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Growth and population structure in the infaunal bivalve *Yoldia eightsi* in relation to iceberg activity at Signy Island, Antarctica

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Abstract. Growth rates in the infaunal nuculanid bivalve mollusc *Yoldia eightsi* (Couthouy) were assessed for field populations in Factory Cove, Signy Island, Antarctica, between February and April 1992. Daily increments in length (maximum shell dimension) ranged from $2.3\ \mu\mathrm{m\,d^{-1}}$ for a 30 mm individual to $5.1\ \mu\mathrm{m\,d^{-1}}$ for a 10 mm specimen. These growth rates were converted to annual increments, based on a growing season for the Signy population of around 5 mo, and ages for the largest individuals in the population (35 mm in length), were calculated to be $\simeq 65$ yr. Specimens of 43 mm in length have been found near this site and, if their growth rates are similar to this population, their ages would be in the order of 120 yr. Size distributions from two sites in the same *Y. eightsi* bed 300 m apart showed significant differences. At the more exposed site the distribution was dominated by small juveniles, with 86% of the population <10 mm in length, while 13% were >20 mm in length. At the less exposed site the values were 27% <10 mm and 56% >20 mm. Icebergs have often been seen grounded on the *Y. eightsi* bed in this study, especially on the exposed outer portion. This factor, in association with inhibition of larval settlement by high densities of large individuals, is proposed as an explanation of the observed population distributions and the absence of very large specimens in the Factory Cove population.

Introduction

Ice is now recognised as a major force in shaping the ecological characteristics in cold-water environments. In particular, there has recently been much work on the ecology and biology of biota associated with sea-ice. Sea-ice algae reach very high biomasses, often exceeding 100 mg chlorophyll *a* $\mathrm{m^{-2}}$ (Grossi et al. 1987, Palmisano et al. 1988). They are known to assist in the seeding of summer blooms of phytoplankton in the water column (Garrison et al. 1986). Microbial activities in sea-ice are also becoming increasingly studied (Sullivan and Palmisano 1984, Delille et al. 1988, Delille 1992) and the importance of sea-ice biota is now being examined in relation to global climate change (Legendre et al. 1992).

The effect of ice on benthos has received less attention, although zonation patterns in organisms inhabiting hard substrata are dominated by ice-scour and anchor-ice effects. Intertidal and shallow subtidal habitats generally have very few organisms present (Hedgpeth 1971, Dayton 1990), while areas beyond this (to ~30 m depth) are affected to a lesser degree by ice, and there are characteristic zonations of algae and invertebrates (Gruzov 1977, Heywood and Whitaker 1984, Hooper and Whittick 1990).

Studies of soft-bottom benthos in polar latitudes have shown that sediment type, productivity and the history of biological disturbance are important factors in determining species compositions and abundances. High density and diversity have been related to areas of high productivity, while the converse of low diversity and biomass in relation to low productivity has also been documented (Richardson and Hedgpeth 1977, Dayton et al. 1986, Barry and Dayton, 1988). The effects of ice on communities of organisms inhabiting soft sediments are almost totally unknown.

Yoldia eightsi is an infaunal nuculanid bivalve inhabiting soft-sediment habitats between 4 and 824 m depth, but is most common at depths shallower than 100 m (Dell 1990). Its distribution is thought to be circumpolar (Dell 1964, Nicol 1966), although records around the continent are few and discontinuous. It burrows relatively shallowly compared to other *Yoldia* species (Davenport 1989) and feeds mainly on organic material present in the surface layers of sediments (Yonge 1939, Davenport 1988). In the present paper, data are presented on size distributions and growth rates of *Y. eightsi* at Signy Island, Antarctica. The results are interpreted in relation to the effects of iceberg trampling and scour in the local nearshore soft-bottom habitats.

