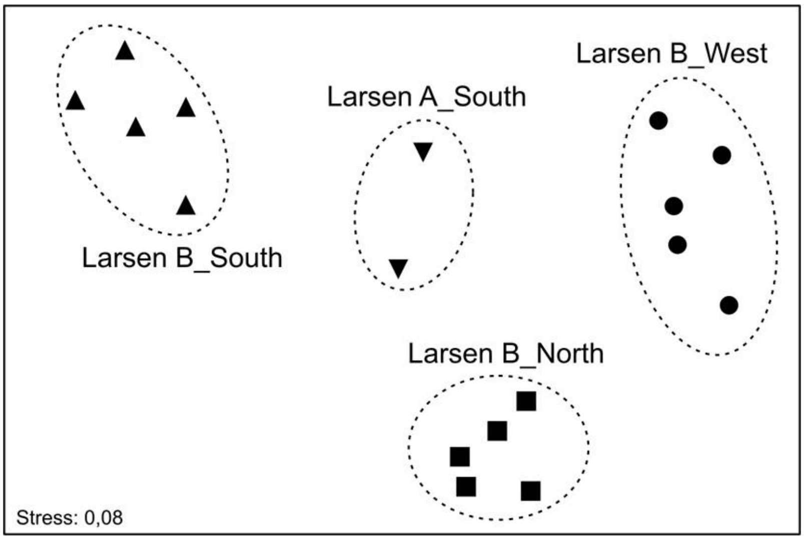

Fig. 10. Non-metric multidimensional scaling biplot of nematode data.

Both for meiofauna (overall R = 0.849 and $p = 0.001$) and nematodes (overall R = 0.994 and $p = 0.001$; R = 1 for all pairwise comparisons), all stations were well-separated from each other (**Figs. 9, 10**). On a higher taxon level, the most pronounced differences were found between the stations with high densities (Larsen B_South; Elephant Island) and those with low densities (Larsen B_West; Larsen A_South): the R-value for all 4 combinations was 1, indicating a perfect separation of the groups. A second nMDS with relative data (log(x+1) transformed) confirmed this trend. Within the Larsen area, differences were most pronounced between Larsen B_West and B_South (R = 1; $p = 0.008$) and Larsen A_South and B_South (R = 1; $p = 0.008$). Larsen B_South and B_West/A_South were most different from each other, with Larsen B_North intermediate between both groups, which was mainly explained by differences in the abundance of nematodes (SIMPER analysis). To rule out any density effects, the same analyses were carried out with relative (standardized) data, which yielded similar results.

Nematode samplings from stations A_South and B_North are most similar to each other, and those from B_South are most different from the other samplings (**Fig. 10**). Pairwise dissimilarity values were lowest between A_South and B_North (43.56), and highest between B_South and B_West (63.79). The dissimilarity between the latter two stations was mainly attributed to the absence of *Microlaimus* at B_West (explains 12.14 % of dissimilarity) and the much higher relative abundance of *Halomonhystera* at this station (explains 10.59 %).

Meiofauna and nematode community structure was also not entirely identical in each sediment layer. Overall, the dominance of nematodes was significantly lower in the upper cm (Kruskal-Wallis ANOVA; df = 1; $p = 0.009$). Genus composition of the upper sediment layer was comparable to that of the entire depth profile, except for station B_West, where the upper cm was dominated by *Thalassomonhystera* (33.81 %) instead of *Halomonhystera*, which was, however, by far the most abundant genus in the deeper sediment layers (relative abundance: 85.24 %). Overall, the relative abundance of *Halomonhystera* in the first cm (17.59±14.15 %) was lower than in the deeper sediment layers (42.89±29.36 %) (Kruskal-Wallis ANOVA; df = 1; $p = 0.0068$).

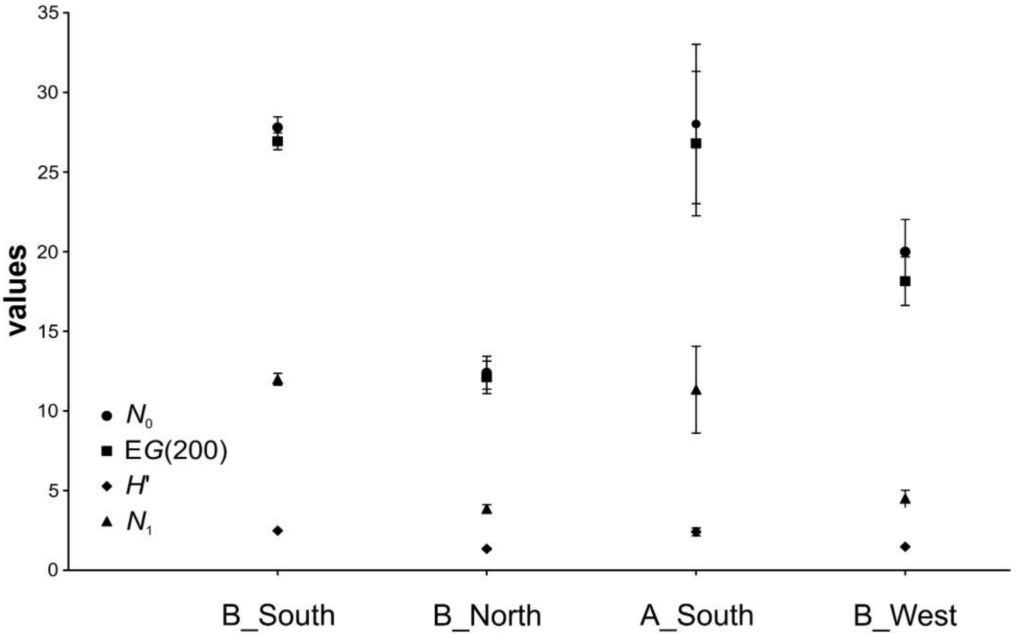

Fig. 11. An overview of several key biodiversity indices for the four Larsen stations (average with standard error flags).

A total of 23 meiofauna taxa was encountered in the Larsen area, ranging between 14 (Larsen B_North) and 19 (Larsen A_South) taxa per station. Taxon richness at Larsen B_North was significantly lower than at the other stations (Kruskal-Wallis ANOVA; df = 1; p = 0.0023). This trend was confirmed for the density-independent index ET(1000): diversity was significantly higher at Larsen A_South and significantly lower at Larsen B_North (Kruskal-Wallis ANOVA; df = 1; p = 0.002). At the Elephant Island station, 17 taxa were recorded. The total number of genera was highest at Larsen B_South (49) and lowest at Larsen B_North (24). Even though only half the number of individuals was identified at Larsen A_South, the station still yielded 38 genera. In comparison, the expected number of genera for 451 individuals (*i.e.* the no. of individuals at station A_South) is 37 at station B_South and 18 at station B_North, respectively. The average values of genus richness N_0, the expected number of genera EG (200), the Shannon Wiener index H' and Hill's N_1 all followed the same trend: highest values for B_South and A_South, and lowest values for B_North (**Fig. 11**). In contrast, evenness (N_{inf}, J') was lower at B_West compared to B_North.

