Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica

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ABSTRACT: Ice disturbance is possibly the major structuring element of polar nearshore biological communities. Effects range from encapsulation by ice forming on rock substrata to gouging and trampling by bergs. Some 15 to 20% of the world's oceans are affected by this phenomenon, yet measurements of the extent of biological destruction from iceberg impacts and subsequent community recovery are very rare. Communities can be held at early successional stages, or even completely destroyed by scouring, and these effects occur from the intertidal to depths around 500 m in Antarctica. The wide scales of disturbance intensity are thought to add to the overall high levels of Antarctic benthic biological diversity, which has recently been shown to be similar to tropical areas. Data here indicate >99.5% removal of all macrofauna and >90% removal of most meiofauna by iceberg impact on a soft-sediment habitat at Signy Island, Antarctica. Species return was via locomotion, advection or larval recolonisation, and all 3 mechanisms worked on different timescales. Locomotion caused groups to return within 10 d of an impact. Storms with wind speeds around 100 km h^{-1} induced water movements intense enough to advect meiofauna to the 9 m depth site. However, it was only during the strongest storm which occurred during the study (maximum wind speed 148 km h^{-1}) that water movements were powerful enough to redistribute small macrofauna such as the bivalve *Mysella charcoti*.

KEY WORDS: Antarctica · Iceberg · Community · Benthos · Macrofauna · Meiofauna · Diversity

INTRODUCTION

Biological diversity is currently a major topic of interest worldwide, especially in relation to environmental changes on global scales. Terrestrial biodiversity increases towards the tropics (Pianka 1987), and one of the best known trends in the marine environment is that of reduced biodiversity from tropical localities to the Arctic (Thorson 1957, Kendall & Aschan 1993). Recently there was shown to be no similar trend in the southern hemisphere, mainly owing to high diversity in Antarctic waters (Clarke 1992, Poore & Wilson 1993, Brey et al. 1994, Gray 1997). A factor which underpins biodiversity is habitat and environmental heterogeneity, and in some areas physical disturbance has been shown to enhance environmental or landscape hetero-

geneity (Huston 1979, 1994, Connell & Keough 1985). In Antarctica ice disturbance is a dominant structuring factor in the marine environment (Dayton et al. 1970, 1994, Dayton 1990). Disturbance effects in Antarctic benthic marine systems vary with latitude, depth, site exposure and local current regimes. This produces a mosaic of habitat variability in terms of physical disturbance on both spatial and temporal scales, which may account for the unexpectedly high levels of biodiversity found. In this context it is surprising that few studies exist on the effects and recovery of species and communities in relation to disturbance from ice.

