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Links between the structure of an Antarctic shallow-water community and ice-scour frequency

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Abstract Ice is a major structuring force in marine and freshwater environments at high latitudes. Although recovery from scouring has been quantified in time, the frequency of scouring in the Antarctic has not. We placed grids of markers at 9–17 m depth at two sites, to study ice-scouring over 2 years at Adelaide island (Antarctic Peninsula). We quantified the time scale of scour frequencies, and linked this to community mortality, age and diversity. Markers were hit from zero to at least three times in 2 years. At the least disturbed site (South Cove) 24% of markers were destroyed per year, whereas in North Cove 60% of markers were destroyed. There were significant differences in scouring frequency between our two sites: a given area in North Cove was on average hit twice as often as one in South Cove. Compared with near shore environments elsewhere, faunas of both sites were characteristic of high disturbance regimes, exhibiting low percent cover, diversity, ages and a high proportion of pioneers. Aspects of the encrusting communities studied reflected the differences between site disturbance regimes. North Cove was scoured twice as often, and bryozoan communities there had half the number of species, two-thirds the space occupation and twice the mortality level of those in South Cove. Maximum age in North Cove bryozoans was also half that in South Cove. Although there are natural disturbance events that rival ice-scouring in either frequency or catastrophic power at lower latitudes, none do both nor across such a wide depth range. We suggest that ice scour effects on polar benthos are even more significant than the same magnitude of disturbance at lower latitudes as recovery rates of high latitude communities are very slow. Climate warming

seems likely to increase iceloading of near shore polar waters, so that some of the world's most intensely disturbed faunas may soon suffer even more disturbance.

Keywords Ice · Age · Bryozoan · Disturbance · Diversity

Introduction

The frequency and scale of disturbance in environments and community recovery are major factors governing diversity and structure of ecosystems from forests (Garwood et al. 1979; Borkaw 1985) to oceans (Dayton 1971; Connell 1978; Paine 1979; Conlan et al. 1998; Gutt and Starman 2001). The coastlines of nearly one-third of the globe, the polar and sub-polar regions, experience often catastrophic disturbance from ice scour. This was probably more than 50% of global coastlines during recent glacial maxima, when icebergs in the northern hemisphere ranged at least as far south as 41°N (Bond et al. 1992). It is likely, therefore that large proportions of current coastal communities on earth are either influenced directly by ice scour, or were shaped by this process in the recent evolutionary past.

When polar oceans are not frozen, billions of pieces of ice float at the sea-surface, ranging in size from <1 g to millions of tonnes. The collisions between these pieces of ice and the sea floor result in one of the most destructive natural forces experienced by benthic communities (Dayton 1990), even at depths of greater than 500 m (Lien et al. 1989; Gutt et al. 1996). At high polar latitudes where near-permanent shelf ice overlays benthic environments, anchor ice (ice attached to and growing on the seabed or benthic biota) is the major cause of ice-mediated disturbance (Dayton et al. 1970). Ice scour is responsible for the near denudation of the intertidal zone and strong subtidal zonation in near shore waters both around the Antarctic Peninsula and outlying archipelagos (Shabica 1972; Zamorano 1983; Gallardo 1987; Barnes 1995; Gambi et al. 1994; Nonato et al. 2000; Gutt 2001; Barnes and Brockington 2003) and most of the Arctic coastline where

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ice shelves are not present (Ellis and Wilce 1961; Bolton 1983; Dowdswell et al. 1993; McCook and Chapman 1997; Conlan et al. 1998). Ice-scour may even result in mortality long after the physical abrasion event, as gouges can develop into superhaline anoxic 'pit-fall' traps (Kvitek et al. 1998). Although there have been estimates made on the frequency of near shore impacts (Barnes 1999) and some attempts to quantify how common deep water scours are (Gutt and Starmans 2001), direct experimental measurements of ice scouring frequency and its consequences on long-term community structure have not to date been reported. There is considerable interest in the frequency of ice scour in the Arctic due to the risk of damage to man-made subsea structures, but very few data are currently available (e.g. Surkov 1998)

The consequences of ice scour to Antarctic benthos differ with the type of substratum hit, the taxa involved and the frequency and intensity of impacts. In soft sediments the population structure of bivalves can show missing cohorts of recruits (Peck and Bullough 1993). However, community response differs between meio- and macro-fauna and seems to be dictated by the mobility of taxa (Peck et al. 1999). On hard substrata, ice-mediated disturbance can play a critical role in preventing competitive dominants from monopolising space (Barnes 2002a, b). In the present study we measure the frequency of iceberg scouring on a series of markers in two adjacent coves, one being considered a priori ice-sheltered and the other ice-exposed, due to prevailing exposure to wind driven ice. From the frequency of hits at each site we can address the following hypotheses: (1) the frequency and probability of ice disturbance to the sea floor is influenced by topography and bathymetry, but some patchiness would also be likely from the effects of wind/wave and current action. We aim to evaluate that background patchiness in two similar sites near Rothera Point, Antarctica, and (2) that biological communities differ markedly in relation to the frequency of ice disturbance. We compare our ice scour data to a range of community variables within and between these coves.