Average taxonomic distinctness with abundance data (Δ*) was highest at stations B_South and A_South, whereas stations B_North and B_West yielded significantly (Kruskal-Wallis ANOVA; df = 1; $p \leq 0.001$) lower values. In contrast, average values for variation in taxonomic distinctness (Λ^+) were highest at B_North and lowest at B_South (Kruskal-Wallis ANOVA; df = 1; p = 0.045). The Λ^+ value for the pooled data at this station plots above the 95 % probability funnel. A deviation from a random selection of the regional genus pool at this station was confirmed by a TAXDTEST analysis (p = 0.032).

Highest pigment concentrations were found at stations B_North and A_South (0.46 ± 0.17 µg/g and 0.43 ± 0.19 µg/g, respectively), lowest concentrations at station B_West (0.32 ± 0.09 µg/g). At the latter station, almost all pigments were concentrated in the upper cm (97.38 ± 5.25 %). The contribution of phaeopigments was comparable at most stations (22.52 ± 9.93 - 37.58 ± 8.15), except for Larsen A_South, where it was significantly lower (2.87 ± 4.06 %; Kruskal-Wallis ANOVA: df = 1, p = 0.03). Mean grain size ranged from 10.03 ± 1.63µm at station B_West (significantly lower: Kruskal-Wallis ANOVA; df = 1; p = 0.002) up to 64.25 ± 19.72µm at station A_South (significantly higher: Kruskal-Wallis ANOVA; df = 1; p = 0.03). The pellite (clay + silt) fraction was significantly lower at station A_South (Kruskal-Wallis ANOVA; df = 1; p = 0.03); the other fractions (very fine sand, fine sand, medium sand, coarse sand) were significantly higher at this station (Kruskal-Wallis ANOVA; df = 1; p = 0.03 for all fractions).

A BIO-ENV procedure revealed that the environmental variables considered did not match in any combination the biological patterns emerging from the nMDS (correlation 0.056).

Our meiofauna data from the Larsen area indicate a distinction between station B_South on the one hand, and B_West and A_South on the other hand, with station B_North as an intermediate. Our nematode community results suggest a slightly different classification of the investigated stations in three groups: (1) station B_South, dominated by *Microlaimus*; (2) stations B_North and A_South, dominated by *Thalassomonhystera* and (3) station B_West, dominated by *Halomonhystera*.

We consider four factors related to ice coverage which could have had an influence on the investigated meiobenthic communities (incl. nematodes): (1) length of the period for which each station has been free of shelf ice cover, (2) distance of each station from a rich source of nematodes for colonization, (3) primary production in the water column above the stations, and (4) local environmental factors, such as sediment granulometry and pigment concentration.

Food availability certainly is a major structuring factor for meiobenthic and nematode populations and communities (**Vanhove *et al.*, 2000**; **Gutzmann *et al.*, 2004**), and oligotrophic conditions are known to negatively affect meiobenthic and nematode abundance (**Vincx *et al.*, 1994**; **Vanreusel *et al.*, 2000**). Extensive and long-term ice cover impedes or, in case of sea ice persisting only for weeks or months, delays phytoplankton production, in this way severely impacting the entire pelagic ecosystem (**Arrigo *et al.*, 2002**) and, hence, benthic communities. Still, living (and even rich) benthic communities can exist underneath large ice shelves (**Oliver *et al.*, 1976**; **Riddle *et al.*, 2007**; **Post *et al.*, 2007**). In the area of Larsen B_South, a pre-collapse benthic community was also present at the ocean floor, judging from the low number of iceberg scour marks and the age of sponges collected here (**Gutt *et al.*, *submitted***). The meiofauna here was probably impoverished in abundance and diversity, relying entirely on advected food from open water. The low densities at station B_West and the nematode community at this station, characterized by a low genus richness and a high dominance of *Halomonhystera*, indicate pre-collapse conditions. *Halomonhystera* was also more abundant in the deeper sediment layers, which generally contain less organic food. *Halomonhystera disjuncta* is known for its high resistance to environmental stress (**Vranken *et al.*, 1989**) and might have actively adapted to changing food conditions by trophic specialisation (**Van Gaever *et al.*, 2006**). Only the densities at station B_South were higher or in the range of densities found at other locations in the Weddell, Scotia and Ross Seas (**Herman & Dahms, 1992**; **Vanhove *et al.*, 1995**; **Fabiano & Danovaro, 1999**; **Vanhove *et al.*, 2004**; **Gutzmann *et al.*, 2004**; **Ingels *et al.*, 2006**), whereas the inner stations were still impoverished 5 years after the 2002 Larsen B ice shelf collapse. After ice shelf disintegration, density increase at the inner stations has been a slow process, related to increased food supply, and/or colonization from adjacent ice-free areas. At a colonization rate of 60.8 m.y^{-1} (**Lee *et al.*, 2001**), it would take more than 1000 years for the nematode community at station B_West to fully recover its abundance levels. Time needed for the first colonizers to reach the inner Larsen stations seems to be in the order of magnitude of at least a decade or more. This agrees well with recovery speed of macrofauna after iceberg scouring, compiled by **Barnes & Conlan (2007)**.

The significantly higher densities, higher diversity and significantly different community structure at B_South in comparison with the inner stations, can be explained by the longer period free of ice cover and, hence, open to potentially increased food supply from sea-surface phytoplankton blooms, in combination with the proximity of the open, western Weddell Sea as a nearby source for advected food and colonization. Quick colonizers might have seized the opportunity to swiftly invade the new space. *Microlaimus* is a rather important and usually (sub)dominant genus in the Antarctic and subantarctic (**Vanhove *et al.*, 1999**, **Vanhove *et al.*, 2004**, **Ingels *et al.*, 2006**, **Sebastian *et al.*, 2007**). It is also known as an opportunistic genus that benefits from increased but unpredictable organic food input (**Van Gaever *et al.*, 2004**; **Van Gaever *et al.*, 2006**), and a successful and fast colonizer (**Lee *et al.*, 2001**).

