

Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs

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ABSTRACT: Analysis of seabed video-strips on the Weddell Sea shelf provided evidence that the effects of iceberg scouring on megabenthic assemblages differ, depending on spatial scale. At a local scale (1 to 100 m), undisturbed glass sponge-associated habitats were significantly more diverse than disturbed ones; at a regional scale (1 to 100 km), increased habitat heterogeneity caused by iceberg scouring enhanced species diversity. The pace and succession of the recolonization exhibits high variability and is difficult to predict. The results not only underpin the concept that disturbance events are essential factors in the regulation of ecosystem dynamics, but also emphasize the relevance of scale in the evaluation and explanation of diversity patterns.

KEY WORDS: Biodiversity · Intermediate-disturbance hypothesis · Mosaic cycle

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INTRODUCTION

Catastrophic disturbances such as forest fires, tree falls or hurricanes are recognized to be fundamental to ecosystem functioning (Naeem et al. 1994, Grime 1997, Hooper & Vitousek 1997, Tilman et al. 1997, White & Jentsch 2001), since their disastrous initial impacts are followed by positive effects on biodiversity (Dayton & Hessler 1972, Huston 1994).

According to a recent assessment, iceberg scouring is one of the 5 most significant impacts on any ecosystem on Earth (Garwood et al. 1979, Gutt & Starms 2001). It has most likely been a major driving force in structuring Antarctic benthos since the continent began to cool and glaciers extended up to the coast approx. 25 to 30 million yr ago (Hambrey et al. 1991). Mainly quantitative effects of scouring on meio- and macrobenthos have been described and reviewed by Gutt et al. (1996), Conlan et al. (1998), Peck et al. (1999), Gutt (2001) and Lee et al. (2001a,b).

The intermediate-disturbance hypothesis predicts a high diversity caused by intermediate levels of disturbance (Huston 1979). In the event of frequent disturbances, only a few species will persist, i.e. those that are able to attain maturity fast. If disturbances

are rare, competitive elimination results either from an efficient exploitation of limited resources by some species or from direct interspecific interference, whereby only the most robust competitors will survive. Consequently, diversity is expected to be highest at intermediate levels of disturbance (Connell 1978). Evidence for the intermediate-disturbance hypothesis predictions has been provided by several studies, predominantly those on terrestrial plant communities. Size-dependent effects on the relationship between ecosystem functioning and biodiversity are well recorded (Huston 1994, Chase & Leibold 2002).

In contrast, according to the stability-time hypothesis initially developed for deep-sea fauna (Grassle & Sanders 1973), species do not have to adapt to a changing environment and can occupy narrow non-overlapping niches. Consequently, the evolution of species that are highly adapted to each other and the maintenance of their long-term co-occurrence is only possible under stable conditions. This concept has also partly been applied to explain the high diversity (Clarke & Crame 1997, Gray 2001) of the deeper Antarctic benthos (Picken 1985, Dayton et al. 1994, Arntz & Gallardo 1994).

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The coincidence of large-scale background stability on the one hand and local catastrophic events on the other has led to the approach of using iceberg scours as natural experiments in ecology. The present study makes use of a benthic video-strip database from the eastern Weddell Sea to evaluate the effect of disturbance on diversity at different spatial scales. There are 2 reasons for conducting such a study in Antarctic waters. Firstly, iceberg scours are discrete events, and can thus be separated from the background variance of all other impacts. Secondly, anthropogenic effects can mask original conditions in most other marine systems, while the high Antarctic is probably the least anthropogenically affected on Earth (although endangered in regard to large-scale climatic changes; Kerr 2002, Rignot & Jacobs 2002).