Materials and methods

Iceberg scour frequency assessment

Experimental work was carried out in North and South Cove, Rothera Point, Adelaide Island Antarctica ($67^{\circ}34'07''\text{S}$, $68^{\circ}07'30''\text{W}$, Fig. 1). Sites of similar water depth (Fig. 2, North Cove 10.0 m–14.7 m, South Cove 9.6–16.5 m below chart datum) and bottom profile but with very different exposure to prevailing winds (and hence ice presence) were selected in North and South Cove. The mean monthly wind direction recorded at Rothera during the period over which the current experimental work was carried out was $46 \pm 2^{\circ}$ (range $34\text{--}68^{\circ}$) with a mean wind speed of 12.6 ± 0.5 knots (range 7.2–18.7 knots). A square grid of concrete markers was accurately laid out in both coves using SCUBA divers. Each grid consisted of 100 markers, placed 2 m apart and arranged in rows of 10, with each grid consisting of ten rows. Therefore, the completed grid measured 18 m \times 18 m and covered an area of 324 m². The grids accounted for approximately 0.6% of the seabed area of South Cove (approximate area 50,000 m²) and 0.3% of the seabed area in

North Cove (approximate area 108,000 m²). The markers were made by filling plastic disposable drink cups (height 97 mm, top diameter 70 mm, base diameter 45 mm, mean mass 428 ± 5 g) with concrete and attaching a unique label to allow identification. The site in North Cove was operated from 10 June 2000 to 21 April 2002 while the South Cove site was operated from 4 October 2000 to the 16 September 2002. After the grids were established they were visited by SCUBA divers at intervals ranging between 21 and 414 days (Table 1). The divers recorded the number of destroyed markers and replaced all damaged markers. Originally it was intended for divers to assess iceberg damage to the grids at approximately 3-monthly intervals; however, the loss of our diving facility in a fire (September 2001) terminated diving operations for approximately 1 year. This interruption of diving precluded detailed recording of berg damage at the sites and resulted in a large variation in the time intervals between ice scour assessments (Table 1). However, comparisons between sites over a similar range of summer and winter periods were possible, as well as long-term evaluations on impact rate.

Community and population measurements

The substratum at both localities (North and South Cove) ranged from boulders (~100–1,000 cm² diameter) through boulders overlain by (~4 mm) silt. Encrusting communities on boulders were sampled in the two localities in January 2002. Samples were taken at 12 m depth at each of three randomly selected sites within each locality. Each sample comprised 42 rocks. From each rock we measured the following whole assemblage parameters: (1) percentage cover by fauna (using a non-elastic net marked in mm²), and (2) the number of species present. We also recorded two measures of direct impacts on fauna; firstly, (3) the number of scars (calcareous base) of previously impacted bryozoan colonies, used as a measure of

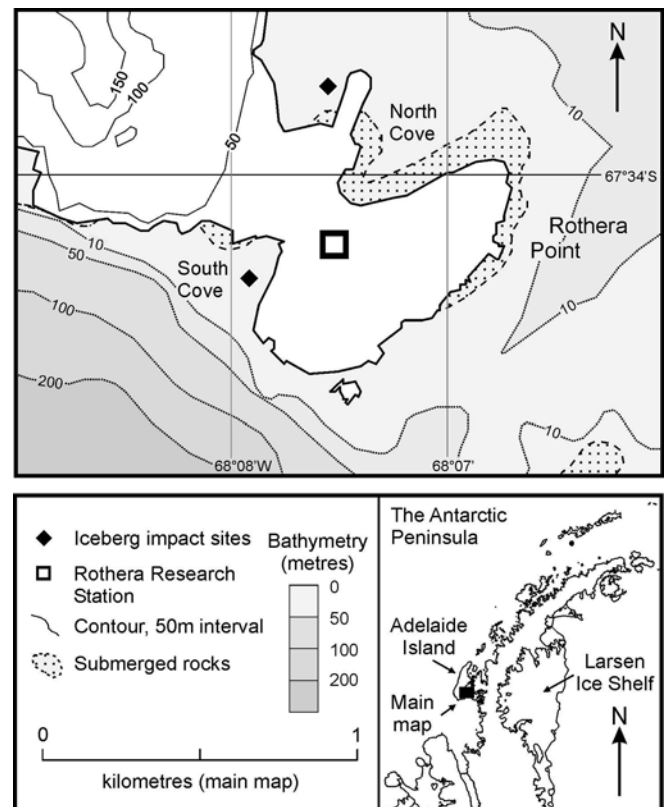


Fig. 1 Location of the study site on the Antarctic peninsula and specific locations of the ice scour assessment grids in South and North Cove, Rothera Point, Adelaide Island

