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Biodiversity change after climate-induced ice-shelf collapse in the Antarctic

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The marine ecosystem on the eastern shelf of the Antarctic Peninsula was surveyed 5 and 12 years after the climate-induced collapse of the Larsen A and B ice shelves. An impoverished benthic fauna was discovered, that included deep-sea species presumed to be remnants from ice-covered conditions. The current structure of various ecosystem components appears to result from extremely different response rates to the change from an oligotrophic sub-ice-shelf ecosystem to a productive shelf ecosystem. Meiobenthic communities remained impoverished only inside the embayments. On local scales, macro- and mega-epibenthic diversity was generally low, with pioneer species and typical Antarctic megabenthic shelf species interspersed. Antarctic Minke whales and seals utilised the Larsen A/B area to feed on presumably newly established krill and pelagic fish biomass. Ecosystem impacts also extended well beyond the zone of ice-shelf collapse, with areas of high benthic disturbance resulting from scour by icebergs discharged from the Larsen embayments.

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1. Introduction

A widespread habitat in Antarctic waters lies beneath floating ice shelves that cover one-third of Antarctica's continental shelf (Clarke et al., 2007). Such sub-ice-shelf ecosystems are among the least known on earth because of their general inaccessibility, and are diminishing as a consequence of climate change (Cook et al., 2005).

Most marine communities depend on both a gravitational (i.e. vertical) and advective flux of food, especially in habitats deeper than the euphotic zone. In the process of sinking to the seafloor, phytodetritus produced in the euphotic zone undergoes decomposition, and nutritional quality changes with depth and advection distance (Levin et al., 2001). In the Antarctic, proximity to sources of primary production, both vertically and horizontally, may enhance species richness and biomass of consumers, e.g., macrobenthos, krill, and apex predators (Gutt et al., 2004; Knox, 2007). Sub-ice-shelf habitats far from the euphotic zone are colonized by communities relying mainly on horizontal advection of their primary food source. An example is a site located underneath the Ross Ice Shelf, 475 km from the ice-shelf edge, where rates of heterotrophic turnover and benthic faunal abundance were measured to be extremely low (Azam et al., 1979; Bruchhausen et al., 1979; Lipps et al., 1979). In contrast a 'diverse benthic assemblage' was observed under the Amery Ice Shelf, 100 km from open water (Riddle et al., 2007; Post et al., 2007).

The collapses of the Larsen A/B Ice Shelves at the eastern coast of the Antarctic Peninsula in 1995 and 2002 (Fig. 1) are the largest ice-shelf failures ever recorded. These collapses are attributed to an air temperature increase above the global average (Scambos et al., 2000) and provided the first opportunity to explore the structure of formerly ice-shelf covered ecosystems 5 and 12 years after ice-shelf loss.

The objectives of the survey presented here were (1) to search for faunistic elements attributed to the former oligotrophic ice-shelf-covered conditions, (2) to assess the direct impact of the ice-shelf collapse on the benthos, (3) to identify biodiversity patterns of different benthic and pelagic ecosystem components, and to

explore their differential responses to abrupt environmental change following the climate-induced ice-shelf disintegration.

This study was a major contribution to the "Census of Antarctic Marine Life" and the "International Polar Year 2007–2008" providing the first comprehensive results on the biodiversity of formerly ice-shelf-covered areas.

2. Material and methods

2.1. Sampling strategy

The Larsen A/B embayments were the targets of the first macroecological to formerly sub-ice-shelf habitats east of the Antarctic Peninsula (Gutt, 2008). Benthic core and trawl samples, seafloor photos and physical measurements were taken during the expedition ANT XXIII/8 with R/V *Polarstern* in January 2007 at six core sites within the Larsen embayments (A-North, A-South, B-North, B-Seep, B-West, B-South) and at two reference sites (Snow Hill and Dundee Island), approximately 200 km from the original limits of the ice shelves (Fig. 1). At each site, both hard and soft substrates were targeted (if present) to sample a broad range of taxa. Geochemical analyses at B-Seep, where Domack et al. (2005a) discovered a cold seep, revealed a decreased seepage activity (Niemann et al., 2009). Pelagic apex predators (whales and seals) were surveyed by helicopter. Additional seafloor photos were obtained from palaeo-ecological investigations between 2000 and 2005 aboard the RVIB "*N.B. Palmer*" and the "*RV L.M. Gould*".

2.2. Physical oceanographic measurements.

Physical properties of the water column were measured with a CTD Sea-Bird 911 plus (Sea-Bird Electronics, Bellevue, Washington, U.S.A.). Current velocity and directions were measured at B-South every 10 min with an RCM 9 current meter (Aanderaa Data Instruments, Bergen, Norway) deployed for 19 days at 20 m above bottom. The sea-floor was mapped using the multibeam sonar system "Hydrosweep" (Atlas Elektronik, Bremen, Germany) to optimize sampling design and contribute to an integrated interpretation of data (Fig. 2 and S1-7). After navigation control, data were edited with "CARIS HIPS and SIPS" software. Results on sediment parameters such as pigments and grain size, analysed within this project, will be published elsewhere (Sañé Schepisi et al., submitted for publication).

2.3. Meiobenthos and sediment

A 12-tube multicorer (25.5 cm² per tube) was deployed 4–5 times at each Larsen core site. The upper 5 cm was subdivided in 1-cm-slices and sieved on nested 1000- and 32- μ m sieves. Meiofauna was extracted from the sediment by density gradient centrifugation, using Ludox HS-40 as a flotation medium (Heip et al., 1985).

2.4. Macro-epibenthos

Samples were taken by Agassiz trawl (AGT, mouth opening 3 \times 1 m, 10 mm cod-end mesh size) at eleven stations. On average, the AGT was hauled over ground for approximately 25 min at averaged 1.9 km h⁻¹. Trawl lengths ranged from 407 to 1667 m, and were calculated on the basis of the ship's GPS position at the beginning of a haul and when the AGT left the bottom. On deck, a total catch of less than 80 L was completely sorted or a 80-L subsample was taken. Subsamples were sieved on