MATERIALS AND METHODS

A seabed video-strip survey was carried out to examine the bottom fauna of the SE Weddell Sea shelf off the 220 km long coast from 70 to 72° S and 4 to 12° E with a remotely operated vehicle (ROV). Clusters of grounded icebergs of various sizes occurred in the study area between 100 and 283 m water depth. Accordingly, the seafloor of the study area (covering a total area of 4900 km² at water depths >300 m) was classified into 3 topographic strata according to the abundance of grounded icebergs. (1) 'Small iceberg banks' comprising ≥10 icebergs (with heights of >10 m above the sea surface), i.e. with an average abundance of >0.15 icebergs km⁻²; the highest value recorded was >0.45 icebergs km⁻²; 10 such banks were recognized, covering a total area of 610 km². (2) A 'large iceberg bank', which was treated separately due to its significantly larger extent (280 km²) and higher iceberg abundance (44 icebergs). (3) A level plateau, comprising the remaining area (4010 km²). The presence of icebergs was derived from bridge observations made during expeditions of the RV 'Polarstern' between 1988 and 1998, helicopter flights in 1998 (authors' pers. obs.) and aerial photographs from 1975 and 1986 (Grosfeld et al. 1989).

Based on the analysis of the video images, 4 disturbance categories of faunal assemblages were discriminated: 1 undisturbed and 3 at various stages of recolonization. Characteristic features in the small-scale bottom topography and an abrupt change in the megabenthic species composition were used to differentiate scours from the surrounding undisturbed area (Gutt & Starmans 2001). The 2 early stages of recolonization, R0 and R1, were identified by the reduced number of dominant species relative to surrounding areas. The third, late stage of recolonization, R2, was identified by the

absence of large hexactinellid sponges that serve as indicators for an undisturbed situation (UD) because of their extremely slow growth (Gutt & Starmans 2001). A subsample of 113 standardized strips (size 0.5 × 40 m) was selected from 36 stations (total strip length 49200 m) distributed over the entire study area. In order to obtain similar sample sizes for a comparison between stages of succession, the 4 disturbance categories were sampled almost equally and random selection of the standardized strips was performed to the same extent in each of the 3 topographic strata.

A total of 57 taxa were identified in the video images by comparison with animals collected from concomitant trawl samples (Gutt et al. 2000). Individuals and single colonies were counted, with the exception of 2 bryozoan taxa for which the proportional coverage of the seafloor was taken as an equivalent for abundance. Taxa were defined as (1) identifiable species; (2) organisms which obviously belonged to 1 species but could not be named; (3) organisms belonging to a higher taxon comprising only a few species, e.g. Hemichordata spp. *Scolymastra joubini* and *Rossella racovitzae* (both Hexactinellida), which were placed into 3 separate 'taxa' according to their size (small, intermediate, large). Gross systematic units that probably comprised a greater number of species, such as Ophiuroidea spp. or Demospongiae spp., were excluded from our analysis.

Diversity was analyzed at different spatial scales: alpha, beta and gamma (Gray 2000). Alpha diversity is traditionally used to describe diversity on a local scale, i.e. at 1 site, which in this study is represented by a standardized area of 0.5 × 40 m. The data was displayed as cumulative dominance plots that provide detailed information and emphasize the abundance of the dominant species. To test the intermediate-disturbance hypothesis at this local scale, the gradient of decreasing significance of rare species was examined by counting species numbers (S) and computing 2 additional parameters (N_1 and N_2). N_1 (the Shannon index) is a function of both number and abundances of species, and N_2 is a measure of evenness describing only numerical species proportions (Magurran 1988). The 2 latter indices, as well as the cumulative dominance plots, are especially suited for the video technique because neither this kind of sampling nor this method of data analysis emphasizes rare species. In addition, these indices and the resultant curves are more sensitive to effects of environmental change than are absolute species numbers. Since the most interesting aspect of the intermediate-time hypothesis is the assumption of a decrease in diversity with increasing competition during a late phase of faunal succession, only values of S , N_1 , and N_2 from R2 were compared with those of UD using Mann-Whitney U -tests.