Even though Larsen A became free of ice cover in 1995, station A_South was still covered by shelf ice in 2002 and its community composition was still very similar to that of station B_North in 2007. We conclude that the inner stations B_West, B_North and A_South were not yet (or, in the case of B_North, only to a small extent) colonized by nematodes from the open Weddell Sea at the moment of sampling. Differences between these stations should be the result of changes in the local genus pool in relation to environmental conditions. The considerable difference in densities between B_North and A_South could also be related to differences in sediment composition, as muddy sediments (B_North) yield the highest meiobenthic densities and coarser sediments (A_South) are considered less favourable for nematodes (**Tietjen, 1977**; **Heip *et al.*, 1985**; **Fabiano & Danovaro, 1999**; **Brandt *et al.*, 2007**).

Stations A_South and B_North are physically separated by the Drygalski Glacier cliff, so faunal exchange between both stations is impossible. Thus, only the recent availability of fresh food could resulted in the comparable nematode community composition and dominance of *Thalassomonhystera* here. *Thalassomonhystera* is known as an opportunistic genus, which could have taken advantage of the fresh food input, outcompeting several other taxa. The food-rich environment at these stations is most likely the result of a recent phytoplankton bloom in the area. The close proximity of land and increased run-off of meltwater from its glaciers create excellent conditions for the development of large summer blooms (**Dierssen *et al.* 2002**; **Clarke *et al.* 2007a**).

In terms of taxon richness, the meiofauna in the Larsen area was not less diverse than at another subantarctic station, which was not influenced by ice-shelf collapse events.

The very high diversity at station A_South, both for the meiofauna on a higher taxon level, and for nematodes on the genus level, seems remarkable for an inner station. The striking contrast with B_North, characterized by very low diversity, could be related to a combination of environmental factors: (1) a higher amount of fresh food (higher fraction of fresh chlorophyll a) at A_South, and (2) the significantly coarser sediment at this station. Nematode communities tend to be more diverse (high richness, low dominance) in coarse, sandy environments (**Tietjen, 1977**; **Heip *et al.*, 1985**).

The significantly lower average values of taxonomic distinctness (Δ^*) at B_North (and B_West), and the significantly higher value of variation in taxonomic distinctness (Λ^+) for the entire nematode community at station B_North indicate both a low taxonomic spread in the community at this station (i.e. relatively more similar taxa), and a high unevenness in its phylogenetic structure, related to an increase in abundance of an opportunistic genus (*Thalassomonhystera*). The station is also characterized by a high dominance of nematodes. A negative correlation between evenness and a combination of abundant food and fine sediment could be an explanation for the low diversity at B_North (**Tietjen 1977**; **Sebastian *et al.* 2007**).

Our BIO-ENV analysis revealed no perfect match between environmental variables and the observed biological patterns. In our opinion, these patterns can only be explained by a combination of historical (length of ice-free period), geographical (position in the Larsen area) and present-day environmental (food supply, sediment granulometry) effects.

In conclusion, the meiofauna in the Larsen A and B areas has been strongly influenced by the presence and sudden removal of the ice cover in this region, and is only slowly replenished through colonization from the open Weddell Sea. Full recovery would even take more than 1000 years. The station closest to the open Weddell Sea has already been ice-free for at least 12 years and is comparable with other Antarctic stations in terms of nematode abundance and community composition. Stations located deeper inside the Larsen embayments are not yet or only little influenced by new colonizers, and probably structured by local environmental conditions, related to food input and sediment granulometry. This study provides first insights about the response of benthic communities after ice shelf disintegration and the rate of colonization of these areas.

Echinoids

The only three species collected in Larsen A&B areas (unpublished data) are known as indirect developers (or at least non-brooders), consistent with high dispersal capabilities. Moreover, this is congruent with the wide Antarctic distribution of these species (**David *et al.*, 2005**). On the contrary, it departs from other Antarctic echinoids which are known as direct developers that brood their young and, accordingly, are supposed to present low dispersal capacities. Secondly, the three species are deposit feeders with a varied diet that can even include small epibenthic organisms (algae, foraminiferans, bryozoans, corals…). This 'generalist' feeding behaviour can be considered as characteristic of pioneering species. Therefore, considering echinoid life and feeding strategies, the three species are good candidates as pioneering species in a changing marine environment.

Direct temperature effects

In November 2007, a laboratory temperature experiment was carried out at the Dallmann laboratory, Jubany station, located near the coast of Potter Cove on King George Island, close to the Antarctic Peninsula, one of the fastest warming regions on earth. Clearly, this area is very suitable for performing experiments dealing with the influence of temperature changes on marine benthos. There were two different incubation periods: one of 14 days (start: 15/11/2007) and one of 10 days (start: 19/11/2007).

The aim of this experiment was to investigate the influence of temperature increase, by steps of 2°C, on the respiration of the Antarctic benthos: microbenthos, meiobenthos and macrobenthos. Four different temperatures were considered: 0°C (ambient temperature), 2°C, 4°C and 6°C. For each temperature, four replicate cores were incubated. To keep the closed cores at these fixed temperatures, they were placed into buckets with water that was kept at a constant temperature by means of thermostats. Water temperature fluctuations were kept to a minimum by frequent inspection and adjustment. Every day, 10ml of water was sucked out from each core, at 5cm from the sediment surface. The oxygen content of this 10ml water sample was then measured using the Winkler method with a spectrophotometer. The same amount of water, incubated separately but at the same temperature as the respective core, was added again subsequently.

All cores were incubated for 14 days, except for the water samples of the 2°C treatment. This incubation was stopped after three days because of a temporary heat (7°C) shock, which clearly affected the results. The sediment cores were kept for further examination in spite of the temperature failure, however, and a new series of 4 sediment and 4 water cores was added for an incubation period of 10 days. Sediment was collected the day of sampling (Day 0), after 5 days and at the end of the incubation period. From each core, a small amount of sediment was taken for bacterial counts and ATP measurements. The remainder of the core was sliced as follows: 0-1cm, 1-2cm, 2-3cm, 3-4cm, 4-5cm, 5cm-rest.

The absorption data are summarized in **Fig. 12**. There is a strong decline in oxygen concentration (expressed as an absorption coefficient) for all sediment treatments, although the rate of decrease becomes higher with each temperature increase. Whereas the 6°C treatment reaches the 'anoxic' phase after 7 days, the 0°C treatment has not reached this phase yet after 14 days. Although the same trend is clear for the water samples, it is less pronounced and subject to small fluctuations. When comparing the sediment and water cores, the oxygen-consuming effect of the benthos is obvious.