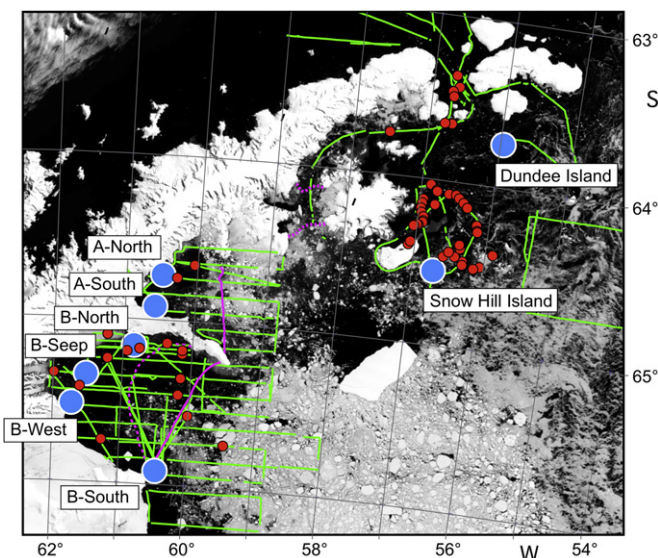


Fig. 1. Area of investigation and sampling sites for *Polarstern* ANT XXIII/8 (PS 69) with sea-ice conditions for 21/01/2007 (MODIS image). Blue circles: core and reference sites for benthic and water column investigations, red circles: whale sightings (observations of individuals or groups) along helicopter transects (green lines). Pink line: ice-shelf edge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

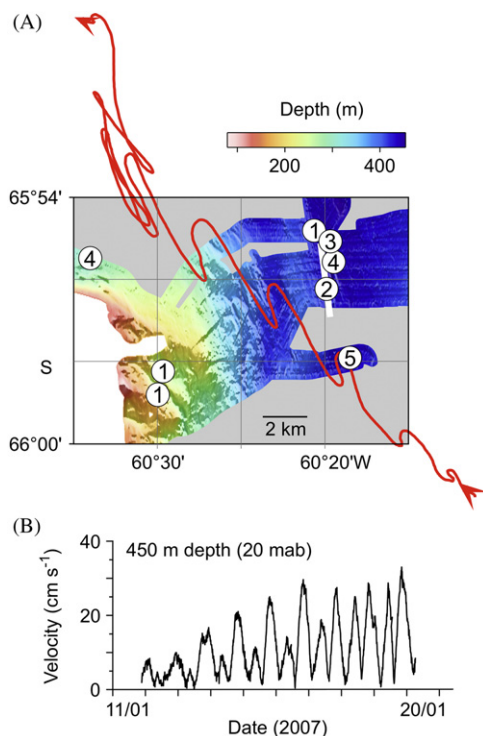


Fig. 2. Current velocity and bathymetric at B-South (A) Bathymetric map (grey: no soundings, white: Jason Peninsula; © AWI, bathymetric working group) with sampling casts; 1: Remotely Operated Vehicle (ROV) stations, 2: bottom trawl (white bar indicates path), 3: multicorer station, 4: Agassiz-trawl station, 5: current meter mooring with current direction depicted as a vector plot (red line) for the time interval 11–20 January 2007, (B) current velocity measured at 450 m water depth, 20 m above sea bottom, by a current meter for the same period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

nested 1000- and 500- μ m mesh. The remainder of the catch was sorted by hand to collect all sponges and fish.

2.5. Megafauna

A Remotely Operated Vehicle (ROV, “Cherokee”, sub-Atlantic, Aberdeen, U.K.) with video and still cameras was deployed to the seafloor at 17 stations. Megafauna is defined here as “animals readily visibly” in video footage sensu Grassle et al. (1975). To assess the length of all transects combined (17.9 km) it was assumed that the ROV followed the GPS-defined ship’s track. With an average width of analysed video strip of 80 cm, this resulted in a total coverage of 2397 m² in Larsen A, 9506 m² in Larsen B, and 2415 m² at the reference sites. These areas were used to analyse: iceberg disturbance (following Gutt and Starman, 2001) and occurrence of rare key taxa such as large glass sponges, stalked crinoids, and aggregations of krill and fish. For community and biodiversity analyses, 42 approximately 60-m² subareas were selected. Due to visibility problems and icebergs scour marks, some of these were not continuous. All visible organisms were counted and identified to the lowest possible taxon. Additional sea-bed images were analysed to study the change in abundance of the deep-sea holothurian *Elpidia glacialis* between 2000 and 2008. Seven photographs, each 1.5 m² in area, were taken during expedition NBP_00_03 with RVIB “Nathaniel B. Palmer” at Larsen A between 690 and 899 m depth in 2000. At Larsen B, 5 photographs were taken at the former ice front, representing 1.46 m² each (NBP_01_07, R/V “Nathaniel B. Palmer”, 2001), and another 20 at different stations formerly covered by the ice shelf between 483

and 963 m depth, representing 3.8 m² each (LMG_05_02, R/V “Laurence M. Gould”, 2005).

2.6. Fish

A commercial bottom-fish trawl (BT), with a mouth opening of 18 \times 3 m and cod-end mesh size of 40 mm, was used at four stations. Trawl speed was 6.5–7.4 km h⁻¹ and average distance trawled per haul was 3.3 km. Total fish catches were analysed.

2.7. Pelagic apex predators

Aerial surveys following representative tracklines were conducted with a helicopter from R/V “Polarstern” (altitude: 180 m; speed: 150 km h⁻¹) (Gutt, 2008). The survey length covered 646 km (6726 km²) in Larsen A, 2388 km (14,381 km²) in Larsen B and 1159 km in the reference areas. Seals were recorded when visible on sea ice and their species identification was done at a representative sub-sample of the sightings data. A detection function was fitted to the perpendicular distances of the sightings data of the different taxa to determine effective strip width (Buckland et al., 2004) for all seal and penguin species pooled. For Killer whales, the number of sightings was too low, so sightings per km effort were calculated. Factors to correct for availability or detectability bias of animals were not collected, so all resulting densities are minimum estimates.

2.8. Statistics

Software package PRIMER 6 was used for numerical analyses (Clarke and Gorley, 2006): diversity (Hill’s N₂: Reciprocal Simpson’s index = 1/ $\sum p_i^2$ with p_i = proportion of individuals in the i th species with alpha diversity referring to single samples, gamma diversity to summed data for core sites), non-metric Multidimensional Scaling (nMDS) to describe faunistic assemblages, ANOSIM ($p < 0.05$) to identify faunistic differences between station groups using Bray-Curtis similarities (square-root transformation for mega- and macrobenthos), BEST/BIOENV for correlations between square-root transformed faunistic abundances and normalized environmental data. Differences between meiobenthic densities and diversities tested by Kruskal-Wallis ($p < 0.05$, PAST software package).

2.9. Data storage and management

Repository reference (ANT-XXIII/8): DOI: 10.1594/PANGAEA.702107 (bathymetry, CTD-data, sea-bed photographs, sea-bed-videos, macrobenthic presences/absences, megabenthic abundances). Data on apex predators are submitted to SCAR-MarBIN.