In contrast to the analysis of local diversity, the study on a larger spatial scale (beta and gamma diversity) requires samples that are representative of the entire investigation area, which is approx. 220 km long and 40 km wide. Consequently, diversity was computed by merging a number of samples over a larger spatial scale. A subsample of 40 of the 113 video-strips was randomly chosen with replacement weighted according to the proportions of recolonization stages and topographic strata (for data see Gutt & Starman 2001). This resulted in 7.2% for R0, 4.4% for R1, 23.0% for R2, and 65.4% for UD averaged for the entire investigation area over all 3 topographic strata. Such a single data set does not sufficiently cover the faunistic variability within the relatively rare stages R0 and R1; however, these stages are essential for this study. We therefore performed 30 random permutations of this draw prior to further analysis. To test the intermediate-disturbance hypothesis at the regional scale, S , N_1 , and N_2 were calculated for a representative data set and compared with a data set of similar sample size comprising UD only. Beta diversity quantifies the differences in faunal composition between sites or areas. It was measured by Bray-Curtis dissimilarities between the faunistic information from all video-strips. The overall resemblance of the pattern within and between the disturbance categories is shown as an MDS (multi-dimensional scaling) plot. To test the intermediate-disturbance hypothesis at the level of beta diversity, the approach described above was repeated to create a representative data set, and resulting faunistic dissimilarities were compared with dissimilarities between undisturbed samples only.

RESULTS

In the original data set (Table 1), species abundance was low in R0 but not in later stages of recolonization. Also, later stages contained a large number of taxa that were not present in highest abundance in the undisturbed stage. Dominance patterns were especially uneven in the 2 early stages of recolonization (R0 and R1), with relative abundance (= dominance) of the 5 most abundant taxa ranging from approximately 65 to 100% (Fig. 1). This pattern tended to be more even in the later recolonization

stage R2 and in UD, with abundances of 55 to 100% and 45 to 95%, respectively. This tendency is equivalent to an increase in alpha diversity during succession; it represents a biological process which is generally expected, but is partly biased by our definitions of R0 and R1 (see 'Materials and methods').

The most interesting aspect of the intermediate-disturbance hypothesis, however, is the assumption of a decrease in diversity with increasing competition during a late phase of faunal succession, in our case from R2 to UD. Our data showed local (alpha) diversities that were significantly higher in UD than in R2 with regard to S , N_1 , and N_2 (Fig. 2a).

Table 1. Abundance ($n = 100 \text{ m}^{-2}$) in study area (SE Weddell Sea shelf) of 30 most abundant taxa in entire data set plus additional species being among the 20 most abundant per single successional stage of recovery (R0, R1: early stages of recovery after disturbance event; R2: later recovery stage; UD: undisturbed [= final stage]). Together they comprise approx. 95% total abundance. Bold-face indicates species whose abundance was not highest in the undisturbed stage (i.e. 'pioneer species'). HEX: Hexactinellida; DEM: Demospongiae; HYD: Hydrozoa; GOR: Gorgonaria; BRY: Bryozoa; POL: Polychaeta; ECH: Echinoidea; HOL: Holothuria; ASC: Ascidiacea; nos. in parentheses = no. of video-strips (20 m^2 each)