Natural disasters and environmental disturbance, including the effects of ice on biological communities, occur over wide ranges of spatial and temporal scales. Local freezing in temperate zones may be ephemeral, with little effect on organisms present, but glaciers and ice shelves may remove completely underlying biota and can persist for millennia. In shallow polar habitats
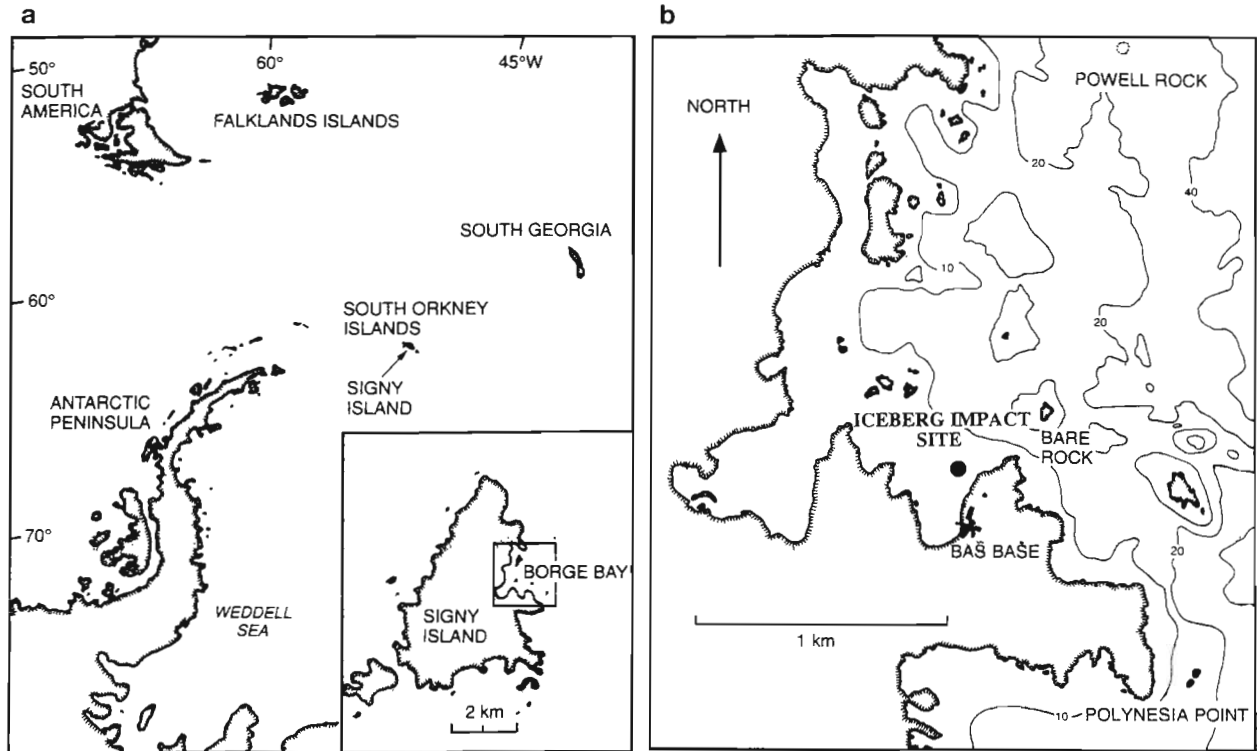
Fig. 1. Map showing (a) the position of Signy Island in the South Orkney Chain, off the Antarctic Peninsula, and (b) the position of the iceberg impact site in Borge Bay

(<50 m depth) hard substratum benthic community diversity and abundance are related to exposure and depth (Dayton et al. 1970, 1974, 1994, Dayton 1990, Arntz et al. 1994, Barnes et al. 1996), reflecting the frequency of ice disturbance. Such disturbance was much more widespread in recent geological history, with evidence of icebergs ranging as far as 41°S during the last glacial period (Bond et al. 1992). This implies that a significantly greater proportion of shallow marine environments worldwide were impacted by ice within the last 70000 yr, and illustrates the importance of ice effects over evolutionary timescales.

Icebergs impact the seabed to 400–500 m depth in polar oceans (Lien et al. 1989, Gutt et al. 1996). Community diversity is elevated in disturbed deep water areas compared with surrounding sediments (Dayton & Hessler 1972), and Gutt et al. (1999) described higher between habitat (beta-) diversity due to iceberg scouring in the Weddell Sea. Enhanced diversity associated with disturbance at deep sites superficially conflicts with reduced diversity in shallow impacted hard substratum habitats. However, disturbance frequencies were estimated at ~230 yr in Antarctica, at depths between 100 and 500 m, based on known organismal growth rates and estimated community development times for fauna inhabiting gouge marks (Gutt et al. 1996). Enhanced community diversity in deeper water was a result of increased habitat diversity combined

with extended times between impact events which allowed longer recovery periods. On shallow hard substrata more frequent impacts hold communities at early successional stages (McCook & Chapman 1991, Barnes 1995a,b), and in some Arctic sites disturbance-associated faunas have been identified associated with scoured areas, as distinct from surrounding benthos (Conlan et al. 1998). Secondary factors, such as the development in scours of hypoxic seafloor brine pools, which produce lethal conditions for benthic and demersal organisms long after the impact event, have also been identified under certain conditions (Kvitek et al. 1998). Between the extremes a wide range of disturbance levels exists.