3. Results

3.1. The benthos

The highest meiobenthic densities were found at the exposed core site B-South near the former ice-shelf edge, and lowest at the sheltered sites B-West and A-South (Table 1; Table S1). B-North revealed intermediate values. Overall densities, taxon richness, and Hill’s N₂ diversity differed significantly among the core sites (Kruskal-Wallis), though no significant results were obtained from any pairwise comparison (after Bonferroni correction). The highest numbers of taxa was found at A-South and B-South, and lowest at B-North. One-way ANOSIM revealed significant faunistic differences between all core sites in total and for each pairwise

Table 1

Impact by iceberg scouring, meio-, mega- and macrobenthic key-taxa, including demersal fish, krill, pelagic fish, and apex predator counts. Rare key species were analysed on total video-transects (Table S4), megabenthic key species were analysed on representative 60 m² video-areas (Table S2), macro-epibenthic key species and fish were sampled by bottom trawl (BT) and Agassiz trawl (AGT), apex predators were surveyed by helicopter transects. Diversity between-core sites (gamma) were calculated by N₂: Reciprocal Simpson's diversity index. R0–R2: stages of recolonization after iceberg scouring according to Gutt and Starman (2001). HEX: Hexactinellida, DEM: Demospongiae, CAL: Calcareia, HYD: Hydrozoa, OCC: Octocorallia, BRY: Bryozoa, GAS: Gastropoda, CRU: Crustacea, CRI: Crinoidea, OPH: Ophiuroidea, AST: Asteroidea, HOL: Holothuroidea, ECH: Echinoidea, ASC: Ascidiacea, PIS: Pisces. n: number of individuals, esw: effective strip width; DI: Dundee Island, SH: Snow Hill Island. +: presence, 0: absence.

| | B-South | B-West/North | A-South/North | DI/SH | Remark |
|--|------------------|----------------------------|---------------|-----------|-----------------------|
| Depth (m) | 177–446 | 152–310 | 152–309 | 146–309 | |
| Area scoured by ICEBERGS, R0–R2 (%) | 4.2 | 6.3 | 2.0 | 99.6 | |
| MEIOBENTHOS | | | | | |
| Abundance range (n/10 cm ²) | 2421–3870 | 359–723 | 308–859 | | |
| Gamma-diversity (N ₂) | 1.14 | 1.38 | 1.76 | | |
| No. of taxa | 18 | 16 | 19 | | |
| RARE KEY SPECIES | | | | | |
| CRI <i>Bathycrinus australis</i> (n/1000 m ²) | 0.3 | 4.7 | 0.0 | 0.0 | Deep-sea |
| CRI <i>Dumetocrinus antarcticus</i> (n/1000 m ²) | 0.0 | 0.7 | 11.6 | 0.7 | Deep-sea family |
| HEX Hexactinellida spp., > 25 cm (n/1000 m ²) | 0.3 | 0.7 | 11.6 | 0.7 | Slow growth |
| CRU <i>Euphausia superba</i> & <i>E. crystallorophias</i> (abundance / no. of patches) | 5 / 0 | 512/7 | 349/7 | 72 / 3 | Trophic key species |
| MEGABENTHOS | | | | | |
| Total abundance (n/100 m ²) | 1349.1 | 1131.3 | 4238.1 | 3979.3 | |
| No. of species (bulk groups excluded) | 30 | 37 | 29 | 63 | |
| Gamma-diversity (N ₂) | 2.90 | 6.37 | 4.83 | 6.73 | |
| KEY SPECIES (n/100 m²) | | | | | |
| HEX Hexactinellida spp., < 10 cm | 0.4 | 0.8 | 41.6 | 5.4 | Pioneer |
| HEX Hexactinellida spp., > 25 cm | 0.0 | 0.0 | 0.7 | 0.0 | Slow growth |
| DEM <i>Stylocordyla borealis</i> (spheric) | 0.0 | 0.0 | 0.0 | 19.8 | Pioneer |
| DEM <i>S. borealis</i> (oblong) and <i>Homaxinella</i> spp. | 2.7 | 0.3 | 26.0 | 779.6 | Pioneer |
| DEM <i>Tetilla</i> sp. | 0.0 | 0.0 | 0.0 | 3.3 | Pioneer |
| HYD <i>Monocaulus microrhiza</i> | 13.7 | 1.1 | 52.2 | 3.2 | Pioneer |
| BRY <i>Melicerita obliqua</i> | 0.0 | 0.0 | 0.0 | 4.4 | Pioneer |
| CRI <i>Dumetocrinus antarcticus</i> | 0.0 | 0.8 | 2.3 | 0.0 | Deep-sea family |
| AST <i>Brisinga</i> cf. <i>distincta</i> | 0.0 | 0.8 | 0.0 | 0.0 | Deep-sea sp. |
| AST <i>Freyella fragillissima</i> | 1.0 | 0.8 | 0.0 | 0.0 | Deep-sea sp. |
| HOL <i>Protelpidia murrayi</i> | 0.4 | 7.6 | 0.0 | 0.0 | Deep (shelf) species |
| HOL <i>Elpidia glacialis</i> (2000: NBP) ^a | No data | No data | 3361.1 | No data | Deep-sea sp. |
| HOL <i>Elpidia glacialis</i> (2001: NBP) ^a | No data | 8.2 ^b | No data | No data | Deep-sea sp. |
| HOL <i>Elpidia glacialis</i> (2005: LMG_05_02) ^a | No data | 38.4 ^b | No data | No data | Deep-sea sp. |
| HOL <i>Elpidia glacialis</i> | 0.0 | 0.6 (1278.9 ^b) | 0.0 | 0.0 | Deep-sea sp. |
| ECH <i>Sterechinus</i> spp. | 11.9 | 16.7 | 72.6 | 17.5 | Invader from shallow |
| ASC <i>Corella eumyota</i> | 0.7 | 58.2 | 1054.8 | 0.1 | Pioneer |
| ASC Cf. <i>Molgula pedunculata</i> | 0.7 | 249.8 | 524.6 | 0.0 | Pioneer |
| ASC <i>Synocicum</i> sp. 1 | 0.0 | 0.0 | 0.0 | 361.2 | Pioneer |
| MACROBENTHIC KEY SPECIES | | | | | |
| No. of species (BT excluded) | 108 | 52 | 46 | 148 | |
| HEX <i>Caulophacus</i> sp. 1 | +(dead) | 0 | 0 | 0 | Deep-sea genus |
| CAL <i>Clathrina</i> "primordialis" (juvenile) | + | 0 | 0 | 0 | Pioneer, 2 mm large |
| DEM <i>Abyssocladia</i> sp. 1 (putative n. sp.) | + | 0 | 0 | 0 | Deep-sea genus |
| DEM <i>Polymastia invaginata</i> (juvenile) | 0 | + | 0 | 0 | Pioneer, 3–5 mm large |
| GAS <i>Sequenzia antarctica</i> | 0 | + | 0 | 0 | Deep-sea |
| GAS <i>Calliotropis</i> sp. 1 | 0 | +(dead) | 0 | 0 | Deep-sea genus |
| AST <i>Brisinga distincta</i> | 0 | + ^b | 0 | 0 | Deep-sea |
| AST <i>Freyella fragillissima</i> | + | + | 0 | 0 | Deep-sea |
| AST <i>Hymenaster perspicuus</i> | 0 | + | 0 | 0 | Eurybath |
| ECH <i>Pourtalesia debilis</i> | 0 | + ^b | 0 | 0 | Deep-sea |
| ECH <i>Sterechinus antarcticus</i> | + | + | 0 | 0 | Invader |
| ECH <i>Sterechinus neumayeri</i> | + | + | + | + | Invader |
| ECH <i>Cystocrepis</i> aff. <i>setigera</i> | 0 | 0 | 0 | 0 | West coast Americas |
| FISH (n/1000 m²) | | | | | |
| PIS <i>Pleuragramma antarcticum</i> | Larsen B 0.99 | | Larsen A | DI/SH | Most abundant fish |
| PIS <i>Trematomus</i> spp. (no. of spp.) | 0.70 (6) | | | | |
| Total abundance (no. of spp.) | 1.83 (18) | | | | |
| APEX PREDATORS | | | | | |
| Transect length (km) | 2388.0 | | 645.7 | 1159.3 | |
| Antarctic Minke (n/km ²); esw: 1.07 km | 0.014 | | 0.007 | 0.073 | |
| Orca (n/km) | 0.0 | | 0.0 | 0.028 | |
| Penguins (n/km ² on ice / n/km ² total); esw: 0.45 km | 0.014/0.014 | | 0.0/0 | 0.0/8.647 | |
| Seals (n/km ² on ice); esw: 0.54 km | 1.459 | | 1.861 | No data | |