Species	R0 (22)	R1 (28)	R2 (31)	UD (32)
<i>Rossella racovitzae</i> , small (HEX)	0	0.7	17.4	85.2
<i>Rossella racovitzae</i> , large (HEX)	0.2	0	2.3	32.8
<i>Scolymastra</i> spp., small (HEX)	0.2	7.7	65.0	120.2
<i>Scolymastra</i> spp., intermediate size (HEX)	0.2	0.4	2.3	24.4
<i>Scolymastra</i> spp., large (HEX)	0.2	0.9	1.3	41.7
<i>Cinachyra barbata</i> (DEM)	0	1.6	11.1	240.9
<i>Homaxinella</i> spp. (DEM)	0	19.1	182.7	0.3
<i>Isodictya</i> spp. (DEM)	0	0	0.2	24.7
<i>Monosyringa obliqua</i> (DEM)	0	0.2	5.5	43.1
<i>Stylocordyla borealis</i>, oblong (DEM)	1.8	54.3	49.0	15.3
<i>Stylocordyla borealis</i>, round (DEM)	0.7	10.0	180.5	153.9
<i>Tetilla leptoderma</i> (DEM)	0	1.3	56.0	5.0
<i>Corymorpha</i> sp. 1 (HYD)	5.2	16.4	10.2	7.5
<i>Corymorpha</i> sp. 2 (HYD)	0.2	26.4	0.2	0.5
<i>Oswaldella antarctica</i> (HYD)	0	70.5	24.8	11.3
Anthozoa spp.	10.2	45.5	61.8	39.4
<i>Ainigmaptilon antarcticus</i> (GOR)	0.9	72.9	27.9	4.8
<i>Arntzia</i> sp. (GOR)	0	44.6	62.3	0
Gorgonaria spp.	20.2	27.3	33.9	29.2
<i>Primnoella antarctica</i> (GOR)	5.2	97.3	150.0	7.2
<i>Primnoisis</i> spp. (GOR)	12.7	474.6	127.9	74.2
<i>Thouarella/Dasystenella</i> (GOR)	1.4	53.8	75.3	69.5
<i>Camptoplites</i> cf. <i>tricornis</i> (BRY)^a	0.2	13.8	4.0	5.2
<i>Melicerita obliqua</i> (BRY)	0.7	16.4	351.9	43.4
<i>Perkinsiana</i> cf. <i>littoralis</i> (POL)	0.7	7.3	27.4	12.2
Polychaeta, Sedentaria	2.5	290.4	103.9	12.5
<i>Pista</i> sp. (POL)	15.2	116.3	92.1	11.1
Hemichordata spp.	0.2	1.4	39.5	43.9
<i>Sterechinus</i> spp. (ECH)	10.7	5.2	5.6	4.1
Dendrochirotida (HOL)	5.5	21.6	34.2	62.7
Crinoidea spp.	53.4	38.2	62.9	93.1
Synascidiacea spp. (ASC)	0	0	1.3	42.8
<i>Sycozoa</i> sp. 1 (ASC)	0	4.5	18.2	8.3
<i>Synoicum adareanum</i> (ASC)	3.2	8.6	60.8	346.6
Synascidiacea spp. (ASC)	14.5	14.1	64.7	32.2