Despite the above there has been little work on the effects of icebergs on shallow soft sediment communities, and no data exist on the timescales or mechanisms of community recovery following iceberg impacts. Here we present such data following a scouring event at 9 m depth at Signy Island, South Orkney Islands.

MATERIALS AND METHODS

Initially an iceberg with a maximum height of 3 to 4 m was observed on its track on the south east side of Factory Cove, Signy Island, South Orkney Islands, until it grounded near Berntsen Point (60°42′25″ S,

45°35'20" W) in a depth of 9 m (Fig. 1). It remained grounded for approximately 36 h and then drifted away to the northwest. An impacted area roughly 30 m in diameter was left behind. Samples were taken from the impacted site and a control (undisturbed) site 5 m away from the impact event within 24 h of the departure of the iceberg, and on Days 10, 20, 30, 50, 78, 102, 150, 200 and 250 after the event. The whole field sampling period lasted from 18 December 1993 to 3 August 1994. A second iceberg impact was monitored in September 1994 at another site in Factory Cove, but 500 m distance from the first grounding. At the second site no meiofaunal analyses were made, and only the immediate effects of the iceberg impact were measured.

Samples for macrofauna were collected from 0.25 m² quadrats using a suction sampler fitted with a 1 mm mesh retaining bag (Luxmoore 1981, Peck & Bullough 1993). Two replicate samples were taken from the impact site on each date sampled. Replicate samples were also taken from the control site on Days 1 and 175. After collection material was returned to the laboratory, sorted and counts made immediately. Samples for meiofauna analysis and material for sediment organic content assessments were taken from sites adjacent to the macrofaunal sampling sites. They were obtained using 5 cm diameter acrylic coring tubes which were pushed into the sediment and capped before extraction. Again duplicate samples were taken and material collected this way was preserved in 4% formol seawater and transported to Belgium for analysis. Analyses of organic content were made on cores collected as above. The top 10 cm of sediment was removed and either analysed whole or passed through graded sieves to allow organic analysis of different sediment size fractions. Organic contents were assessed as the difference in mass between samples dried to constant weight at 60°C and ignited in a muffle furnace at 475°C for 24 h.

RESULTS

At Signy Island the iceberg impact removed >99.5% of all macrofauna at an 8 to 10 m depth soft sediment site. 100% of 6 groups (bivalves: *Yoldia eightsi*, *Cyamiomactra laminifera* and *Laternula elliptica*; nephtyid polychaetes; isopod: *Serolis polita*; and gastropod: *Eatoniella* sp.), 96.0% of amphipods and 96.3% of the bivalve *Mysella charcoti* were removed (Fig. 2). Amphipods were predominantly of the genus *Cheirimedon* (G. Chapelle pers. comm.), but identification to species was not conducted for all samples. Abundances in controls of individual groups ranged to 78000 m⁻² for the small (<3 mm length) bivalve *M. charcoti*.

At a second grounding event (data not shown), 500 m from the primary study site in September 1994, 9 mo after the first impact, only the immediate effects of the impact were measured, but there was again 100% removal of 6 of the 8 most common macrofaunal groups (*Yoldia eightsi*, *Cyamiomactra laminifera*, *Laternula elliptica*, *Serolis polita*, nephtyid polychaetes and *Eatoniella* sp.). Removal of the other 2 groups (*Mysella charcoti* and serolid isopods) was >97.7% at this second site. Samples taken 5 d post impact at the second site showed no change from Day 1.