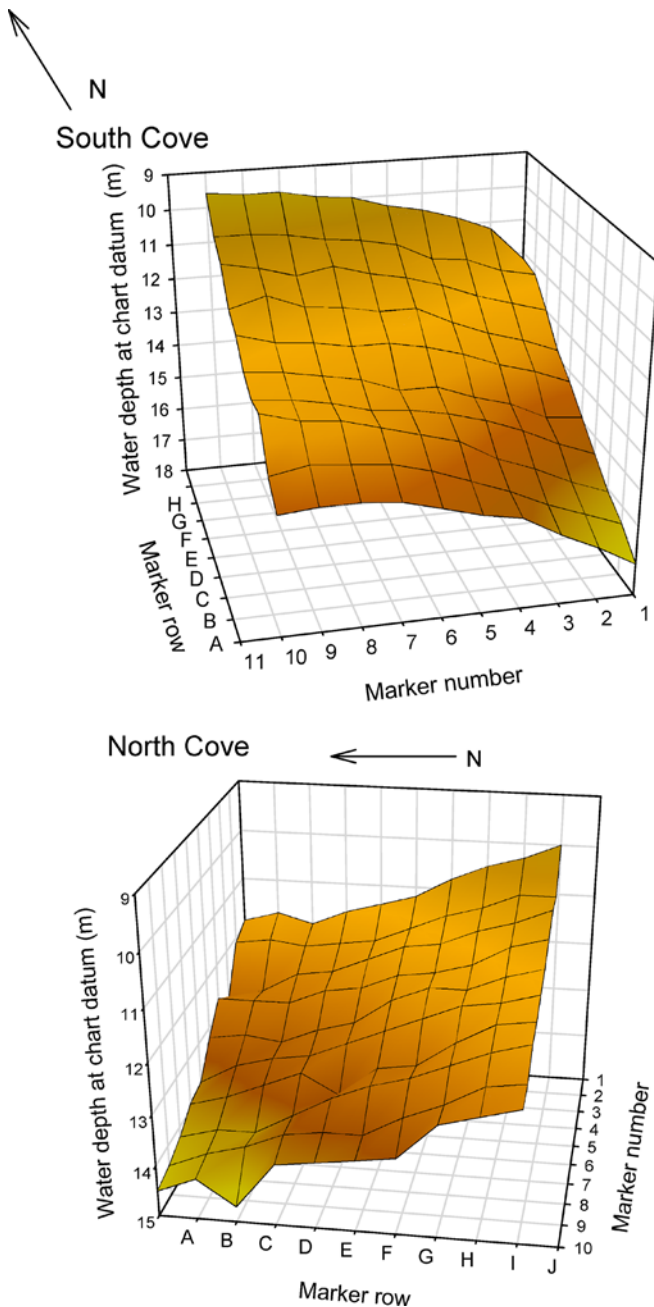


Fig. 2 Bathymetry of sites used for ice scour assessment grids in South and North Cove, Rothera Point, Adelaide Island, Antarctica

disturbance induced mortality (dying naturally leaves a skeleton and their main predators—pycnogonids and nudibranch molluscs seem to rarely eat more than small parts of colonies, personal observation); previous examination of freshly scoured rocks has revealed minor remains of calcareous fauna that were present prior to scouring. The high frequency of shallow water scouring and recolonisation suggests such traces of previous colonies are likely to last only 1–2 years. Secondly, (4) we examined rocks for the number of bryozoan colonies with asexual origins. This indicates they have regenerated from fragments (termed ‘partial mortality’ here) rather than being budded from a sexually produced ancestrula; the normal mode of reproduction. In addition to community measurements we also investigated population structure of the most common encrusting species.

Table 1 The dates of, and time intervals between iceberg scour grid measurements

Date	Cumulative time period from start of experiment (days)
North Cove	
10.6.2000	0
1.7.2000	21
6.9.2000	89
21.12.2000	196
5.3.2001	271
3.7.2001	392
21.4.2002	685
South Cove	
4.10.2000	0
14.2.2001	134
12.5.2001	222
29.6.2002	636
16.9.2002	716

On each rock the age of colonies of a particularly common bryozoan *Fenestrulina rugula* were recorded (faint growth check lines are laid down with annual frequency, see Barnes and Arnold 2001). Growth of the current season in *F. rugula* is much more translucent than that of previous years, so growth after scouring can easily be separated from old fragments. If not completely removed by scouring, it was still usually possible to age colonies as long as part of each annual ring remained. We analysed the mean and maximum age of *F. rugula* colonies collected on rocks (*F. rugula* are rarely larger in ice-sheltered overhangs, as undisturbed areas as colonies are virtually all overgrown by competitive dominants such as *Beania erecta* bryozoans or sponges). We plotted survivorship of year classes for this species and used this as a proxy measure for mortality levels (as Barnes and Clarke 1998).