^aAbundance present as % cover on seafloor

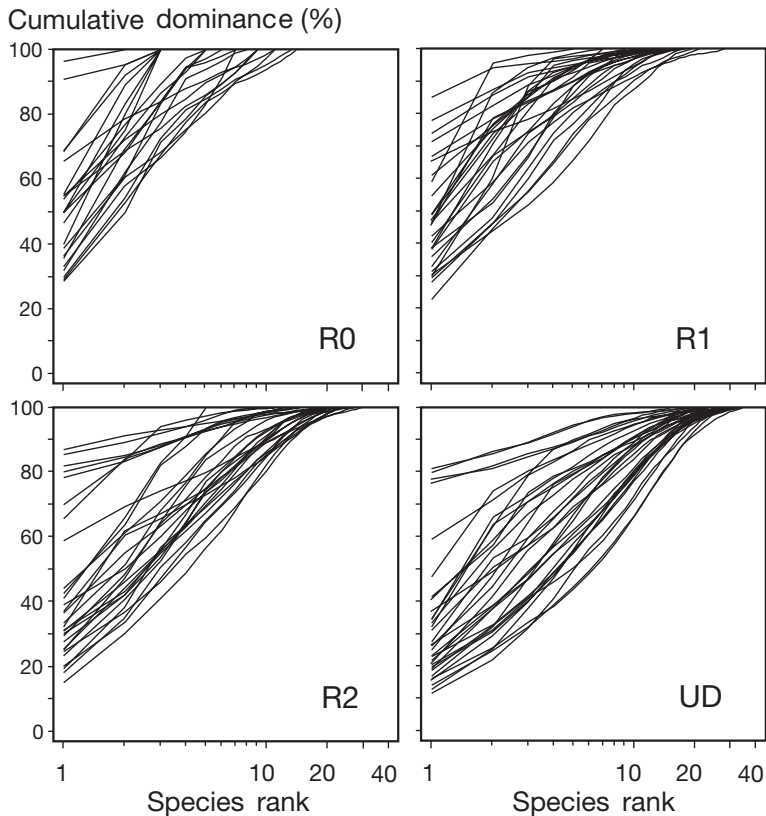


Fig. 1. Cumulative dominance plots using all 113 video-strips of study area on SE Weddell Sea shelf for recolonization Stages R0, R1, (early stages) and R2 (late stage) and undisturbed areas (UD)

To analyze large-scale regional (gamma) diversity, samples were selected from the entire study area in such a way that they comprised adequate data for both disturbed and undisturbed areas. These representative samples had higher species numbers, as well as higher values for N_1 and N_2 , than those drawn from the undisturbed assemblages only (Fig. 2b).

Faunal heterogeneity was higher in the recolonization stages than in undisturbed samples. This is reflected in the MDS plot (Fig. 3a) by the larger area over which the disturbed samples were dispersed. Consequently, between-habitat diversity was higher in a situation that representatively included both disturbed and undisturbed sites than in a situation representing undisturbed sites only (Fig. 3b).

DISCUSSION

Our findings strongly indicate that 2 processes, operating on different spatial and temporal scales, regulate the diversity of Antarctic shelf benthos. According to the stability-time hypothesis, the high local diversity of undisturbed Antarctic shelf

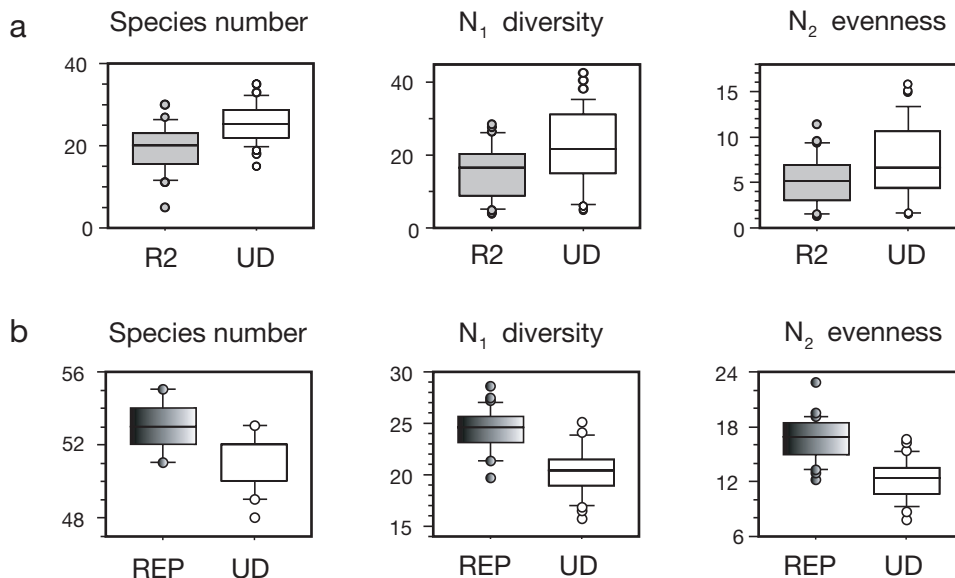


Fig. 2. Alpha and gamma diversity in study area. (a) Alpha diversity: Mann-Whitney U -tests ($p < 0.05$) used to compare number of species (S) and Hill's N_1 and N_2 diversity indices for R2 ($n = 31$) and UD ($n = 32$) areas. (b) Gamma diversity: faunistic data for 40 representative strips (REP) were pooled and an average of 30 permutations statistically compared (Mann-Whitney U -test, $p < 0.05$) with a similar data set of equal size from UD samples only