Meiofauna numbers were also dramatically reduced following the first impact event (Fig. 2). Meiofaunal densities at control sites were similar to those from a nearby study of meiofauna in Factory Cove (Vanhove et al. 1998). Over 90% of all meiofauna groups (nematodes = 98.5%, ostracods = 98.1%, bivalves = 96.0%, turbellarians = 94.6%, nauplii = 92.3%) except copepods (86.4%) were removed. Nematoda were most affected with a 98.5% reduction in numbers, from in excess of 1 million to less than 10000 per core sample.
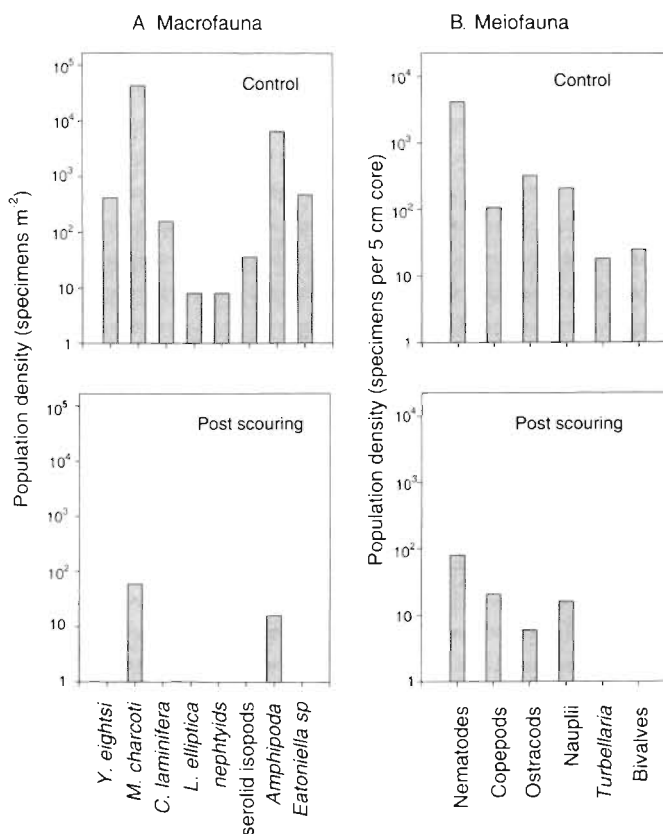

Fig. 2. Effects of iceberg scour on organismal abundance. (A) Macrofaunal abundances for the 8 most common taxa from control sites (unimpacted values) and following the scouring event (note logarithmic axes). (B) Control and post iceberg impact abundances (specimens m⁻²) for the 6 most common meiofaunal groups (note logarithmic axes). Data are only for the first impact site. No collection was made for meiofauna following the second impact
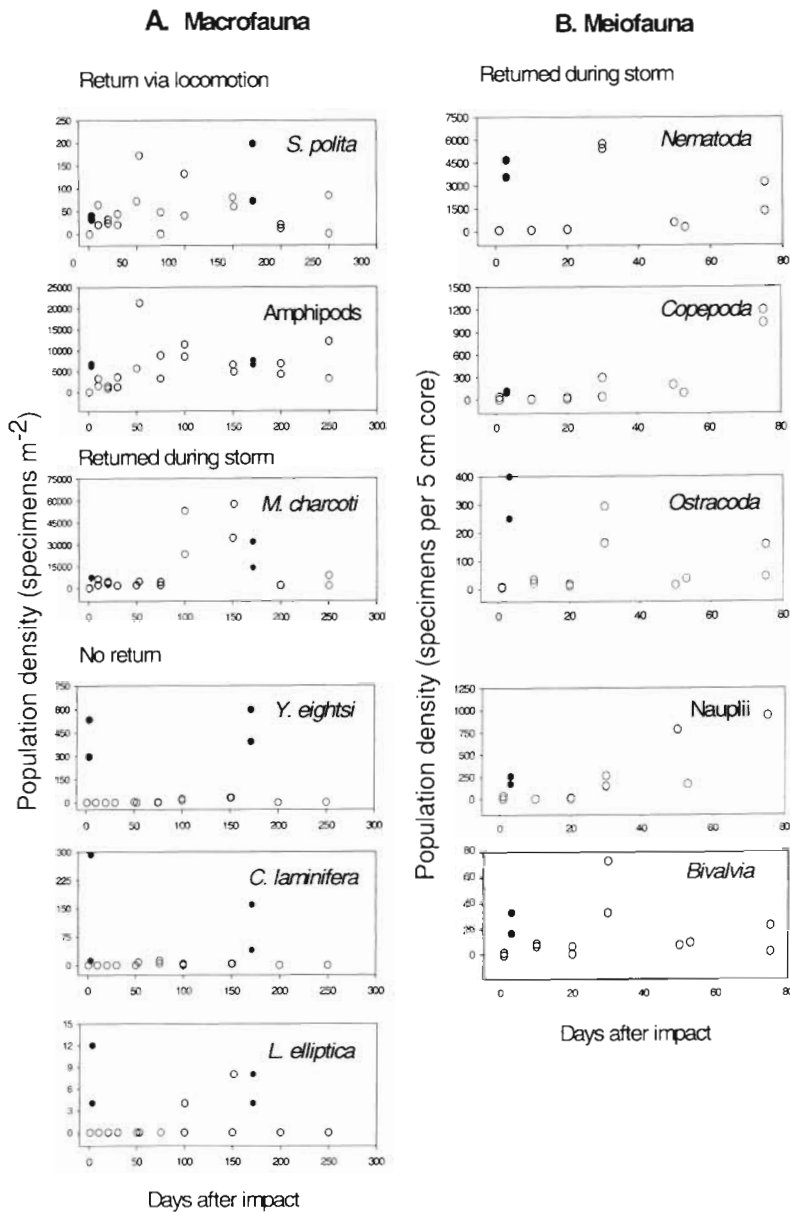
Fig. 3. Timings of return of faunal groups following an iceberg impact. Organismal density is plotted against day after the impact event. (O) Impact area values, (●) densities at the control site. Data shown are for the period following the first impact only. (A) Macrofauna. Data shown are for the most common species present. (B) The most common meiofauna groups (see Fig. 2) all returned 20 to 30 d after the impact. Numbers varied somewhat after this time, because of seasonal factors. Other meiofauna groups (including turbellarians and halacarids) were present in some samples, but in too small numbers for analysis