^a For differences in data acquisition between expeditions see "Material and methods".

^b Sampled at B-Sea.

test except between A-South and B-West (after Bonferroni correction), visualized by the nMDS-plot (Fig. 3). The dominance of nematodes (93%) at B-South caused a low alpha-diversity. Their relative abundance was also high at B-North (92%), but significantly lower at B-West (85%) and A-South (74%). Nematodes, nauplii and harpacticoid copepods (adults and larvae) were consistently most abundant.

The macro-epibenthos at B-South, the original ice-shelf edge, was more than twice as rich in taxa compared to all other Larsen core sites, with cnidarians and echinoderms being especially speciose (Fig. 4A; Table S3). Average densities and species numbers were much higher than those at the inner shelf site B-West, which, however, had higher diversity values. According to video observations, the shallow depths (< 300 m) at B-South were dominated by hard substrata, especially where the sea-bed was steep, and soft bottoms with gravel and dropstones were only found in a sea-floor depression > 400 m depth (Fig. 2). At the > 800-m deep station B-Seep, located in the centre of the inner Larsen B embayment, macro-epibenthic taxon richness was relatively low while megabenthic densities were still high compared to the poorest station B-West due to the abundant deep-sea holothurian *Elpidia glacialis*, leading to low alpha and gamma diversity (Table S2). At Larsen A, this species was

abundant five years after the ice-shelf collapse in 1995 but rare at Larsen B (B-Seep) four years after the ice-shelf disintegration. Values remained low until 2005 but increased on average to almost 1300/100 m² by 2007 everywhere along two 1.4 and 1.5 km long video transects. The two core sites North and South of the strip of ice between both Larsen embayments, B-North and A-South, had high proportions of gravel and boulders, visible on video and photographs of all six ROV stations. Macro-epibenthic richness at A-South was three times as rich as that of B-North and had the highest megabenthic abundance dominated by the hydrocoral *Errina laterorifa*, sponges and two ascidian species (Table 1; Tables S2–3). Megabenthic density at B-North was dominated (40%) by cf. *Molgula pedunculata*, being also abundant at A-South, (Fig. 4B). At A-South, densities of all three size classes of hexactinellid sponges was highest, while mostly large specimens occurred at B-South and B-West and then in low abundances. The surface sediment of station A-North was predominantly soft. Macro- and megafaunal abundances were similarly poor in taxa and abundance. Macro-epifauna was dominated by infaunal actinians, polychaetes and suprabenthic mysids.

The two reference sites, Snow Hill Island and Dundee Island, were generally richer in density and species number of macro- and megabenthic taxa than the Larsen core sites (Fig. 4C). Alpha diversities (N₂) ranged from 1.77 to 12.44 resulting from either locally high abundances of demosponges and ophiuroids or from an even distribution of specimens over the species. Hexactinellid sponge density was extremely low with only 2% and 18% of the generally low abundances recorded in the formerly ice-shelf covered A-South core site (Table 1, Tables S2–3).

The composition of the meio-, macro- and megabenthos showed distinct assemblages especially at B-Seep and the reference sites for the mega- and macrofauna but also between all Larsen core sites (Fig. 3; one-way ANOSIM). For the megabenthos, the only non-significant difference was that between B-South and A-South/A-North. Early stages of megabenthic recolonization were spread most widely over the nMDS-plot, indicating a high species turnover (beta-diversity). The correlation between the abundance data of the megabenthos and environmental parameters was best for the following variables: sediment type (Fig. 3), distance from former ice shelf edge, and water depth ($\rho=0.728$; 21 samples, replicates within stations not considered). The fourth parameter, a latitudinal gradient, did not play a significant role. The best correlation using a single environmental parameter ($\rho=0.600$) was obtained for the distance between station and the former ice shelf edge.

In addition to macrobenthic taxa that are well known to occur on the Antarctic shelf, 16 species or genera were found that are typical for the deep sea. Most of them belonged to the echinoderms (Table 1, Fig. 4D), together with representatives of gastropods and sponges. Although a certain proportion of specimens have not differentiated to species level, the number of < 10 macrobenthic species thought to be new to science was low. A different result was obtained for the meiobenthos. One sample from B-South contained 35 species of harpacticoid copepods, 32 of which are new to science. Virtually no meiofaunal overlap existed between stations B-South and B-West (only 70 km apart) with only one shared species. At B-West, a further 13 putative new species were found.