Materials and methods

Size distributions of *Yoldia eightsi* (Couthouy) were investigated at two sites in Factory Cove on the east side of Signy Island, Antarc-

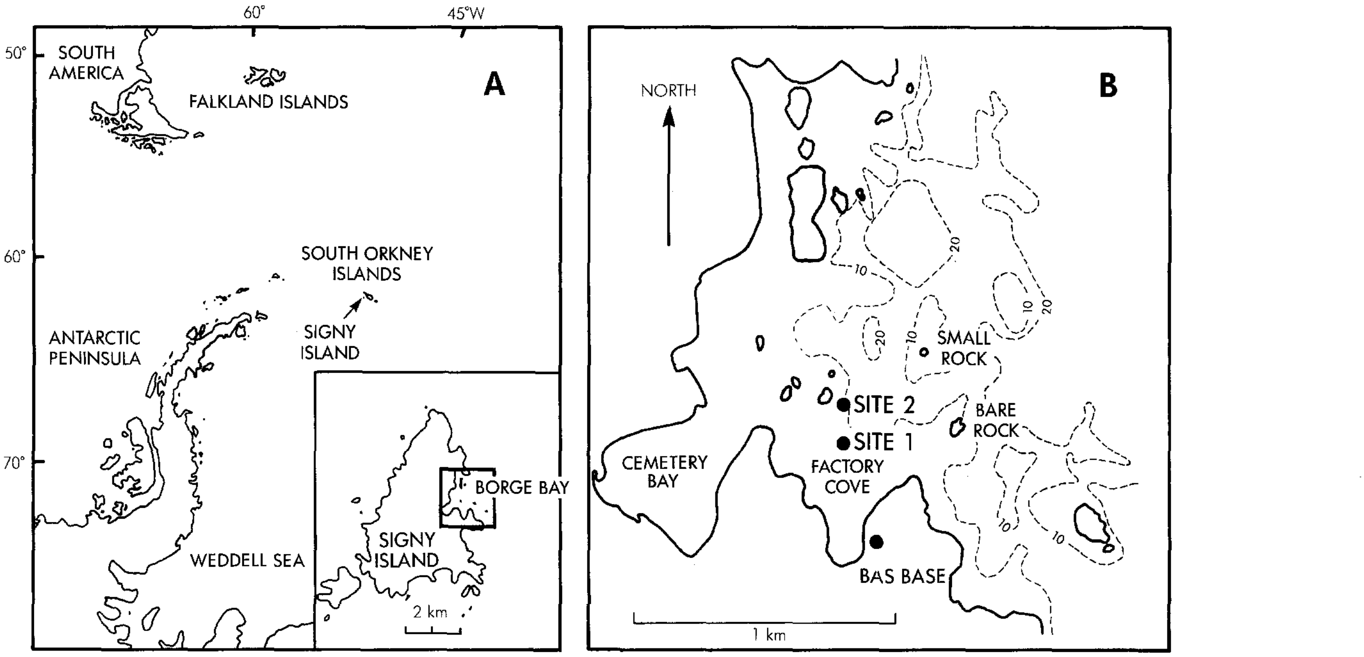

Fig. 1. (A) Position of Signy Island in South Orkney group; inset is Signy Island itself, showing position of Borge Bay. (B) Details of Factory Cove experimental sites in Borge Bay and position of British Antarctic Survey (BAS) base; both sites were at 8 to 10 m depth below spring low tide level; depth contours are at 10 m intervals

tica (60°43′ S; 45°36′ W) between February and April 1992. The population studied was living at ~9 m depth in Factory Cove (Fig. 1). Specimens for study were collected from 0.25 m^2 areas of sediment by a sampling device which removed the bivalves and sediment from the seabed using suction generated by an air lift and then trapped the bivalves in a 1 mm-mesh bag. Sediment passed through the bag and was carried away via a 5 m long airlift pipe. Bivalves collected in this way were returned to the laboratory, and held in mesh baskets suspended in a flow-through aquarium system at 0.0 to 1.0 °C. All the individuals collected were measured for shell length, breadth and height, to the nearest 0.05 mm using vernier callipers.