benthos is primarily the result of the evolution of sponge-dominated assemblages (Fig. 4a) over long and stable time spans. Long-lasting absence of iceberg disturbance and, as a consequence, the influence of competitive displacement during a late stage of succession, obviously does not reduce local diversity and species richness of Antarctic megabenthos. Instead, the values for all 3 diversity parameters increased from a late stage of recolonization to an undisturbed community. Consequently, the intermediate-disturbance hypothesis cannot be confirmed by our results. This is surprising, since a high coverage (>50%), particularly of large sessile animals, occurs in the habitat classified as undisturbed. Possible explanations for this finding are: (1) Diversity-reducing interspecific competition does not play an important role in this context due to exceptionally slow growth. Therefore, areas classified as 'undisturbed' do not attain true equilibrium for 3 possible reasons: (i) the system will never reach dynamic equilibrium; (ii) the disturbance occurred too long ago and is no longer detectable by our methods; (iii) recolonization has not come to an end since the last glacial era, when most shelf areas were covered by grounded ice shelves. In the 2 latter cases, it could be only a matter of time before a diversity optimum will be reached, and subsequently competitive displacement leading to a reduction in diversity will set in. (2) Competition for space and other limited resources actually exists and would lead to a reduction in diversity, but its effect is masked by a counteracting effect which is in accordance with the stability-time hypothesis. In Antarctica, a 3-dimensional biogenic habitat provides further niches that are occupied by additional species as a result of interspecific adaptation (Gutt & Schickan 1998). This applies both on an ecological time scale, in which migration and recruitment play a role, and on an evolutionary time scale, in which long-term speciation is the most important process. (3) Intensive predation especially on fast-growing organisms, as observed by Dayton et al. (1974) in McMurdo Sound, can generally control competition for space in areas not affected by icebergs and consequently result in high local diversity.

In contrast to the local scale, diversity on a regional scale is strongly increased by catastrophic disturbances, possibly even encompassing the entire Antarctic shelf (<300 m; Fig. 4b,d). Species that are obviously displaced in a near-equilibrium stage may develop very successfully during recolonization, e.g. the demosponge *Homaxinella* spp. (Porifera), the hydrozoans *Oswaldella antarctica*, *Corymorpha* sp. 1 and sp. 2, and the gorgonians *Ainigmaptilon antarcticus*, *Primnoisis antarctica* and *Primnoisis* spp. As a consequence, within a cyclic process including disturbance and recovery, a mosaic-shaped heterogeneous habitat would develop due to the co-existence of different succes-