The macro faunal community in/on the sediment was dominated by the burrowing bivalves *Laternula elliptica* and *Yoldia eightsi* and the regular echinoid *Sterechinus neumayeri*. Previous scientific collections of the bivalves coupled with their rarity in South Cove negated meaningful analysis of these species. Macro faunal measurements were, therefore, restricted to *S. neumayeri*. We assessed the density of *S. neumayeri* in both North and South Cove with multiple random quadrats (0.25 m²) dispersed throughout each cove. We measured test diameters of *S. neumayeri* individuals using vernier callipers in at least six population samples, with a minimum sample size of 17.

Statistical analysis

Data are expressed as mean \pm SEM unless otherwise stated. All data were normally distributed (after arc sine transformation in the case of proportion data) and were analysed using general linear model (GLM) analysis or Student’s *t*-test. Spatial hetero- or homogeneity of ice scours within grids was analysed using the Moran statistic (Cliff and Ord 1973). The Moran statistic is a weighted correlation coefficient used to detect departures from spatial randomness. It is used to determine whether neighbouring areas are more similar than would be expected under the null hypothesis i.e. in the current case whether ice scours are hetero- or homogeneously distributed within a grid.

Results

Ice scour frequency, patchiness and probability of impact variability in space

Over the 2 year study period, the range of ice scouring events observed on each marker ranged from zero to three (Fig. 3). There was a significant difference in the frequency of ice scouring events per marker between North and South Cove (Student's *t*-test, *df*=192, *T*=7.72, *P*<0.001). The mean number of ice scouring events per marker in North Cove over 2 years was 1.18±0.06 whereas in South Cove it was 0.47±0.07, a 2.5-fold difference. This means that in North Cove approximately 60% of the site is scoured per year whereas in South Cove only 24% is scoured.

Despite the marked general relationship between ice scour and depth, the small difference in the water depths of the grids placed in North and South Coves had no significant effect on the frequency of scouring (Fig. 2, Table 2). There was also no overall significant correlation in our data between water depth and the likelihood of ice scouring in either North Cove (Pearson correlation coefficient =0.186, *P*=0.064) or South Cove (Pearson correlation coefficient =0.068, *P*=0.503). However, the grids in both North and South Cove covered only very small depth ranges.

Spatial analysis demonstrated that the distribution of iceberg scouring events in both North (Moran statistic observed 0.1608, expected -0.01010, *P*<0.01) and South Cove (Moran statistic observed 0.1506, expected -0.01010, *P*<0.01) were significantly different to random distributions (Fig. 3). This implies a high degree of

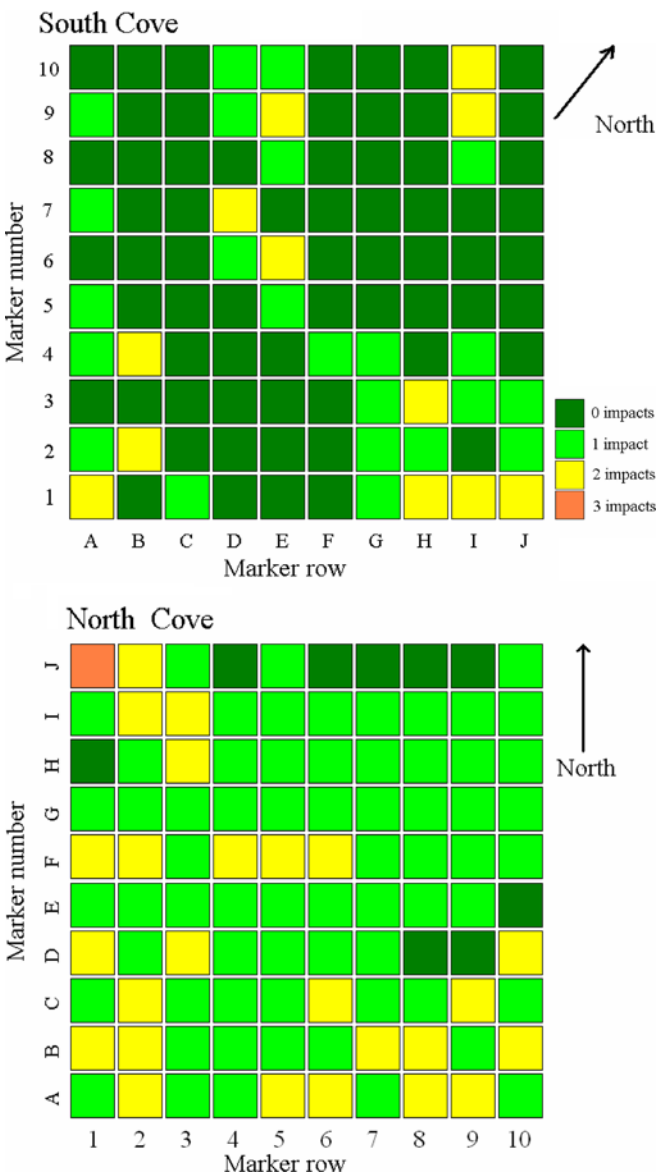


Fig. 3 Location and frequency of ice scour events within assessment grids sited in South and North Cove, Rothera Point, Adelaide Island, Antarctica over approximately 2 years