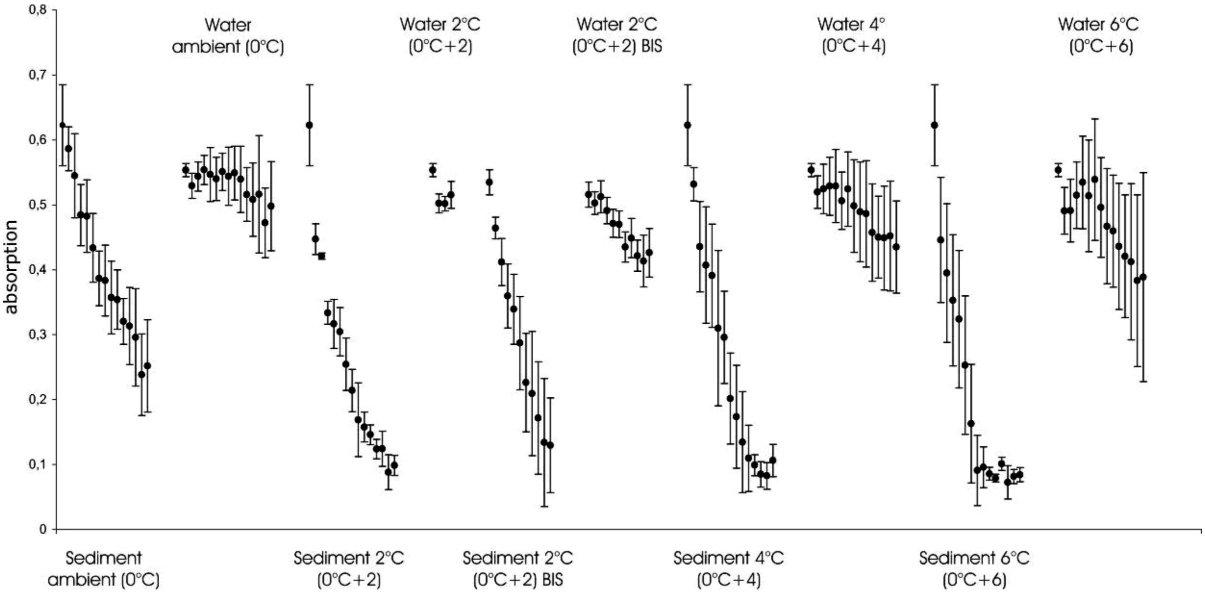

Fig. 12. Absorption data for the temperature experiment.

More data (densities, biomass, ATP…) will become available when the sediment samples are analysed.

The impact of increased food availability on benthic respiration was also investigated.

On 19/11/2007, the sediment of some cores was covered by a thick, dark-yellow-green layer of benthic diatoms. Four such cores were incubated at 0°C and compared with the sediment cores taken on 15/11/2007, which did not have any observable diatom layer. Although the initial oxygen concentration (Day 0) was not the same for both treatments, there still was a pronounced trend: benthic respiration was higher in the food-enriched cores, resulting in a faster decline in oxygen concentration in these cores, compared to the 'normal' (not-enriched) sediment cores.

In order to test the set-up of the experiments, and to enable a bipolar comparison, analogous experiments were carried out at Koldewey station, Spitsbergen (78°55'N; 11°56'E). Although the ambient temperature was higher here (4°C), and temperature steps of 4°C were used instead of steps of 2°C, the experiments yielded similar results.

CO_2 and skeletogenesis

Anthropogenic CO_2 emissions have been largely absorbed by oceans. This results in a surface pH which is already 0.1 units lower than during pre-industrial times and is expected to decrease by 0.3-0.4 units by the end of the century. As a consequence, oceans are experiencing a reduction in CO_3^{2-} concentration, which is leading to a drop in calcium carbonate saturation. The Southern Ocean will suffer even lower concentrations of CO_3^{2-} due to lower surface temperatures and the presence of large amounts of upwelled deep water rich in CO_2.

The main goals of this work are: (1) to determine the impact of sea water acidification on larval and adult sea urchins and (2) to establish dose-effect relationships for the most significant effects.

Paracentrotus lividus. The first experiments were done using *P. lividus*, a temperate species, in order to adjust the techniques. Controlled lower pH values were obtained by bubbling CO_2 in seawater. The total alkalinity and pH (total scale) were measured and the pCO_2 and total inorganic carbon calculated, as well as the magnesium-calcite saturation state. The larvae were grown at pH between 8.0-7.0 until the echinopluteus stage (3 days) and their development was characterized using embryotoxicity protocols to distinguish normal and altered morphologies. At lower pH, significantly more larvae showed an abnormal morphology and a reduced size. The spicules development will now be quantified.

Adult sea urchins were grown at pH values between 7.8-7.3 during one month. The internal pH, measured immediately after collection of coelomic fluid, decreased significantly with the decrease of the external seawater pH, indicating that sea urchins have a poor acid-base compensation mechanism. Spine regeneration was experimentally induced in order to have a measurement of calcification rate in these structures. However, contrary to our expectations, no significant difference was found between treatments, as well as in their magnesium content.

Arbacia dufresneii. The same type of experiments was carried out using the sub-antarctic species *A. dufresneii*: larvae were raised for a week at pH 8.0-6.8 and adults for 3 weeks in pH 8.0, 7.7 and 7.4. The larvae data are under analysis.

Adults coelomic fluid pH was measured and again it decreased significantly with the decrease of the external seawater pH indicating no acid-base regulation. Additionally, the magnesium content of the coelomic fluid was also measured and no significant differences were found between treatments, showing that no skeleton dissolution mechanism takes place to compensate the coelomic fluid acidosis. Spine regeneration was induced in this species too and it was verified that neither calcification rate neither skeleton magnesium concentration showed significant differences between treatments. Yet to be analyzed is the growth rate of test plates, labeled with calcein at the beginning of the experiment. We hypothesize that calcification in the endoskeleton of adult sea urchins does not seem to be affected in medium-term low pH exposure. As these animals seem unable to regulate their acid-base internal equilibrium, further experiments should be designed to evaluate the metabolic state of other physiological functions behind calcification. Furthermore, the individuals seem to be able to maintain a normal calcification rate on a first stage, but after a longer exposure of the animals to a lower pH this function should be studied and the cost to maintain it should be evaluated. Consequently, the RNA/DNA ratio is currently being studied in order to evaluate the metabolic well-being of the studied individuals. Additionally, the body wall activity of carbonic anhydrase, an enzyme that has an important role in calcification, among other functions, was evaluated and it did not differ significantly between treatments.