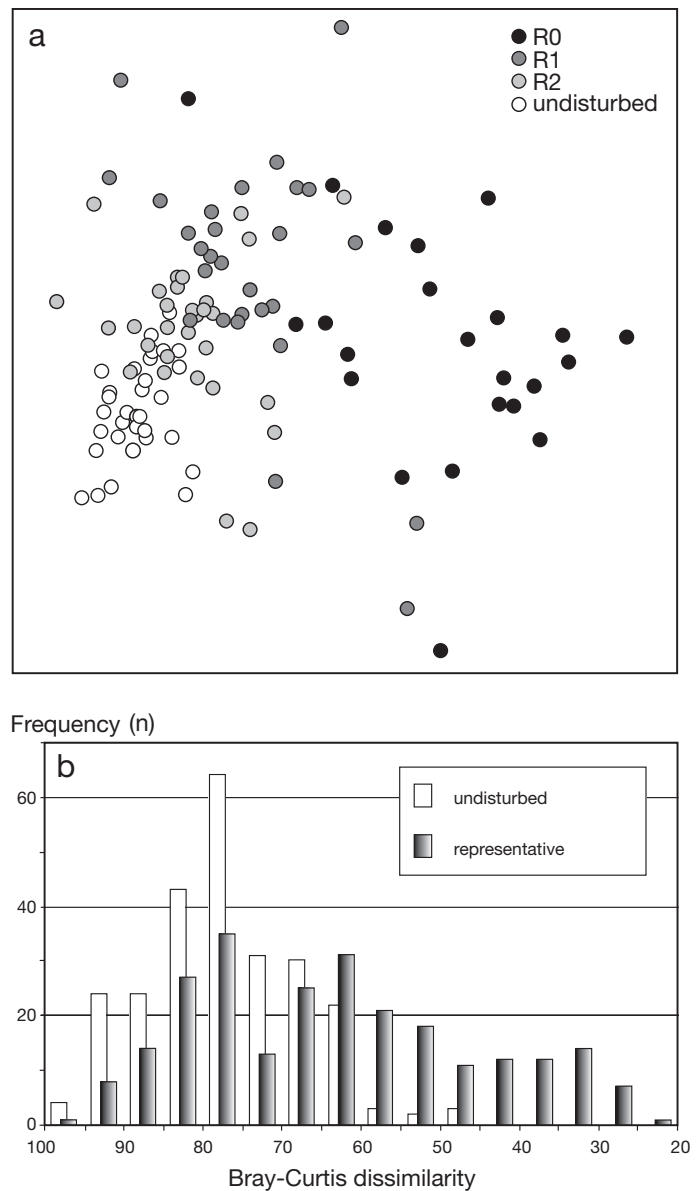


Fig. 3. Beta diversity in study area. (a) Multi-dimensional scaling plot (stress = 0.21) showing pronounced faunistic heterogeneity, especially within early (R0 and R1) stages of recolonization, and relatively homogenous species composition of undisturbed samples. (b) Analysis based on 23 400 Bray-Curtis dissimilarities between permuted samples (after Magurran 1988); random selection of 250 dissimilarity values was statistically compared with similar data set of undisturbed samples only (Mann-Whitney *U*-test, $p < 0.05$); coincidental pairings of same strip were excluded

sional stages, and would prevent a true steady-state climax at the level of the entire community (Pickett & White 1985, Remmert 1991). A corresponding diversity maximum would result. High beta diversity could represent another optimum at the regional scale, since maximum local diversity in the undisturbed stage provides a high potential for variation in species composi-