Table 2 ANOVA table of ice scour frequency with locality and depth

Source	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
Locality	1	25.21	25.21	59.34	0.000
Depth	1	0.06	0.06	0.13	0.718
Locality × depth	1	0.36	0.36	0.85	0.359
Error	196	83.25	0.42		
Total	199	108.88			

heterogeneity in the distribution of ice scouring events at these sites.

Variability in encrusting boulder communities between localities

Boulders did not significantly differ in size by either locality or site (GLM ANOVA *df*=1.2 *F*<0.1, *P*>0.86). Community composition at the two localities (i.e. North and South Cove) and six sites was similar. Both were characterised mostly by tubicolous polychaetes and cheilostome bryozoans colonising the lower most surface of rocks. Most space on boulders was not utilised by fauna; just over 6% of surfaces were colonised in South Cove and nearly 4% in North Cove. This difference was significant (*F*_{1,2}=15, *P*<0.001). All the species found on North Cove rocks were also found in South Cove but a few others were additionally present on South Cove rocks, e.g. the cheilostome bryozoan *Klugarella antarctica*. Significantly more (*F*_{1,2}=123, *P*<0.001) species were found on South Cove rocks (3.99±0.15 per rock) than North Cove rocks (1.89±0.0.13 per rock).

The proportion of bryozoan colonies which had asexual origins (grown from fragments) was significantly higher on rocks from North Cove (*F*_{1,2}=19.4, *P*<0.001). Nearly a third of all living colonies had grown from mechanically damaged former colonies (0.32±0.02) in North Cove, compared with one fifth (0.21±0.02) in South Cove. The proportion of scars of former colonies relative to living

Table 3 ANOVA table of *F. rugula*

Source	df	SS	MS	F	P
Mean age with locality, site and sample					
Locality	1	1.935	1.935	104.4	0.000
Site	2	0.565	0.565	15.3	0.000
Sample	41	0.596	0.596	0.8	0.822
Error	207	3.837	0.018		
Total	251	6.934			
Maximum age with locality, site and sample					
Locality	1	52.480	52.480	126.9	0.000
Site	2	1.738	0.869	2.1	0.125
Sample	41	12.274	0.299	0.7	0.891
Error	207	85.615	0.414		
Total	251	152.107			

colonies (our proxy of mortality) differed between localities ($F_{1,2}=32.7$, $P<0.001$) but not sites. The proportion of scraped (dead) colonies in South Cove was 0.13 ± 0.01 , half of that in North Cove (0.27 ± 0.02). In total, therefore, more than half of all recent bryozoan colonists, for which there was evidence from North Cove, had been damaged; 32% killing only part of the colony and 27% killing the whole colony. At South Cove, these values were much lower, with a third of all colonies affected (21% partially and 13% completely destroyed). Evidence of predation was very low, with less than 1% of zooid (module) death being attributable to predators, and in no cases did colonies appear to have been entirely killed by predators (such as pycnogonids, nudibranch molluscs or regular echinoids).

Variability in *F. rugula* populations between localities

One species, *F. rugula*, dominated the encrusting community (~80% in terms of numbers) in all three sites at each of the localities. Although there were significant differences in the mean age of *F. rugula* between the two locations, this was confounded by significant differences between sites, within the locations (Table 3, upper ANOVA). Nevertheless the *F* ratio associated with locality was nearly an order of magnitude higher, and so clearly explained much more of the variability in age (Table 3, upper ANOVA). The oldest *F. rugula* colonies in South Cove were aged four while, of the 126 samples collected from North Cove all were 2 years old or less with the exception of one 3-year-old colony. ANOVA on maximum age values showed a highly significant influence of locality and no confounding effect of site (Table 3, lower ANOVA). With sites as replicates, we plotted regression lines of survivorship for each locality using the number of colonies represented by each year class (Fig. 4). Although there were too few colonies of the next most abundant bryozoan species, *Celleporella bougainvillei* and *Inversiula nutrix* to analyse statistically, in both species the oldest colonies were present in South Cove.