the genera *Lissarca, Laevilacunaria, Margarella* and *Nacella*, sabellid and spirorbid polychaetes, and priapulids. Earliest recovery was by amphipods and the isopod *Serolis polita*, both motile macrofauna, which showed significant recolonisation within 10 d of the iceberg departing. None of the other macrofauna showed a significant return to the site within the first 100 d after the scouring event. The second group to return was meiofauna. Nematodes, ostracods, nauplii and bivalves <1 mm length all returned between Days 20 and 30 after the impact event (Fig. 3), when their numbers were not significantly different from control values (paired *t*-test, T = 1.39, n = 10, p = 0.197). Numbers of the small bivalve *Mysella charcoti*, which grows to approximately 3 mm length, returned to control levels in the sample taken 102 d after the iceberg impact. This was the third group to recover.

Numbers of the final group which could be identified showed no significant recovery during the 250 d experimental period (Fig. 3). This category comprised 3 moderate to large sized bivalve molluscs, all >5 mm length (*Cyamiomactra laminifera, Yoldia eightsi* and *Laternula elliptica*). There were small variations in numbers sampled in this group, and on Day 150 after impact 2 specimens of the largest bivalve present, *L. elliptica*, were collected. However, these were close to a rock outcrop within the scoured area.

Fig. 4 shows the maximum wind speeds of storms which occurred in Factory Cove throughout the study. Meiofauna recovery (between Days 20 and 30 post scouring) coincided with the first storm with wind speeds in excess of 100 km h^{-1}, on Day 23. Return of the small bivalve *Mysella charcoti* on Day 102 immediately followed the largest storm recorded during the study (on Day 100) when a maximum wind speed of 148 km h^{-1} was recorded. The sampling date was delayed to Day 102 because of the intensity of the storm. Species usually only associated with hard substrata (including the gastropod *Margarella antarctica* and sabellid polychaetes) were also advected to the scouring site by this large storm. These species were not observed in the scoured area following lesser storms.