Specimens for the growth study were taken from the above samples and their shells were labelled. The shells of small individuals (<15 mm length) were numbered using Staedtler permanent markers, while in larger specimens numbers were engraved onto the shell valves using a Radio Spares professional engraver. Shells were dab-dried using tissues before being numbered; the engraving tool was used only to remove the periostracum. Small amounts of shell matrix were also accidentally removed by this process in some specimens. After numbering, a thin coat of Radio Spares cyanoacrylate gel adhesive was spread over the area to protect the label from physical abrasion while *Yoldia eightsi* moved through the sediment. Setting times for the adhesive were reduced to $\simeq 30$ s by the use of an activator, which was painted onto the shell prior to the application of the glue. This was necessary because the bivalves were held in sea water at 0 °C and setting times for cyanoacrylate adhesives are extended at low temperatures.

After being marked and measured, individuals used in the growth experiments were returned to the sediment at the study sites. They were placed in enclosures to facilitate collection at a later date. The enclosures were made from 3.5 mm-thick polycarbonate sheet; they were circular, with an enclosed area of 0.25 m^2 and were 300 mm deep. Enclosures were pushed into the sediment by divers to a depth of 200 to 250 mm, leaving 50 to 100 mm exposed above the surface. This stopped the study individuals from burrowing out of the area, or climbing over the enclosure rim to escape, while leaving only a small amount of polycarbonate exposed at the surface. Any *Yoldia eightsi* in the enclosures when they were set up were removed. Three enclosures were set up at each of the two experimental sites, near to where the original samples had been collected. Each enclosure had 50 *Y. eightsi* put into it, ranging in size from around 7 to 35 mm in length. Thus, the density of specimens in the enclosures was 200 m^{-2}, which was within the range of natural population density, but below the mean density for the area. After the bivalves used in the growth experiments were returned to an enclosure they were covered with surface sediment from the surrounding seabed. This was to replace material removed earlier and replenish the food supply for the experimental individuals. Sediment placed over bivalves in the enclosures was passed through 2 mm-mesh sieves held 50 to 100 mm above them. This avoided the accidental placement of any unmarked and unmeasured *Y. eightsi* into the enclosures from the surrounding area.

Experimental bivalves were returned to the seabed in mid-February 1992. They were then left in situ for 2 mo, until mid-April, before being collected once more and remeasured. Differences in length between initial measurements and those obtained 2 mo later were used to calculate growth rates.

Results

The data on density and size of *Yoldia eightsi* for each of the 0.25 m^2 samples collected at the two study sites are summarised in Table 1. Mean densities at Site 1 were 90.2 individuals per 0.25 m^2 (361 m^{-2}). The density at Site 2 was much higher, at 167.2 per 0.25 m^2 (669 m^{-2}), and ranged as high as 1540 m^{-2} in one of the samples. Maximum lengths were similar at each site, but minimum lengths were lower at Site 2. The numbers of small individuals were nearly seven times higher at Site 2 than at Site 1, as shown by data for specimens <10 mm in length. The reverse was the case for large specimens, with Site 1 having over 2.5 times as many *Y. eightsi* >20 mm in length as Site 2.

The size-distribution patterns of the populations at the two sites were markedly different (Fig. 2). At Site 1 there

Table 1. *Yoldia eightsi.* Data on densities and sizes (length, mm) for individual 0.25 m^2 samples from each of the two sites studied

Site, sample no.	No. in sample	Mean length, mm (SE)	% <10 mm in length	% <20 mm in length	Length (mm)	
					min.	max.
Site 1						
1	95	18.85 (0.88)	23.2	62.1	2.90	34.90
2	55	18.45 (1.04)	21.8	65.4	3.30	32.10
3	108	16.64 (0.82)	32.4	52.8	3.20	31.00
4	91	17.34 (0.95)	16.5	70.3	3.40	34.00
5	102	18.39 (0.81)	24.5	58.8	3.30	32.90
Mean	90.2	17.93 (0.88)	24.1	61.1		
Site 2						
1	151	9.65 (0.83)	78.1	17.9	2.70	32.90
2	131	9.55 (0.91)	73.3	25.2	1.50	32.80
3	61	10.91 (1.40)	67.2	31.1	2.20	31.70
4	108	6.24 (0.63)	89.8	9.3	2.65	31.10
5	385	4.91 (0.25)	94.8	3.9	1.40	32.20
Mean	167.2	8.25 (0.80)	85.8	12.4		