3.2. Water masses and dynamics

CTD-profiles at five Larsen core sites showed a high temperature - low salinity surface layer, which was slightly more obvious in the central Larsen B embayment at B-Seep with temperatures

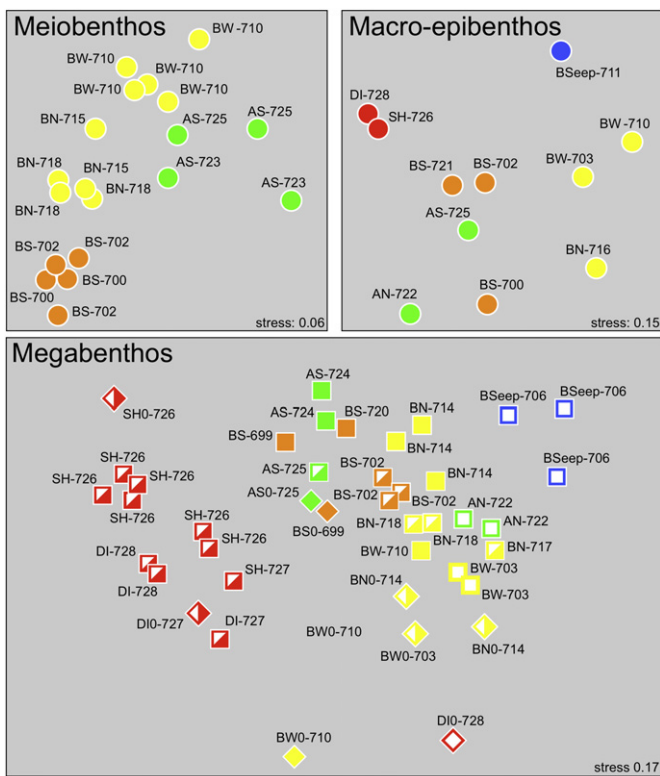


Fig. 3. Plots of non-metric Multi-Dimensional Scaling (MDS) of benthic assemblages; orange: B-South (BS), yellow: B-West (BW) and B-North (BN), blue: B-Seep, green: A-South (AS) and A-North (AN), red: reference areas (Dundee and Snow Hill Islands, SH/DI). Meiobenthos (Bray-Curtis similarities, square root data transformation, taxa present in ≤ 2 samples excluded). Macro-epibenthos (Sørensen similarities, presence/absence data, all 304 taxa considered); Megabenthos (Bray-Curtis similarities, 73 out of a total of 107 taxa considered, systematic bulk groups and rare taxa present in ≤ 2 samples excluded), squares: undisturbed areas, diamonds: disturbed areas; filled symbols: predominantly hard substratum, semi-filled: mixture of hard and soft sediments, empty symbols: predominantly soft sediments. Among the above mentioned colour coded station groups only the faunistic difference between B-South (orange) and A-South/A-North (green) is non-significant; ANOSIM, $p < 5\%$, fresh iceberg scours (BNO, BW0, BS0, BNO, AS0, DIO, SH0) not considered. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

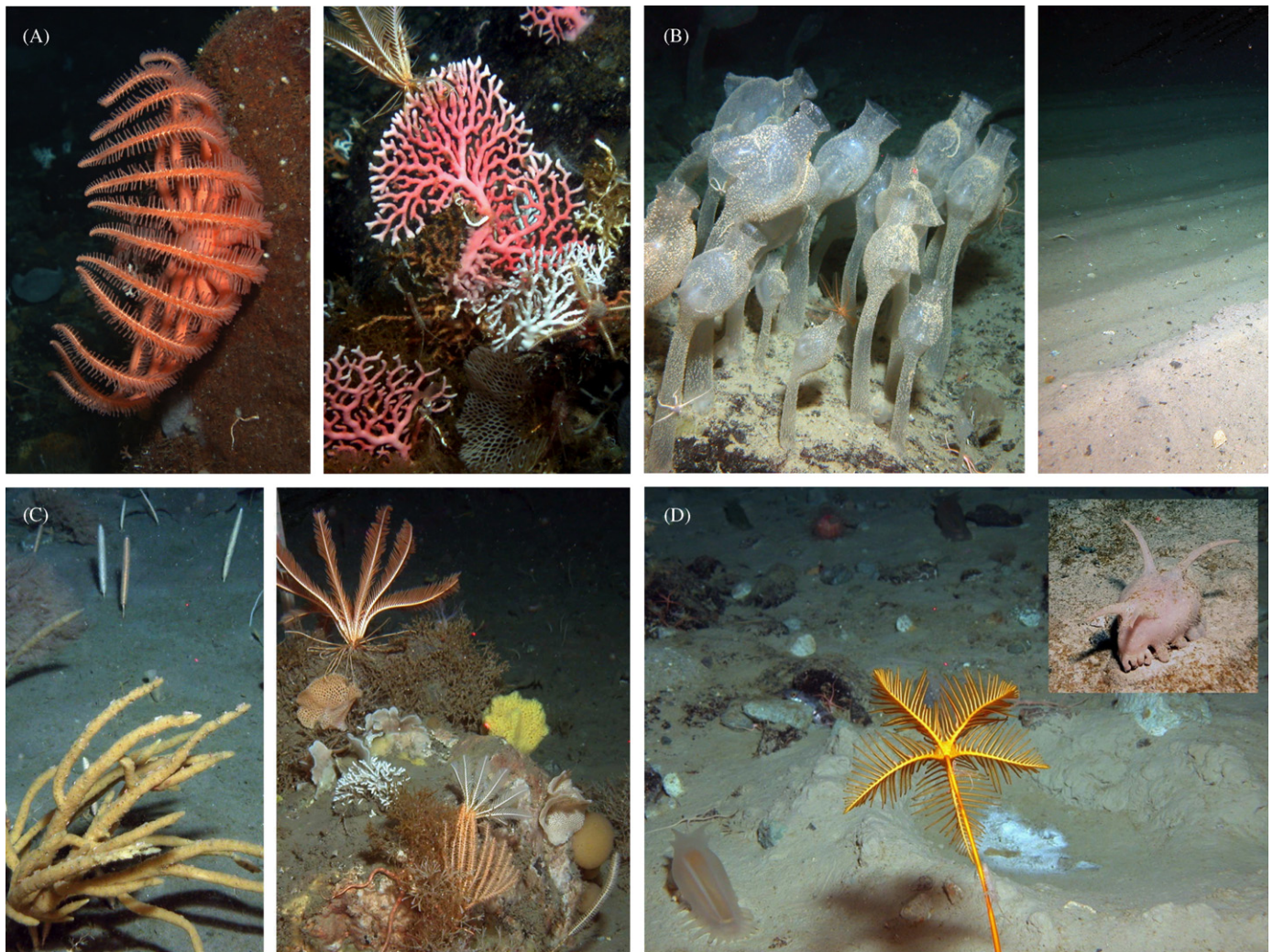


Fig. 4. Sea-bed photographs (A) species preferring hard substrata (B-South): the asteroid *Freyella fragillissima* (left), the hydrocoral *Errina laterorifa* (right), (B) B-North, ascidians cf. *Molgula pedunculata* growing on a hard substratum (left), iceberg scour mark (right), (C) early stage of recolonization (left) with the demosponge *Homaxinella* sp. (foreground) and juvenile cnidarians (background) as pioneer organisms (Snow-Hill Island) with an unidentified sponge (yellow), compound ascidians, cnidarians, and different bryozoans, growing on a boulder and being used by a crinoid as substratum, (D) deep-sea fauna (B-West): the crinoid *Dumetocrinus antarcticus* of the deep-sea family Hyocrinidae, the eurybathic elasipod holothurian cf. *Penagone vignioni* (lower left) and the deep-sea elasipod holothurian *Protelpidia murrayi* (upper right); the white layer inside the small crater could be bacteria of unknown origin. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Photographs: J. Gutt and W. Dimmler, © AWI/MARUM, University of Bremen.

above 0 °C (Fig. 5) and below a homogenously low temperature very close to the freezing point. At the reference sites, the profiles indicated a slightly warmer and mixed water column. Near-bottom currents at B-South had a high net velocity heading from off-shore into the Larsen B embayment, which was superimposed by strong tidal cycles (Fig. 2).