Recovery of faunal groups after the impact was indicated by abundances in samples collected during the 250 d following the scouring event (Fig. 3). Data shown in Fig. 3 are for the commonest groups present only. Other groups recorded during the study were in small numbers, or were aberrants normally inhabiting rocky substrata. These included pycnogonids, gastropods of

Unexpectedly, sediment organic content was un-affected by iceberg gouging either immediately after impact (ANOVA, 1,11 df, $F = 1.94$, p = 0.19), or 150 to 200 d later (ANOVA, 1,11 df, $F = 1.34$, p = 0.28; Fig. 5). There was also no trend in total organic content throughout the study (regression, slope = −0.0014, t = −0.70, p = 0.50). However, this was because organic matter in the smallest size class (<0.25 mm) dominated, which did not vary during the study (regression, slope = 0.00054, t = 0.96, p = 0.36). Organic content of all of the larger size classes except the >5 mm fraction declined seasonally from summer to winter (regressions: >5 mm fraction slope = −0.0261, t = −1.53, p = 0.15, 1 to 5 mm fraction, slope = −0.023, t = −1.94, p = 0.046; 0.5 to 1.0 mm fraction, slope = −0.01 1, t = −2.24, p = 0.38; 0.25 to 0.5 mm, slope = −0.0044, t = −2.83, p = 0.016; Fig. 5). Total organic content at recently im-pacted sites is therefore the same as in control areas, suggesting little decline with depth in the sediment.

DISCUSSION

Icebergs affect soft substrata in 3 main ways. They plough the seabed, which forces surface layers away from the point of contact; they trample it, whereby ice-bergs rock backwards and forwards crushing underlying organisms and seabed; and water flowing around ice-bergs either caused by movements of the berg, natural oceanic currents, or salinity induced water movements can resuspend and transport sediment (Reimnitz & Barnes 1975, Carey & Ruff 1977). These phenomena are all capable of removing or translocating macrobenthos

Fig. 5. Organic content of sediment at the impact site (ash-free dry mass, AFDM, as % dry mass, ●), and from nearby controls (○). Values shown are whole sediment and the size fractions >5 mm, 0.5–1 mm and <0.25 mm. Size fractions 1–5 mm and 0.25–0.5 mm are not shown, but were similar to the 0.5–1 mm fraction

from under or around an iceberg. However, meiofauna removal on the scale seen here by trampling or currents produced by movement of a berg of this size is unlikely, although both probably occurred on smaller scales, be-cause the berg remained grounded for over 36 h. Ploughing was therefore likely to be the major effector. Plough marks over 30 m wide and 5 m deep have been recorded (Barrie 1980), exposing sediment beyond depths where multicellular organisms are abundant. The scouring at Signy Island, in addition to killing large num-bers of macrofauna by trampling, clearly exposed sedi-ments containing few meio- or macrofauna, even though the post-impact depression was only 50 to 75 cm deep.