Cidaroids. The cidaroid primary spines are characterized by the presence of a monocrystalline stereom surrounded by a polycrystalline cortex and when the spine becomes mature the epithelium covering disappears, exposing it to seawater. By that time, the shaft becomes heavily colonized by epibionts making these sea urchins islands of biodiversity, especially in the Southern Ocean. Therefore, we have looked into the morphological differences of cidaroid spines exposed to different saturation states of Mg-calcite. The spine morphology and chemistry of *Ctenocidaris speciosa*, collected from the Weddell Sea, Antarctica, at different depths, was studied in order to evaluate possible differences related to different calcite and aragonite saturation states, using these values as proxies for Mg-calcite. A short-term laboratory experiment using spines from an accessible tropical species (*Phyllacanthus imperialis*) was carried out to understand the effects of lower seawater pH and magnesium calcite saturation state on their well-being.

In the case of *C. speciosa* we observed morphological differences in the cortex, as well as in the later magnesium content, which might turn in an adaptive advantage in order to cope with low magnesium-calcite saturation state. In the case of *P. imperialis*, we observed a certain degree of corrosion that was much higher in young spines at lower pHs, indicating that these structures are somehow more fragile than the mature "naked" spines.

WHAT TO EXPECT?

Creating a model on the response of benthic fauna to environmental change in the Antarctic

At this point, PhD-student Benjamin Pierrat is working on the construction of the GIS model. The frame, based on latitudes and longitudes, is already finished, and sediment and depth data are already added. Data on marine currents and surface + sea floor temperatures are added at the moment. Specific data for echinoids have also been added already: taxonomic information, sampling coordinates, and complementary data on taxon ecology. Taxon ecology includes life mode, nutrition, reproduction and symbiosis.

SUMMARY

Increased efforts to look into the morphological taxonomy of Antarctic amphipods have lead to the discovery and description of several new species. Molecular analyses revealed that at least some circum-Antarctic amphipods are actually complexes of cryptic species. This is especially the case in taxa with low dispersive capacities. This result has important implications for our knowledge of the biogeography and biodiversity of the Antarctic amphipod fauna. On the genus level, nematode diversity is comparable to that in the Atlantic and Mediterranean, and much higher than in the Arctic Ocean. For amphipods, the Weddell Sea, Antarctic Peninsula (+ South Shetland Islands), Ross Sea, South Georgia, Kerguelen Islands and Bouvet Island are recognized as biodiversity hotspots. Out of 900 echinoid species, 79 occur south of the Antarctic Polar Front. In the Southern Ocean, many nematode species are new to science and rare. They can be either very resticted in their distribution, or they can occur in a very broad area. On the species level, nematodes might have a high degree of endemism in the Antarctic, although pathways towards lower latitudes exist. Within the gammaridean and corophiidean amphipods, endemism rates may be as high as 79.8% in the Southern Ocean. Endemism is particularly high in Antarctic echinoids: 68% of the species are endemic to the Southern Ocean. More than 80% of all Cidaridae and Schizasteridae are also endemic. Distribution patterns of the Antarctic zoobenthos are also influenced by bathymetry. Nematode genera might have a wider depth range in Antarctica in comparison to other parts of the world, and eurybanthic distribution patterns might also be common in this group. There are three distinct groups within Antarctic amphipod species, with regard to bathymetry: a shelf group, a deep shelf-upper slope group and a deep slope-abyssal group. Although some species appear to have wide bathymetrical distributions, molecular analyses are needed to rule out cryptic speciation. In echinoids, there are stronger similarities between shelf and upper slope than between slope and deep sea. Biomarker analyses indicated differences in feeding behaviour between pelagic (feeding mostly on flagellates) and benthic scavenger (*de novo* biosynthesis of fatty acids) amhipods. Moreover, the speed of adjustment in body tissue stable isotope ratio as a reaction to new food sources depends on the species and lifestyle. The echinoid *Sterechinus antarcticus* might be well-adapted to cope with change, as it feeds on a variety of food sources (carnivore/scavenger/deposit feeder). It also ingests large amounts of sediment. The gut microflora of this species is not symbiotic or specific, but composed of bacteria occurring in its environment; these are typical for marine sediments or known to be associated with marine invertebrates. In contrast, Cidaridae are typical carnivores/scavengers, feeding on hydrozoans and bryozoans. Cidaridae gut bacterial microflora is poorly developed. These echinoids are probably more sensitive to changes in the environment. The epifauna on Antarctic cidaroid echinoids increases local epibionts diversity, although in the Larsen area, which became recently free of ice cover, the epifauna was low in diversity and comparable to stone epifauna. This might indicate that recolonization by sessile organisms in the area has not yet reached climax conditions. Echinoids in this area are known as indirect developing, non-brooder species with high dispersal capacities, which are also generalist feeders. These attributes are typical for early colonizers with a high potential to cope with change. The meiofauna inside both Larsen A and B has been strongly influenced by the presence and sudden removal of ice cover, and is only slowly replenished through colonization from the open Weddell Sea. Full recovery might take more than 1000 years. The station closest to the open Weddell Sea has been ice-free for at least 12 years and is comparable with other Antarctic stations in terms of nematode abundance and community composition. Stations located deeper inside the Larsen embayments are not yet or only little influenced by new colonizers, and might be structured by local food input and sediment composition. This all demonstrates the indirect impact of warming on the Antarctic zoobenthos, via large-scale ice-shelf collapse events. However, warming also directly intensifies benthic respiration and the decline in local oxygen concentration occurs already at a much faster rate when temperature is increased with 2°C. Increased food availability, *e.g.* in the form of a thick layer of benthic diatoms, also speeds up oxygen consumption. Global warming is also accompanied by increased anthropogenic CO_2 emissions, which result in a lowered water surface pH. Ocean acidification and a reduction in CO_3^{2-}

concentration can lead to a reduced size and an abnormal morphology of echinoid larvae. On the other hand, neither calcification rate nor magnesium concentration of the skeleton changed when the pH was experimentally lowered for three weeks, although coelomic fluid pH decreases significantly with the decrease of seawater pH. Both climatic, environmental and taxon-specific information is currently being added into a GIS model, built to predict the response of Antractic benthic fauna to environmental change.

Have the proposed aims been achieved?