3.3. Iceberg scouring

In the shallowest areas of the Larsen embayments (100–200 m depth), only 7% of the seafloor was disturbed by icebergs (Table 1, results for depth strata not shown; Fig. 4B). For areas with depths < 350 m, the proportion of undisturbed areas at Larsen A and B was very high (94–95%) compared to only 0.4% at the reference sites. The proportion of seafloor area in advanced stages of recolonization, defined by Gutt and Starman (2001) for the eastern Weddell Sea, varied between 4 and 59% at the reference sites, whereas these stages did not occur at the Larsen sites (Table S4).

3.4. The pelagic system

The fish fauna of Larsen B consisted mainly of high-latitude Antarctic species dominated by species of *Trematomus* with additional lower latitude representatives like *Lepidonotothen larseni* and *Gobionotothen gibberiformis*. The pelagic *Pleuragramma antarcticum* was the most abundant fish. Both krill species, *Euphausia superba* and *E. crystallographias*, were registered by the ROV-cameras close to the bottom, even potentially feeding on the sediment surface at B-West and A-North (Table S3). The helicopter survey of apex predators (Table 1) showed highest seal densities, with 1.86 n/km², at Larsen A compared to 1.46 n/km² at Larsen B. Species composition was as follows: 71% Crabeater seal (*Lobodon carcinophagus*), 24% Weddell seal (*Leptonychotes weddellii*) and 5% Leopard seal (*Hydrurga leptonyx*). Emperor penguins (*Aptenodytes forsteri*) were seen in the former shelf-ice regions in a very low density of 0.014 n/km². In the northern reference areas, Adelie penguins (*Pygoscelis adeliae*) were much more abundant but not counted individually. The only cetacean species seen in Larsen A and B was the Antarctic Minke whale

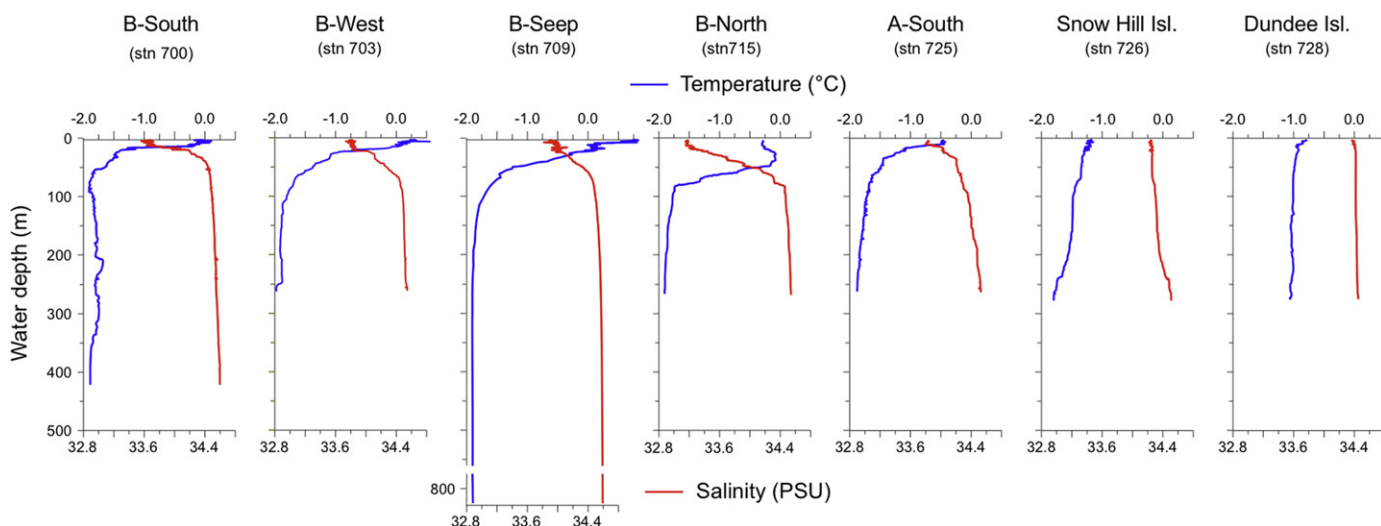


Fig. 5. Salinity and temperature (CTD) profiles of the water column at the Larsen A/B core and reference sites.

(*Balaenoptera bonaerensis*). Its density was about a magnitude lower in Larsen A/B in comparison to the northern reference area. Killer whales (*Orcinus orca*) were only seen north of the Larsen area.

4. Discussion

This first ecological survey in a large area that was until recently covered by permanent ice shelves provided a biological snapshot into ecosystem responses to ice-shelf loss. The results allow conclusions concerning processes occurring before, during and after the climate-induced disintegration of the ice shelves.

4.1. Conditions before the ice-shelf collapse

Before the Larsen ice shelf disintegrated, even the shallow sea floor between 100 and 200 m was mainly covered by floating rather than grounded ice, since the video survey showed only 7% of sea floor disturbed by grounded ice. This evidence is in contrast to earlier modelling indicating a thicker, grounded ice shelf (Sandhäger et al., 2005). In the non-grounded areas, the presence of hexactinellid sponges > 20 cm tall testifies to the existence of suspension feeders before the ice-shelf disintegration because these sponges, especially *Rossella nuda* and to a lesser extent *R. racovitzae*, are known to grow very slowly when adult (Dayton, 1978). The extremely low densities of small and intermediate-sized specimens of these sponges at Larsen B suggest that little recruitment has occurred by five years after ice-shelf disintegration. Further, it suggests that, during the period of ice-shelf cover, very food-poor conditions limited the recruitment of sensitive juvenile stages whilst the few surviving specimens resisted oligotrophic conditions by reaching a threshold in size (Gutt, 2006). Food availability is also a major factor structuring meiobenthic communities in general (Vanhove et al., 2000) and sub-ice oligotrophic conditions obviously affected meiobenthic abundance negatively. Low food conditions probably resulted in low initial densities, with a similar composition of taxa at the most in-shore core site B-West and A-South lying close to the current tongue between Larsen A and B, which locally continued to disintegrate after the big shelf collapses. Only at B-South at the original ice-shelf edge were densities within the range of those found elsewhere in ice-shelf free Antarctic waters (Ingels et al., 2006).