Table 4 Variability in density and test diameter of *S. neumayeri* with locality. Data shown are mean \pm SD

	South Cove (n=212)	North Cove (n=217)
Density/m ²	35.3 \pm 12.4	31.0 \pm 12.3
Size in test Φ mm	18.2 \pm 9.7, range 1–49	23.8 \pm 8.7, range 4–42
Size modality	Unimodal	Bimodal

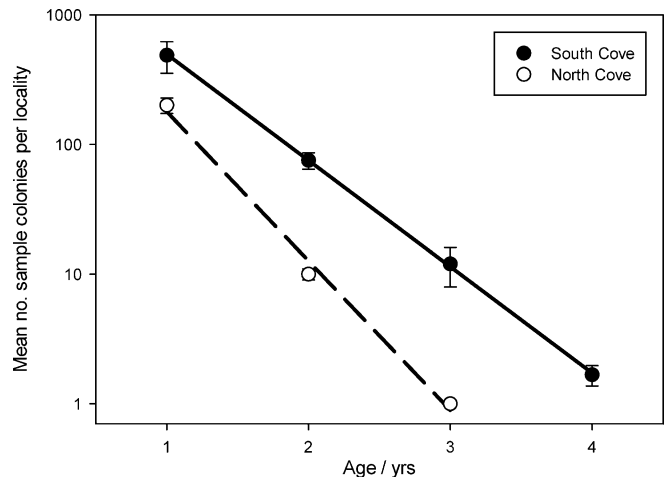


Fig. 4 Mortality plots (log decline in colony age) of *F. rugula* with two localities at Adelaide Island, Antarctica. Data are shown as mean and standard error. Lines shown are significant regressions (log no. colonies=3.52–0.82 age at South Cove and log no. colonies=3.40–1.15 age at North Cove) with both associated $r^2>99\%$ and both associated significances $F_1>173$, $P<0.05$

Variability in *S. neumayeri* between localities

The density of *S. neumayeri* individuals ($30+$ ind m⁻²) was not significantly different between South (six quadrats) and North Cove (seven quadrats) with respect to either the mean or variability (Table 4). Size structure of the populations did, however, differ between the two localities in two ways: (1) North Cove animals were significantly larger than South Cove individuals (Tables 4, 5) being nearly 6 mm wider in diameter, (2) the North Cove population was distinctly bimodal, with modes centred at 15 and 30 mm diameter (Fig. 5).

Discussion

Iceberg disturbance

For more than half a century it has been known that ice is a major structuring force on high latitude shores both in

Table 5 ANOVA table of *S. neumayeri* test diameter with locality

Source	df	SS	MS	F	P
Locality	1	3336.8	3336.8	39.51	0.000
Error	415	35052.2	84.5		
Total	416	38389.0			

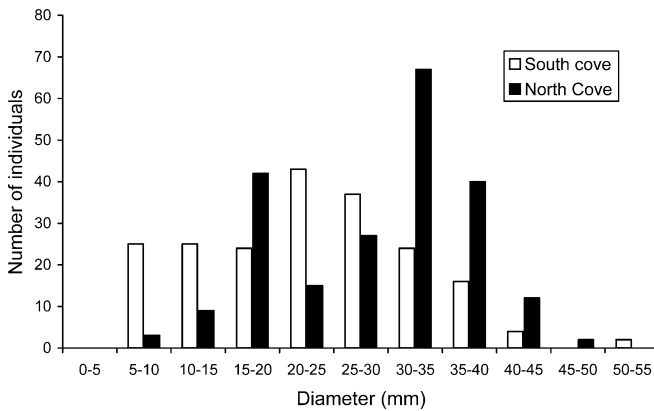


Fig. 5 Size frequency distributions of *S. neumayeri* populations in North and South Cove, Rothera Point, Adelaide Island, Antarctica. Test diameters within size classes range for example from 5.1–10.0 mm or 10.1–15.0 mm

marine and freshwater environments (Nichols 1953). Early studies established the sculpturing power of ice, in particular ice-scour, showing it to be responsible for physical landscaping at many scales by bulldozing pits, troughs, boulder pavements and push ridges (Nichols 1953; Araya and Hervé 1972; Belderson et al. 1973). As well as changing topography, large amounts of sediment can be resuspended and moved by ice scour (Rearic et al. 1990; Woodworth-Lynas et al. 1991). The evidence of past physical scraping is often well preserved in strata—a valuable indication of palaeo-bathymetric, glaciological and glacioclimatic conditions (Dionne 1974, 1977; Vogt et al. 1994).

Our study, for the first time, puts a time scale on scour frequencies, albeit a small and limited data set. The scouring frequencies we found (at 9–17 m) ranged from none to at least three scours in 2 years. All our values must be treated as minima, as we scored a scour if a marker was found to be hit, but it was not possible to identify if it had been hit more than once. At the least disturbed locality 35% of the markers were hit over the 2-year period compared to 91% at the more disturbed locality. Whilst it is intuitively obvious that scouring must be related to bathymetry across a wide range of depths (i.e. 0–100 m) and seems likely to be linked to topography (Gutt 2001), we found no evidence for either across the limited depth scale we studied.