Within the first phase of the project, the consortium already achieved most of its proposed aims (cf. page 4). Benthic life in the Larsen A and B areas (**aim 1**), and the impact of large-scale ice shelf collapse events (**aim 15**) has been studied for meiofauna (Raes et al, submitted), amphipods and echinoids. BIANZO II also contributes to the ANDEEP-SYSTCO project, and *e.g.* the nematode fauna of the Weddell Sea abyssal Plain has been studied in detail (**Sebastian *et al.*, 2007**) (**aim 2**). The biogeography of the Antarctic zoobenthos (**aim 3**; **aim 7**; **aim 9**) is the subject of the joint paper we are currently working on. Phylogeographical information and evolutionary relationships, based on molecular data, are provided for several amphipod taxa (**aim 3**; **aim 11**). The collection of biological and environmental information to be added to the FOREBIO model is underway (**aim 4**), and some of this information has already been inserted in the GIS frame (**aim 22**). The taxonomy of Antarctic amphipods is being thoroughly revised, based on both morphological and molecular features (**aim 6**). A lot of work has been carried out (or is currently been carried out) to unravel both trophic ecology (all taxa) and metabolism (amphipods) of the Antarctic benthos; the resulting information is also being interpreted in the light of possible regime shifts due to global climate change (**aim 7**; **aim 13**; **aim 14**; **aim 16**; **aim 17**; **aim 18**; **aim 19**; **aim 20**). Ectosymbiosis on echinoids has been investigated, including specimens from the impacted Larsen area (**aim 10**). Direct warming effects and indirect effects related to warming (*e.g.* large-scale ice shelf collapse events) were investigated for meiofauna both in a field study (Larsen) and by an experimental approach (King George Island) (**aim 15**). Our group is also working to unravel the effects of seawater acidification on echinoid biology (incl. development) (**aim 21**).

To sum up, the original BIANZO II aims have been met to a great extent, focusing on both biology (biogeography, diversity, trophodynamics, metabolism, symbioses) and resilience (coping with change) of the Antarctic benthic fauna. In the next phase, the focus will be on the development of the FOREBIO model, which will allow us to predict future responses to a changing environment (**aim 23**).

Recommendations for policy makers

Our research has indicated that global climate change, both warming itself and warming-related changes, clearly affects the antarctic zoobenthos. Although some effects, such as the disintegration of large ice shelves, are not considered to be entirely detrimental for the benthic fauna, other effects, such as ocean acidification, have been shown to have a negative effect on the development of benthic organisms, *i.c.* echinoids. The work performed within the framework of the BIANZO II project also revealed the complexity of the intimate interactions between organisms and their environment, and the vulnerability of many Antarctic benthix taxa to a changing environment. BIANZO II provides policy decision makers with additional arguments for the acute threat of global warming and for the promotion of environmentally friendly alternatives for current energy supply.

The project also deals with biodiversity issues. The Antarctic marine benthos is still only fragmentary known and due to the unique BIANZO approach, comprehensive information is provided on all three size groups of the zoobenthos. In order to assess the impact of global warming on marine life, it is essential to record the current or pre-impact situation. BIANZO II also contributes here considerably. In the next phase of the project (see below), our knowledge on the Antarctic zoobenthos will be brought together in a predictive GIS model, which will provide even more useful information to policy makers.

The consortium would like to tighten its connections with policy makers, so that our findings may be integrated more adequately in future decisions.

Prospects for phase 2

In the second phase of the BIANZO II project, the focus will be more on integration of our results and a number of joint actions. In order to achieve these goals, even more research data are needed or at least very welcome. Therefore, ongoing research on the biology of Antarctic benthic organisms and their ability to cope with change will still be continued.

The two most important outputs at the end of the second phase will be:
1. The **FOREBIO model** with climatic, biogeographic and biological data on meiofauna, amphipods.
The current situation of this model has already been explained in detail in the scientific results chapter. The next steps to be taken are the addition of (1) environmental data on marine currents, surface temperatures, sea floor temperatures, salinity etc., (2) taxonomical, biogeographical and ecological (life mode, nutrition, reproduction...) information on nematodes and amphipods and (3) of purchase of GIS software. The separate partner institutes will soon be provided with a template for adding their taxon-specific biological data. Further data management and construction of the model are centered in Dijon (uB).

2. A **joint review paper** on the effects of global climate change on the Antarctic zoobenthos.
During our recent workshop (20/05/2009), the BIANZO II consortium elaborately discussed the structure and contents of our joint paper. We already agreed on the topics to be addressed. At the moment, a template sensitivity table is being constructed for all partners to fill in. Based on this table and a flow chart with causes and effects of climate change on benthic biology, which we constructed during the meeting, the paper will be constructed.

The detailed objectives of the second phase of the project are:
1. to continue the study of the Antarctic zoobenthos' diversity (NOWBIO) and trophic position (DYNABIO) from the shallow subtidal to the deep sea;
2. to continue the study of the impact of climate-related effects on the Antarctic zoobenthos;
3. to integrate results from experimental and field work carried out by the separate institutes (BIANZO II phase 1 + new data), in combination with literature data, and produce a review paper that provides an overview about what is known on potentially climate-related effects, such as change in primary productivity (food quality and quantity), glacier melt (increased sedimentation and freshening), increase in frequency of iceberg scouring, collapse of ice shelves, acidification, on the three benthic groups considered in the project (other taxa might be added);
4. To contribute to the FOREBIO model, by providing data on:
    3.1. Distribution of amphipod, echinoid and nematode species;
    3.2. Climatic/edaphic characteristics (from existing databases and literature);
    3.3. Available specific biological data per taxon (reproduction, feeding, symbionts...);
5. to build a GIS (Geographic Information System) integrating these data;
6. to produce macroecological results for the selected taxa with the newly developed GIS;
7. to forecast potentially climate-related effects on the Antarctic zoobenthos with the newly developed GIS.

Summary of BIANZO II phase 1

Polar regions experience greater rates of climate change than any other region in the world. Especially the Antarctic Peninsula is one of the fastest warming regions on earth. The Antarctic fauna is known to be generally stenothermal and vulnerable to increased temperatures, and might therefore be severely impacted by a changing (warming) environment. Global climate warming also has secondary effects on the environment and its inhabitants, *e.g.* large-scale ice-shelf disintegration events, changes in the availability, quantity and quality of food (regime shifts), ocean acidification, increased glacier melting (incl. freshening and increased sedimentation)… The complexity of effects, responses and interactions can only be understood if we increase our knowledge of the biology of our target group, *i.c.* the Antarctic zoobenthos. It is crucial to establish comprehensive baseline information on Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. It is also imperative to better understand the ecological role of biodiversity in the functioning of the Southern Ocean ecosystem and to assess how its structural and functional characteristics might be affected by a changing climate. These aspects are addressed in the BIANZO II project, by focusing on representatives of three zoobenthic size classes: Nematoda (meiobenthos), Amphipoda (macrobenthos) and Echinoidea (megabenthos).