In general, the macro- and megabenthic communities had a composition typical for non-ice-shelf-covered Antarctic seafloor, including sessile filter feeders such as hexactinellid sponges, cnidarians and ascidians (Gutt, 2007). However, this fauna was impoverished in species richness and density when compared to the shelf fauna of the eastern Weddell Sea studied with the same methods (Gutt et al., 2004). In particular, the mobile fauna (e.g., amphipods and isopods) associated with large filter feeders was extremely poor in the Larsen core sites. In addition, 16 representatives of deep-sea taxa, mainly echinoderms, occurred at depths of 300–800 m in the Larsen A/B area. Deep-sea taxa included the hyocrinid *Bathycrinus australis* previously known only between 1700 and 8300 m depths (Schiaparelli et al., 2007); *Dumetocrinus antarcticus*, also belonging to the deep-sea family Hyocrinidae, known only from deeper than 1000 m; and the asteroids *Brisinga cf. distincta* and *Freyella fragillissima* (Fig. 4A) found previously only at depths > 1000 m (Clark and Downey, 1992). Two echinoids from the deep-sea family Pourtalesiidae were collected at the deepest Larsen station (B-Seep); *Pourtalesia debilis* is known as eurybathic in the Weddell Sea, whereas *Cystocrepis aff. setigera* is new to Antarctica. This latter species was previously recorded in the Pacific (off the coast of Alaska, Equator, Mexico, and Peru) between 2876 and 3800 m depths (David et al., 2003). The holothurians *Protelpidia murrayi* (Fig. 4D) and *Elpidia glacialis* belong to the deep-sea order Elaspoda and rarely occur above 400 m on the Antarctic shelf (Sumida et al., 2008). However, both species were photographed in high abundances at the edge of the Filchner Ice Shelf (Gutt and Piepenburg, 1991). Apart from one questionable record, the hexactinellid sponge genus *Caulophacus* had only been found at > 2400 m depth (Janussen and Tendal, 2007), and the carnivorous demosponge *Abyssocladia* was only known from the Pacific at 1997–6127 m depths (Vacelet, 2006). The gastropods *Seguenzia antarctica* and *Calliotropis* are thought to be true deep-sea taxa (Schwabe et al., 2007). We assume that the decomposition of organic matter during transit from the euphotic zone to the deep sea is similar to that from the open water to areas beneath ice shelves. This allows sub-ice-shelf emergence of deep-sea species adapted for very oligotrophic conditions. Thus, we attribute the occurrence of these deep-sea taxa in the Larsen A/B area in 2007 to reflect the former ice-covered, oligotrophic conditions.

At present, the composition of the macro- and megabenthic species does not suggest a considerable endemic fauna occurred in the sub-ice-shelf habitat. Rather, the high number of

undescribed meiobenthic harpactoid crustaceans and the high spatial heterogeneity in macro- and meiobenthos exhibits a pattern typical of the deep-sea benthos (Brandt et al., 2007; Fonseca and Soltwedel, 2007).

4.2. Direct impact of the ice-shelf collapse

The low proportion of areas assumed to be recently disturbed by iceberg scour indicates that, surprisingly, the collapse events in the Larsen A and B areas did not cause an area-wide impact on the shallow shelf. Obviously, a relatively steep slope in combination with the iceberg's draught and direction of movement impeded more catastrophic devastation of the sea-floor at depths between the groundling line and 250 m, which marks the lower limit of intense iceberg scouring in other Antarctic areas.

Another surprise was the discovery of distinct evidence of benthic ecosystem disturbance at Snow Hill and Dundee Island. Hexactinellid sponges were nearly absent and demosponges, except pioneer species characterized by massive recruitment and fast growth, were rare compared to undisturbed sites in the eastern Weddell Sea (Table 1, Gutt and Piepenburg, 2003). In addition, fast-growing sessile ascidians and sponges, as well as mobile echinoderms, constituted an assemblage indicative of a highly dynamic environment. The sponge *Homaxinella* grows very successfully in the Ross Sea in areas devastated by anchor ice (Dayton, 1978) and near glaciers (Dawber and Powell, 1997), in the eastern Weddell Sea it occurs almost exclusively in former iceberg scours (Gutt and Piepenburg, 2003). The proportion of seabed recently devastated by grounded icebergs exceeded maximum values observed in the eastern Weddell Sea (Gutt and Starmans, 2001). Satellite images following the Larsen ice-shelf disintegration show an enormous number of icebergs moving from Larsen B towards the reference sites (Rack and Rott, 2006). In contrast, studies of icebergs that calved farther south showed northward drift tracks far off-shore along the continental shelf (Schodlok et al., 2006). We conclude that in accordance with patch-dynamics theory (Pickett and White 1985), the massive iceberg calving events at Larsen A/B caused extensive seafloor disturbance along the eastern tip of the Antarctic Peninsula, where, due to the production of megafaunal successional mosaics, beta diversity could reach high values (Table 1).

4.3. Biodiversity change

Taking the investigated environmental conditions at Larsen B, we can conclude that close to the former ice shelf edge at B-South, currents provided the required conditions for a horizontal advection of food from far off-shore. Strong tides are superimposed on the net current, which might resuspend nutritive particles for suspension feeders (Table 1, Fig. 2).

Although the meiofauna at the sites B-South and A-South differs greatly in abundance, they are comparable in taxon richness. Analogous diversity results were found for the nematode communities at the genus level: i.e., highest diversity at B-South and A-South, and lowest at B-North (Raes et al., in press). High densities and a high diversity at B-South might result from a longer period free of ice cover and increased food supply in combination with the long-term proximity of the open Weddell Sea as a source of advected food and new colonizers. The meiobenthic community at this site could be in an intermediate or later stage of succession, with a high dominance of nematodes. High diversity at A-South could be related to a high amount of fresh food and a coarser sediment composition. For the most inshore core sites, Raes et al. (in press) calculated a recovery time of > 1000 years based on nematode data.