Is the sort of disturbance we have measured like that which occurs in other environments? There are natural disturbance events that resemble small scale ice-scouring in their effect, such as impacts of drift logs into the intertidal (Dayton 1971) and feeding by Grey whales and Walruses (Nerini and Oliver 1983). Tectonic and volcanic activity have similar potential of destructive power but generally do not approach the frequency of scours in shallow (<100 m) water.

High energy sandy shores in mid to low latitudes experience possibly the most frequent physical disturbance of any marine sites, because the substratum is disturbed every tidal cycle. However, habitats and communities living there recover rapidly from disturbance events

(Dernie et al. 2003). Probably the most similar disturbance to ice-scour seen in temperate and tropical oceans is due to fishing activity. In areas regularly dredged for benthic catches given areas of North Sea seabed can be impacted up to eight times per year (Jennings and Kaiser 1998). The effects obtained vary markedly with dredge type, and effects vary for species depending on whether they are physically damaged, displaced or pass through the net mesh (Jenkins et al. 2001). Most damage to benthic invertebrates occurred unobserved on the seabed. However, few species of megafauna were markedly affected by the dredging activity, with only two out of ten species studied suffering mortality or damage likely to lead to death at rates over 40% for any dredge pass (Jenkins et al. 2001). This compares with complete removal of six out of eight megafauna groups by a single iceberg impact at Signy Island, Antarctica, and over 96% removal of the other two species (Peck et al. 1999). Iceberg impacts clearly have more profound destructive effects on benthic communities than human fishing activity per event.

Faunal responses to iceberg disturbance

The effect of ice scour on polar benthos is much greater than disturbance at lower latitudes for two reasons relating to the characteristics of the faunal groups present. Firstly, recovery rates of high latitude communities are very slow: colonisation and recruitment can be an order of magnitude lower than in warm water (Stanwell-Smith and Barnes 1997), even by mobile fauna (Gutt et al. 1996) and growth tends to be very slow (Dayton 1989; Brey et al. 1995a, b; Peck et al. 1997, 2000; Barnes and Clarke 1998). Secondly, the structure of competition is more hierarchical at high latitudes (Barnes 2002a, b).

Community responses to disturbance, and its measurement, have proved an important testing ground for field and theoretical ecology especially, since Connell's (1978) and Huston's (1979) theory of intermediate disturbance. In lower latitude environments, increased disturbance often increases biological diversity by preventing dominant species from monopolising or by increasing substratum heterogeneity (Dayton 1971; Dayton and Hessler 1972; Grassle and Sanders 1973; Wethey 1985). Many Southern Ocean coastlines, however, experience the highest winds, wave heights and ice loading resulting in very high levels of near shore disturbance (Barnes 2002b). The rapid frequency of littoral scouring coupled with winter ice-foot formation results in most polar littoral regions being mostly denuded with distinct zonation in the shallows. Fauna that does occur on polar shores and in the shallows tends to be distinctly patchy dependent on the degree of shelter from disturbance (Nerini and Oliver 1983; Dayton 1990; Barnes 1995; McCook and Chapman 1997; Pugh and Davenport 1997; Gutt 2001). This heterogeneity has marked implications for benthic diversity over a range of scales (Dayton et al. 1970, 1974; Shabica 1972; Kaufman 1974; Gallardo 1987). In the last decade the influence that ice has on benthos, and the depth to which it does so, has

been described in fine detail for glacial, Arctic and Antarctic shallow shelf environments (Dayton 1990; Peck and Bullough 1993; Gutt et al. 1996; Pugh and Davenport 1997; Conlan et al. 1998; Barnes 1999; Peck et al. 2000; Gutt 2001). It is possible that distinct depth zonations occur with differing degrees of ice scour influence or conversely that there is a decreasing continuum of ice scour frequency from intertidal depths to as deep as perhaps 1,000 m. Despite quantitative data on areas affected by ice scouring, faunal comparisons of scours of different relative ages (Lee et al. 2001a) and even some 'before and after' comparisons (Peck et al. 1999), to date there has been no direct measure of how often 'berging' occurs in time and its effect against time. Neither have differences in faunal responses of adjacent areas with differing levels of ice disturbance been measured. Various aspects of the encrusting communities we measured reflected the disturbance they experienced: North Cove had twice the scouring frequency of South Cove and North Cove communities had 50% less encrusting species, and occupied 33% less space. There was also evidence of twice the mortality level and bryozoan maximum age was halved in North Cove. Shallow water lithophyllic benthos in both Arctic and Antarctic high polar regions are dominated by pioneer species (Barnes and Clarke 1998; Barnes and Kuklinski 2003). Pioneer species are also highly abundant in certain highly disturbed warm water communities even though they are often poor competitors (Paine 1979; Karlson 1983; Wulff 1995). In comparison with near shore environments elsewhere in the world, the faunas of both sites could be described as characteristic of a high disturbance regime due to the overall low % cover, diversity, ages and high proportion of pioneers (Barnes 2000 and references therein). Mobile species, such as the sea urchin, *S. neumayeri*, are present in the zones studied here, but their major population densities occur in deeper water, where disturbance is less frequent (Brockington 2001)