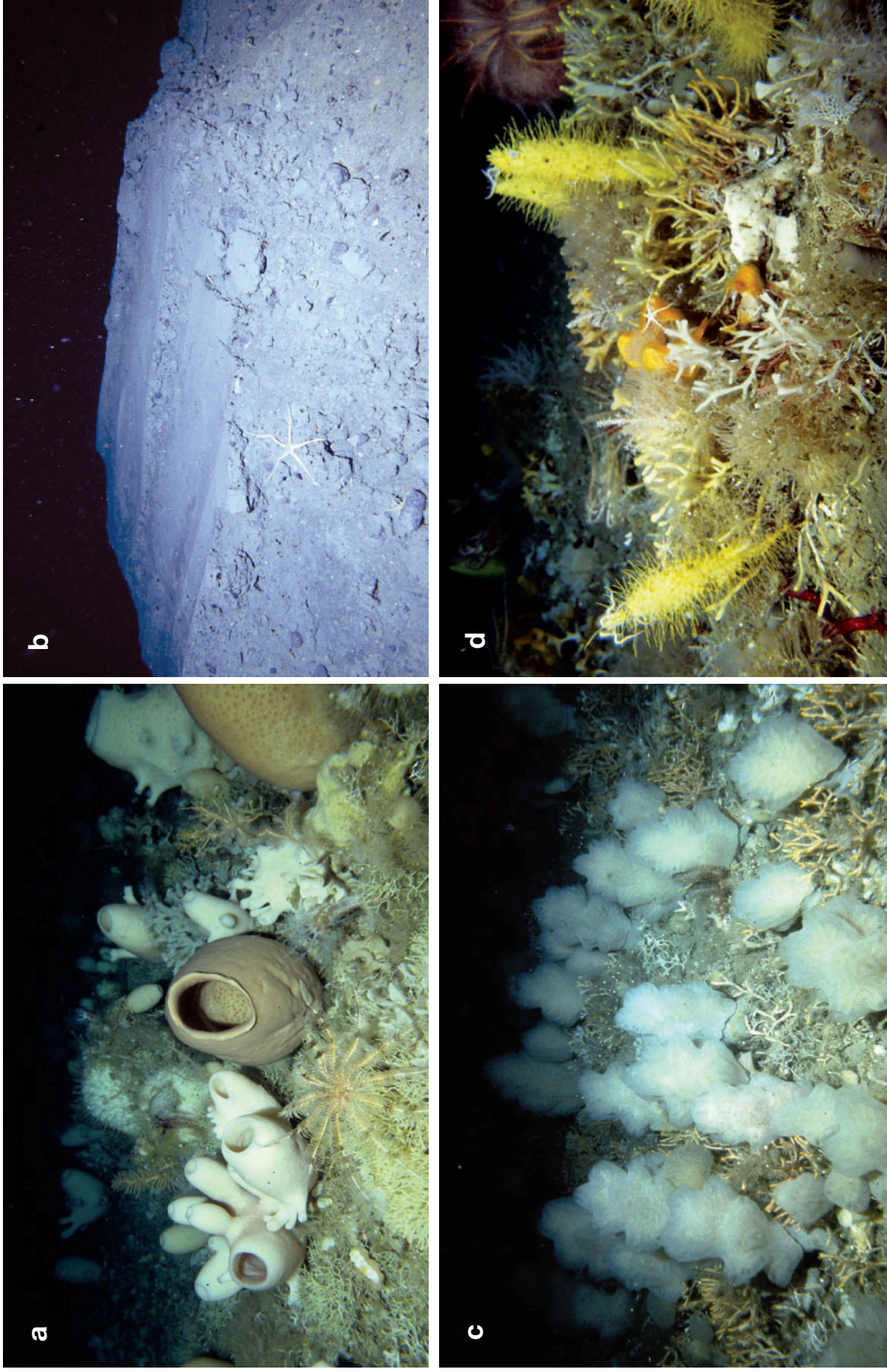


Fig. 4. Seabed photographs of SE Weddell Sea shelf. Oblique views, width in foreground approx. 0.5 m. (a) Hexactinellid sponges *Scolymastra joubini* (left) and *Rossella nuda* (centre) indicate area has not been disturbed for estimated period of > 500 yr (Dayton et al. 1974, Gutt et al. 1996). (b) Sea floor recently scoured by icebergs; sessile epifauna is totally devastated; motile organisms (e.g. ophiuroids) invade such areas soon after impact. (c) High abundance of compound ascidians and low local diversity indicate early recovery stage. (d) Various bryozoan species, gorgonarians, 2 yellow demosponges of genus *Isodictya* and associated mobile fauna such as dark red holothuroid and crinoids (e.g. upper right) indicate late recolonization stage

tion during recolonization. Due to the high variability in abundance of several pioneer species (Table 1, Fig. 3b) and the obvious unpredictability of species succession, the equal-chance hypothesis (Connell 1978) can also be applied. If these pioneers have principally the same potential to invade or to recruit into devastated areas, their occurrence and succession is determined by chance. In addition, indirect effects of iceberg scouring, such as changes in the bottom-water current regime or modification of small-scale seabed topography, may result in further specific ecological conditions.

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