Megabenthic diversity at between-station (alpha) and between-core site (gamma) scales was correlated with species richness (Table 1 and S2). The high values at Larsen B might still reflect the old shelf-ice covered conditions. Low values at B-Seep and A-South are due to the dominance of single species, which responded quickly to the environmental regime shift and allow, similarly to the meiobenthos, the application of the intermediate-disturbance hypothesis (Huston, 1994) for an early stage of biodiversity-change. No latitudinal gradient was found within the Larsen area when environmental factors and the megabenthic pattern were correlated. Obviously, differences in the Holocene food supply for higher trophic levels and a series of advances and collapses of the Larsen A ice shelf (Brachfeld et al., 2003), compared to a permanent cover at Larsen B (Domack et al., 2005b) affects recent regional faunistic differences significantly. The strongest single environmental correlated with the megabenthic community structure was distance to the former ice-shelf edge, suggesting that former ice-shelf conditions substantially influenced benthic community structure 5 and 12 years after ice-shelf collapse.

Food supply for the benthos is considerably affected by ocean current activity, which also shapes the sediment. More directly, food conditions are reflected by the concentrations of chlorophyll *a* and its degradation product phaeophytin *a* in surface sediments. Concentrations of both were low in the Larsen A/B areas (Sañé Schepisi et al. (submitted for publication)). Despite the formation of a polynya three months before the measurements, sea-ice coverage (Fig. 1) probably hampered primary production similar to the observed reduction in primary production due to a giant iceberg in the Ross Sea (Arrigo and Dijken, 2003). The largest seafloor concentrations of phytoplankton pigments occurred at B-Seep, B-North and A-South, probably because higher primary production was facilitated at these sites by the most obvious stratified sea-surface layer (Fig. 5). Stations B-North and A-South could have been influenced by a recent phytoplankton bloom in the area, which might be related to increased run-off and meltwater from the glaciers on the nearby land. Additionally, B-Seep is situated in an inner-shelf depression probably accumulating phytodetritus deposition.

Benthic species likely benefitting from the trophic regime shift after the ice-shelf collapse include the two deep-water holothurians *Protelpidia murrayi* and *Elpidia glacialis*, a phenomenon also known for related species from the deep-sea (Billett and Hansen, 1982; Wigham et al., 2003) and being related to the quality of food affecting their reproduction. Assumed pioneer species were found in several taxa. Two ascidians, *Corella eumyota* and cf. *Molgula pedunculata* (Fig. 4A), were abundant at A-South, which was ice-shelf free 12 years prior to our investigations, and at B-North. At the latter, both species must have started to grow before the Larsen B breakout, because they were rare in iceberg scours which could only have originated after 2002. In addition, one calcareous sponge and one demosponge were found exclusively as juveniles in Larsen B. The population structure of hexactinellid sponges revealed a high percentage of juveniles (98%) at A-South under the former ice shelf, when compared to undisturbed areas in the eastern Weddell Sea (59%) (Table 1, Gutt and Piepenburg, 2003). This indicates unusually successful recruitment and growth under the new ice-shelf-free conditions. In addition, the echinoids found on the newly exposed Larsen shelf, *Sterechinus antarcticus*, *S. neumayeri*, and *Notocidaris mortensenii*, are all non-brooders, two of which have pelagic larvae (David et al., 2003). These spawners are likely to be fast colonizers because of their high dispersal abilities. Their lowest abundance at the innermost B-West site is consistent with a post-ice-shelf colonization gradient. Other shelf-specific echinoids, which are mostly brooders, were absent in the Larsen area but present at both reference sites.

The reference sites had higher faunal diversity than the Larsen stations at both the local and regional scales. The presence of

slow-growing hexactinellid sponges and demosponges shows that they can potentially grow at the sites. However, these indicators of long-term environmental stability were extremely rare, giving evidence for non-equilibrium in the faunal succession, shaped by a high rate of disturbance and leading to high habitat heterogeneity. The local dominance of some sessile pioneer and mobile species such as ascideans, *Homaxinella*-sponges (Fig. 4C), previously known almost exclusively from areas disturbed by ice (Gutt and Starman, 2001) and echinoderms are indicative of a highly dynamic environment with a low alpha diversity. Grounded icebergs were observed at the reference sites in much higher concentrations than further in- and off-shore (author's unpublished observation). As a consequence, the disturbance observed in the megabenthos is likely to be caused by the direct impact of icebergs. These dynamic environmental conditions might have been amplified by the completely mixed water column caused by the high number of grounded icebergs in addition to a heterogeneous current pattern (von Gyldenfeldt et al., 2002) and strong tides (Robertson et al., 1998). Nevertheless, we conclude that the recovery of the megabenthos in terms of abundance and species richness is faster in the reference area due to its generally richer benthos than at the poorer Larsen sites, even if it might need a few hundred years to recover as calculated for the eastern Weddell Sea (Gutt and Starman, 2001).

Pelagic animals showed much more rapid colonization and exploitation of the newly ice-free Larsen area. In terms of species composition, a typical Antarctic fish fauna had become established by the time of sampling; however, abundances were 10 times lower than in the eastern Weddell Sea (Ekau and Gutt, 1991). Evidence of strong pelagic-benthic coupling was found by the benthic presence of the key trophic species *Pleuragramma antarcticum*, even at the deepest site, together with suprabenthic concentrations of both Antarctic krill species, *Euphausia superba* and *E. crystallorophias*, which have obviously invaded after phytoplankton blooms developed following ice-shelf breakout. The abundances and species composition of seals in the Larsen A/B regions were comparable to other areas of the Weddell Sea (Flores et al., 2008). Their higher abundance in Larsen A compared to Larsen B (Table 1, Fig. 1) was potentially caused by higher sea ice coverage providing better haul-out opportunities. The species composition is similar to that in the western Weddell Sea. The higher density of penguins in the northern reference area is related to breeding colonies situated on the ice-free areas of the coast (Woehler, 1993). Densities of Minke whales were similar to those reported west of the Antarctic Peninsula (Ainley et al., 2007). In the reference area, densities were about an order of magnitude higher than in Larsen A/B, possibly because of ongoing migration into the Larsen A/B areas at the time of study. Orcas were observed attacking Minke whales in the reference area within the Antarctic Sound, while none were seen within the Larsen A/B areas.

4.4. General conclusion and outlook

The climate-induced change from an assumed oligotrophic sub-ice-shelf ecosystem to a productive Antarctic shelf ecosystem shows extreme variations in the pace of development of the different ecological subsystems. We predict that the rapid response in the pelagic system will lead to the gradual development of a "typical" diverse benthic shelf fauna, ultimately excluding most deep-sea benthic taxa from depths < 400 m. This gradual shift in benthic ecosystem structure, of which the first stages are now visible, could be interrupted by terrestrial deglaciation and land run-off caused turbidity in coastal waters (Smale and Barnes, 2008). Such conditions are unlikely to be

tolerated by the newly developing suspension feeders, their associated fauna and later colonizers, and could result in a limited number of opportunistic species surviving on the Larsen A/B shelf.

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