Despite being close together, of similar depth and characterised by being very patchy we did find significant differences in the frequency of scouring at our two sites. Although the most striking feature of our scour maps is the patchiness of the benthic environment, North Cove was scoured, on average, 2.5 times as much as in South Cove over the two-year study. Analyses of such data are, however, fraught with problems and must be treated with caution. Most obviously the probability of scouring at one point cannot be completely independent of that at others. We also have to consider that the temporal and spatial scales used have a strong bearing on the results likely to be generated. For example it is possible that a marker or number of markers may be scoured by ice more than once before they are assessed. This inaccuracy will be increased as the time intervals between inspections of the impact grids increases. As the ice scour grid markers are placed 2 m apart it is also likely that some ice scouring events will occur within the grid without destroying any markers. Hence the results presented in this paper should be considered as a minimum estimate of ice scour frequency

at these localities. Despite such restrictions to the interrogation of our data, we were able to quantify faunal difference caused by physical disturbance in two otherwise similar environments. On small spatial and time scales ice scouring removes over 99.5% of species at a given site, dramatically reducing benthic richness and diversity (Peck et al. 1999). At larger scales the patchy scraping of ice may be very important in generating overall high levels of species diversity by producing great environmental heterogeneity (Dayton 1990; Brey et al. 1994; Gutt 2001; Barnes and Brockington 2003). The scale of the disturbance event in terms of area affected has been shown to have a marked effect on recovery rate of both seabed and communities living there in temperate seas (Thrush and Dayton 2002). Recently large-scale (Dernie et al. 2003) and meta-analyses of large datasets (Collie et al. 2000) have become necessary to identify major factors in physical environment and community recovery from disturbance in temperate zones. It is likely that our understanding of ice effects on biological communities will remain incomplete until data are available for such analyses at polar latitudes.

The lithophyllic community was dominated by one pioneer species, *F. rugula*. Amongst the macrobenthic community, one species was also prominent, the echionoid *S. neumayeri*. The invertebrate benthos of polar waters tends to be thought of as reaching great size and age [data on: long lived sponges (Dayton 1989); brachiopods (Peck and Brey 1996); echinoderms (Brey et al. 1995a, b) and bivalve molluscs (Peck et al. 2000); and polar gigantism (Chapelle and Peck 1999)]. In the current work lithophyllic communities of *F. rugula* lived to a maximum age of 4 years in South Cove and just 2 in North Cove. Mortality plots confirmed that encrusting species at the site with twice the average level of iceberg scour had achieved only half the maximum age. Such a result may seem intuitive, yet these are the first data directly linking measured ice scour frequency with community and species attributes. In contrast to the sessile species studied here, the population of *S. neumayeri* at our study sites were not all that young. Brockington's (2001) estimates of size-based age at the same site suggest that the mean size of *S. neumayeri* we found (Table 4) may be more than 2 decades old. Mobile animals, which tend to be the fastest to recolonise scoured areas (Peck et al. 1999; Lee et al. 2001b), may also be adept at avoiding being killed by scours, hence surviving to considerable age. Fresh scours may attract mobile scavengers to exploit organisms killed by the scour event (Richardson and Hedgepeth 1977; Gutt et al. 1996). The density of *S. neumayeri* was higher at the less scoured site, but it was not significantly so. The urchins were however, significantly larger (in test diameter) at the more scoured site and the population was bimodal, rather than unimodal as in South Cove. The larger size test diameter is not an intuitive result, but could be because of an increased availability of energy due to location-specific differences in sediment particle size or energetically rich foods. Indeed Brockington (2001) found that North Cove *S. neumayeri*, which fed entirely on sediment, had (throughout the year)

much higher gut mass than those from South Cove, which had a more varied diet. Bimodality has been noted before in macro-infauna of scoured sites (Peck and Bullough 1993).

Our data show these 9.6–16.5 m depth sites in Antarctica are highly disturbed compared to other sites worldwide not just because of the sub-annual frequency of catastrophic disturbance, but because of the restricted ability of fauna at this latitude to respond. The faunas present were poor, as predicted for such an extreme end of the disturbance continuum (Connell 1978; Huston 1979). It seems likely that the high regional warming (Murphy and Mitchell 1995; King and Harangozo 1998) is likely to result in increased ice sheet collapses and higher iceloading of near shore waters (Doake and Vaughan 1991). Thus these sites that are amongst the most highly disturbed in the world seem set to become even more impacted.

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