The return of species to an impacted site, and the recovery of communities is controlled by several fac-tors. The earliest to return to sites are those that are motile, as shown by amphipods and isopods (Fig. 3). Other groups depended on external forces, or new recruitment via larval forms to recolonise the site. The
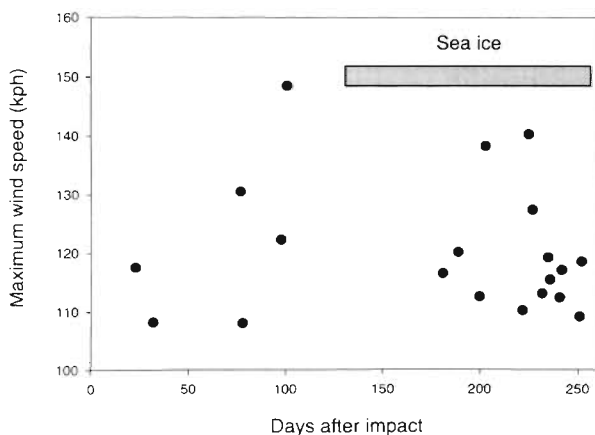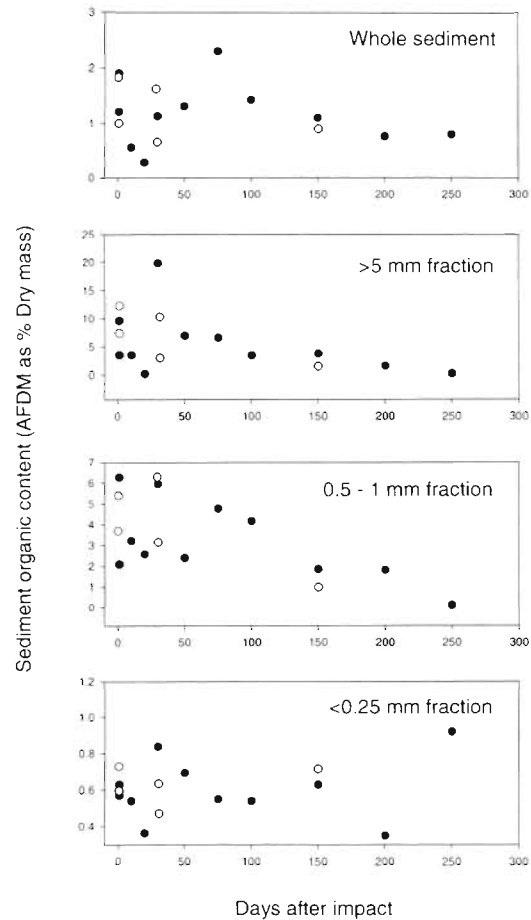

Fig. 4. Maximum wind speeds of storms at the iceberg impact site between 18 December 1993 and 3 August 1994. The site was sheltered from the west and southwest. Only storms with wind directions between 330° and 180° were, therefore, included. Sea-ice presence is indicated by the solid horizontal bar, and the site was covered from approximately Day 130 onwards, which reduced dramatically any storm effects after that date

return of meiofauna was regulated by the magnitude of storm induced water movement close to the seabed, and were advected back to the experimental site by the first storm after the impact event (Figs. 3 & 4). Meiofauna have been shown to be transported passively on strong water currents elsewhere (Sherman & Coull 1980, Fleeger et al. 1995). Macrofaunal densities were not affected by the storm which advected meiofauna to the impact site. Following the early recolonisation by motile forms, the only change in macrofaunal density followed the largest storm of the year (study Day 100; maximum wind speed 148 km h^{-1}, maximum 5 min mean winds >100 km h^{-1}) when large numbers of the small bivalve *Mysella charcoti* (<3 mm length) were advected to the site (Fig. 3) by intense storm induced water movements. Water column turbulence of this magnitude clearly redistributes small non-attached macrobenthos around shallow bays in Antarctica. It should be noted that this type of organism is not moved by moderate storms and strong turbulence is needed to redistribute species like *M. charcoti* around the seabed, as none of the previous storms (some with wind speeds >100 km h^{-1}) succeeded in doing so. A continuum of redistribution of organisms probably exists between light water movement and major storms, and at least 2 levels have been demonstrated here. Between the 100 and 150 d samples sea-ice covered the site and storm effects were much reduced until the end of winter (after Day 250).

Large bivalves must recolonise impacted sites via larval dispersal. This is supported by a study of growth in *Yoldia eightsi* at Signy Island close to the impact site which found regularly impacted areas had populations dominated by small specimens (2 to 10 mm length) at densities up to 1460 m^{-2}, whereas less disturbed populations comprised more mature individuals (Peck & Bullough 1993). It was suggested that recruitment and population structure were maintained by iceberg scour releasing new sites for colonisation, and balancing areas dominated by adults which inhibited larval settlement (Peck & Bullough 1993). It was somewhat surprising here that *Y. eightsi* did not return during storms. It is mobile to a degree, pushing its way through surface sediment, and has a light shell. Small specimens, which can occur in very high densities (Peck & Bullough 1993) were expected to be returned by violent water movements. However, on disturbance *Y. eightsi* burrows and behavioural mechanisms may preclude its return during storms. Three major mechanisms have, therefore, been identified for the recolonisation of iceberg impacted sites on shallow soft sediments: locomotion, dispersal by water currents and via larval recolonisation. The 3 methods act on different timescales.