The project is constructed around three complementary work packages: NOWBIO, DYNABIO and FOREBIO. NOWBIO deals with the characterization of Antarctic benthic biodiversity and its distribution along bathymetric and geographical gradients, and the explanation of its underlying processes. Special attention is devoted to cryptic speciation and ectosymbiosis. The DYNABIO work package focuses on the ecofunctional role of benthic biodiversity and the ability of the benthos to cope with change. This includes the study of trophodynamic and metabolic aspects of the investigated fauna, as well as the impact of temperature-related change, including direct temperature impact, changes in food availability and composition, and seawater acidification, on functional and structural aspects of the benthic communities. Information collected during previous projects and in the first two workpackages are also used to develop a model on the possible changes in benthic communities due to global environmental change (FOREBIO WP).

During phase 1 of the project, the focus of our research was put on biogeography and phylogeography, the trophic position of the three benthic groups, their ability to cope with warming and acidification, and their response to large-scale ice-shelf disintegration.

Samples were collected during several expeditions in the Weddell and Scotia Sea: ANDEEP I, II, III; ANDEEP-SYSTCO; ANT-XXIII-8 and BENTART'06. The meiobenthos was sampled by means of a multicorer (shelf and deep sea) or by divers (shallow subtidal), the macro- and megafauna with a variety of sampling gear, such as Agassiz trawls and Rauschert dredges. Genetic characterization of amphipods was based on the analysis of COI, 28S and 18S sequences. The trophic position of the target groups was investigated by biomarker analyses ($\delta^{13}C$ and $\delta^{15}N$ stable isotopes; fatty acids), gut content analyses, and characterization of the gut microflora. The ability of the benthos to cope with temperature increase, the influence of trophic stress on the energy budget of amphipods, and the impact of acidification on skeletal growth and larval development in echinoids, were investigated by means of a laboratory experiment.

The FOREBIO GIS model is currently being constructed. The frame, based on latitude and longitude data, is already finished (ahead of schedule), and both sediment and depth data are already added. Data on marine currents and surface + sea floor temperatures are being added at this moment. Specific data for echinoids have also been added already, including taxonomic information, sampling coordinates, and complementary data on taxon ecology. Taxon ecology includes life mode, nutrition, reproduction and symbiosis.

A thorough examination of new specimens and museum material of the amphipod genus *Liljeborgia* lead to the description of 15 new species and a detailed revision of the genus. A biogeographical survey of *Liljeborgia* suggests recent faunal exchanges between shelf and abyssal species in the Antarctic, and a certain degree of endemism, with certain species limited to the high Antarctic and others to subantarctic areas. Similar levels of endemism were observed in the family Phoxocephalidae. The absence of eyes in Arctic representatives of the *Liljeborgia georgiana* group suggests an origin of this group on the Southern Ocean shelf and a loss of eyes during migration to the north at abyssal depths. Although *Liljeborgia georgiana* specimens from the same location have the same haplotype, specimens from distant locations and different depth ranges are genetically distinct, even to the extent where the deeper representatives of the species will be described as a new species. An in-depth revision of the Antarctic amphipod fauna also resulted in the desription of two new families: the Alicellidae fam. nov. and the Valettiopsidae fam. nov. A molecular (COI) analysis of representatives of the orchomenid group within the family Lysianassoidea revealed new species, and the species *Orchomenella pinguides* and *O. cavimanus* are now recognized as complexes of cryptic, sympatric species. These findings have important implications with regard to the biogeography and biodiversity of the Antarctic amphipod fauna.

On the genus level, nematode diversity is comparable to that in the Atlantic and Mediterranean, and much higher than in the Arctic Ocean. For amphipods, the Weddell Sea, Antarctic Peninsula (+ South Shetland Islands), Ross Sea, South Georgia, Kerguelen Islands and Bouvet Island are recognized as biodiversity hotspots. Out of 900 echinoid species, 79 occur south of the Antarctic Polar Front. In the Southern Ocean, many nematode species are new to science and rare. They can be either very resticted in their distribution, or they can occur in a very broad area. On the species level, nematodes might have a high degree of endemism in the Antarctic, although pathways towards lower latitudes exist. Within the gammaridean and corophiidean amphipods, endemism rates may be as high as 79.8% in the Southern Ocean. Endemism is particularly high in Antarctic echinoids: 68% of the species are endemic to the Southern Ocean. More than 80% of all Cidaridae and Schizasteridae are also endemic. Distribution patterns of the Antarctic zoobenthos are also influenced by bathymetry. Nematode genera might have a wider depth range in Antarctica in comparison to other parts of the world, and eurybanthic distribution patterns might also be common in this group. There are three distinct groups within Antarctic amphipod species, with regard to bathymetry: a shelf group, a deep shelf-upper slope group and a deep slope-abyssal group. Although some species appear to have wide bathymetrical distributions, molecular analyses are needed to rule out cryptic speciation. In echinoids, there are stronger similarities between shelf and upper slope than between slope and deep sea.

It remains unclear what drives the high local meiobenthic diversity in the deep-sea, although it could be related to primary productivity. This is investigated by comparing the communities at a Polar Front station and at a station located more to the south. There is also growing evidence that bacteria might constitute an important fraction of the food ingested by nematodes. An *ex situ* enrichment experiment with a ^{13}C label was carried out with deep-sea material from Maud rise. First results are still underway, but a parallel experiment in the Arctic Ocean revealed little or no uptake of bacteria by nematodes.

Another *ex situ* feeding experiment was carried out on King George Island, with material from the shallow Potter Cove. The experiment aims to unravel nematode feeding preferences. ^{13}C-labeled bacteria and diatoms were added to sediment cores under controlled conditions. The samples are currently being processed, but a preliminary survey of the natural community composition revealed high meiobenthic and nematode densities (6315 nematodes/10 cm^2 on average), and a nematode assemblage dominated by *Aponema*, *Daptonema*, *Amphimonhystrella* and *Halalaimus*. This might indicate high amounts of organic food.

In the same area, direct temperature effects on Antarctic benthic communities were investigated by means of a laboratory benthic respiration experiment with closed sediment and water cores incubated at 0°C, 2°C, 4°C and 6°C. There is a strong decline in oxygen concentration for all sediment treatments, although the rate of decrease becomes higher with each temperature increase. The "anoxic" phase is reached after 7 days in the 6°C treatment, whereas the 0°C treatment had not yet reached this phase after 14 days. Benthic respiration was also higher in food-enriched cores, and the decline in oxygen concentration occurred much more rapid in these cores.

Peracarid fatty acid composition, focused on amphipods, revealed distinct differences between pelagic species, which are carnivorous or omnivorous and mainly feed on flagellates, and scavengers, characterised by an intensive *de novo* biosynthesis. In Antarctic scavengers, the speed of adjustment in body tissue stable isotope ratio as a reaction to new food sources differs between species and depends on their lifestyle. The Specific Dynamic Activity (SDA) experiment, designed to obtain a detailed picture of post-prandial metabolism increase, encountered many problems. However, it revealed that scavengers have a strong ability to cope with long periods of starvation.