It has been stated that community recovery from iceberg disturbance requires many years (Picken 1985).

In addition colonisation of settlement plates in Antarctica is at least an order of magnitude slower than at temperate or tropical sites (Barnes 1996, Stanwell-Smith & Barnes 1997), and strong interannual variability may be characteristic of recruitment in polar latitudes (Dayton 1989). However, recovery following the iceberg impact at Signy Island varied between faunal groups, both in method and timing (Fig. 3), with some groups returning in a matter of days.

Quantitative assessments of the effect of iceberg scour on shallow biological communities are absent (Clarke 1996). Richardson & Hedgepeth (1977) observed iceberg scouring at Arthur Harbour, Anvers Island, but no quantitative measurements were made. They suggested 5 recovery phases following impacts. Initially a depression formed which filled with macroalgal fragments from vicinal rocky areas. Motile species aggregated to feed on the macroalgae and predators returned to exploit the newly established communities. The depression finally filled via sedimentation from pelagic productivity. Locomotion and advection were major influences controlling recovery in both studies. Clearly in some conditions macroalgal input can be important, but these conditions are probably rare because of the relative scarcity of large macroalgal stands in high Antarctic latitudes, however, locomotion, advective water movement and larval settlement will be of major importance at all sites.

Several factors control soft-bottom community structure, diversity and organismal biomass in polar regions. The most important are disturbance, sediment type and nutrient supplies (Dayton et al. 1970, 1994, Gallardo 1987, Barnes et al. 1996). In stable productive habitats macrofaunal abundances can be extreme, with animal densities >150 000 m^{-2} (Gallardo & Castillo 1969, White 1984) and predation can be important in maintaining such high density assemblages (Oliver & Slattery 1985). Clearly the importance of each factor varies between sites along a continuum from stable high productivity to highly disturbed, low productivity. These are the criteria which have been shown to be of importance in regulating diversity in biological communities in all ecosystems, and have been synthesised into the nonequilibrium 'intermediate disturbance hypothesis' (Paine & Vadas 1969, Connell 1978, Huston 1979, 1994, Connell & Keough 1985). The hypothesis is based on reduced diversity at high or low levels of disturbance, where disturbance is defined in terms of mortality of the organisms present, and can be any mortality factor. The range of physical disturbance in Antarctic benthic systems is extreme, from continual abrasion and ice encapsulation to minor effects which only occur with a frequency of hundreds of years. This is a major factor leading to the observations of high biodiversity in Antarctic marine benthos (Dearborn

1968, Richardson & Hedgepeth 1977), and there is support for the intermediate disturbance hypothesis in the enhanced levels of diversity seen at depths between 5 and 50 m, where physical disturbance levels are intermediate between highly impacted shallow sites and infrequently disturbed deep water localities (Dayton 1990, Arntz et al. 1994, Dayton et al. 1994, Gutt et al. 1996). Longer term environmental cycles such as those recently found to enhance deep sea diversity (Cronin & Raymo 1997) will also enhance habitat diversity in polar oceans on temporal scales.

On Antarctic criteria the system at Signy Island is light to moderately disturbed and productive, which suggests it may be representative of many maritime Antarctic soft sediment environments. The identified mechanisms of recovery from iceberg scouring, locomotion, storm washing and larval recruitment should therefore be widespread and common. During glacial periods iceberg scoured conditions are likely to be amongst the most common in shallow benthic habitats, and the adaptations described here the most common ecological adaptations in shallow marine environments. It may also be the case that species adapted to regular physical disturbance of the type described here may be more resistant to disturbances of human origin than would be expected.

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