The echinoid *Sterechinus antarcticus* from the Antarctic Peninsula is a carnivore and deposit feeder, feeding mainly on a wide range of animals and sediments. In contrast, Antarctic Cidaridae only feed on hydrozoans and bryozoans and the temperate species *Paracentrotus lividus* is either an exclusive herbivore (Mediterranean), or an omnivore feeding on plants, algae and animals (Brittany).

Sterechinus antarcticus is clearly a generalist feeder, and might therefore be well-adapted to cope with changes in food resources that might result from global climate change, whereas Cidaridae are probably more sensitive. Gut content analysis and stable isotopes analysis revealed that *Sterechinus antarcticus* ingests large amounts of sediment (and the organic matter associated with it). Most of the bacteria found in the gut of this species were related to inhabitants of marine sediments, and even bacterial groups occurring in cold-seep sediments. Other bacteria were known to be associated with sea ice, marine water or marine invertebrates. To conclude, the gut microflora of *S. antarcticus* is not symbiotic or specific, but consists of (transient) bacteria occurring in its environment, and probably associated with the sediment ingested by the echinoid. Cidaridae are characterized by a poorly developed gut microflora.

Global climate change may lead to the collapse of large ice shelves. In 2002, 500 billion tons or 3250 km^2 of ice from the Larsen B ice shelf collapsed at the eastern side of the Antarctic Peninsula, and this in only one month's time (31/01-07/03/2002). A few years before, in 1995, the ice shelf of the nearby Larsen A region had already disintegrated completely. Ice-shelf collapse initially leads to increased iceberg disturbance and may have detrimental effects on surface primary productivity, but later, the formerly ice-covered area opens up, leading to increased primary production and the opportunity to enter the area for scientific investigations. The area was investigated between 11/01/2007 and 22/01/2007. Meiofauna was collected at one station close to the former ice-shelf edge (B_South), two stations deep inside the Larsen B area (B_North; B_West), and one station deep inside the Larsen A area (A_South), at depths between 229 and 427 m. Pre-collapse, sub-ice conditions were unfavourable because food was limiting, and the meiobenthic community underneath the ice shelves was, although certainly present, clearly impoverished in abundance and diversity. The situation at station B_West, with low densities, low genus richness and high dominance of *Halomonhystera*, indicate pre-collapse conditions. Meiobenthic and nematode communities at all investigated stations were significantly different from each other. Only at station B_South were meiobenthic and nematode densities higher or in the range of densities found at other sites in the Southern Ocean. The 'inner' stations were still impoverished 5 years after the 2002 Larsen B ice-shelf collapse event. After ice-shelf disintegration, densities increased only slowly as a response to locally increased food availability (phytoplankton blooms) and the arrival of quick colonizers from the nearby Weddell Sea. An extrapolation of iceberg scour recolonization speed by nematodes revealed that it would take more than 1000 years for the nematode community in the deeper parts of the Larsen embayment to fully recover its abundance levels. At the other hand, first colonizers might reach the inner Larsen stations within a decade or more. Quick colonizers might have seized the opportunity to swiftly invade the new space. The nematode genus *Microlaimus*, dominant at station B_South, is a rather important and usually (sub)dominant genus in the Antarctic and subantarctic, and is known as an opportunist, successful and fast colonizer. The inner stations B_West, B_North and A_South were not yet colonized by nematodes from the open Weddell Sea at the moment of sampling. Differences in the local genus pool between these stations are probably the result of changes in local environmental conditions. The close resemblance between stations B_North and A_South, although physically separated by the Drygalski Glacier Cliff, is probably the result of a recent phytoplankton bloom in the area. Differences between these stations are attributed to differences in sediment composition. The high diversity at A_South is related to a high amount of fresh food and relatively coarse sediment at this station. On the other end, station B_North is chracterized by low diversity, which is attributed to high dominance of nematodes and of *Thalassomonhystera* within the nematode community.

Ectosymbiosis on cidaroid echinoids positively influences local epibiont biodiversity. However, in the Larsen area, which became recently free of ice cover, the symbiotic communities on cidaroids are poor and resemble epibionts communities found on stones in the same area. This could indicate that the recolonization of the area by echinoid ectosymbionts is still in an early fase, and that a climax community has not yet been established.

The three echinoid species encountered in the Larsen area are all widely distributed, indirect developing non-brooders, characterized by high dispersive capacities. They are also deposit feeders, which feed on a variety of food sources. Such attributes are typical for quick colonizers, indicating that these species might be pioneers in the recolonization of the formerly ice-covered Larsen area.

Increased anthropogenic CO_2-emission has led to a decrease in ocean surface pH. An experiment with controlled lower pH values was carried out to investigate the effect of ocean acidification on larval and adult sea urchins. At lower pH, significantly more larvae showed an abnormal morphology and a reduced size. In adult sea urchins, the internal pH decreased significantly with the decrease of external seawater pH. This indicates that sea urchins have a poor acid-base compensation mechanism. In the subantarctic species *Arbacia dufresneii*, no skeleton dissolution mechanism takes place to compensate the coelomic fluid acidosis. No significant differences in spine regeneration speed with decreased pH were observed, and it is hypothesized that calcification in the endoskeleton of adult sea urchins is not affected by medium-term exposure to low pH. In the Antarcic cidaroid species *Phyllacanthus imperialis*, a certain degree of corrosion was observed, which was higher in young spines at lower pHs, indicating that these structures, characterized by an epithelium cover, are more fragile than the mature, naked spines.

The BIANZO II project succeeded in achieving most of its aims. Future work within phase 2 of the project includes an increased effort in the integration of the results of the separate partner institutions, and the construction and application of the FOREBIO GIS model. Integration will be achieved by a collaborate effort to synthesize the effects of global climate change on the Antarctic zoobenthos, which will result in a joint review paper on this topic.

Our research indicated that global climate change, both warming itself and warming-related changes, clearly affects the Antarctic zoobenthos. Although some effects, such as the disintegration of large ice shelves, are not considered to be entirely detrimental for the benthic fauna, other effects, such as ocean acidification, have been shown to have a negative effect on the development of benthic organisms, *i.c.* echinoids. The work performed within the framework of the BIANZO II project also revealed the complexity of the intimate interactions between organisms and their environment, and the vulnerability of many Antarctic benthic taxa to a changing environment. BIANZO II provides policy decision makers with additional arguments for the acute threat of global warming and for the promotion of environmentally friendly alternatives for current energy supply.

List of BIANZO II publications

Scientific publications

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