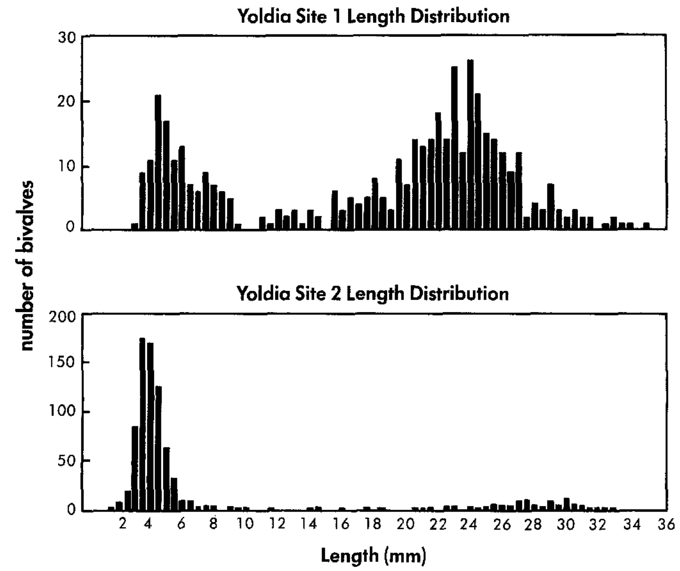

Fig. 2. *Yoldia eightsi.* Population size distributions at two sites in Factory Cove. Data are actual number of specimens found in a given size range and are displayed in 0.5 mm-length groups starting from 0.75 mm in length (i.e., number of individuals between 0.75 and 1.25 mm, between 1.25 and 1.75 mm, etc.). Note difference in *y*-axis scales between sites

was a bell-shaped distribution pattern, with most of the bivalves between 15 and 30 mm in length. There were very few specimens between 10 and 15 mm, but there were significant numbers below 10 mm in length. The distribution at Site 2 was very different, with 80% of the population ≤ 5 mm in length. The differences in proportions of individuals in the various size categories were not only due to the large numbers of small individuals present at Site 2, but also because of a reduction in numbers of large bivalves at Site 2 compared with Site 1. It is also noticeable that at Site 1 there were very few specimens in the 9 to 12 mm size range, and relatively few up to 16 mm in length, while at Site 2 the size range where very few bivalves were present was larger, ranging from 7 to 20 mm length.

Data on growth rates were only obtained from the individuals set out at Site 1, because within 2 wk of setting experimental bivalves out in enclosures at Site 2 the area was heavily impacted by an iceberg. After the berg moved away there was no trace of the enclosures and it was not possible to retrieve any marked specimens which might have survived, since the experimental site had been completely obliterated.

Of the original 150 specimens set out in enclosures at Site 1, 130 were retrieved alive and remeasured. This was a recapture rate of 87%. Nine of the other bivalves were retrieved dead and 11 were not recovered. Thus, there was a known mortality rate of 6%, some of which may have been due to the stress involved with collection and marking, and there was uncertainty about a further 7%. Collection of soft-sediment samples by suction sampler underwater is not totally efficient and it is likely that some of these specimens may have been left in the enclosures. It is also possible that some of the *Yoldia eightsi* in the study were weakened by the marking treatment and were taken by predators, although a return of 87% shows that neither of these effects were important.

Growth increments for the experimental bivalves set out at Site 1 are shown in Fig. 3. The enclosures were not all set out on the same day or retrieved on the same day. Thus, the periods wich specimens in each enclosure were left to grow were 57, 58 and 60 d. The data in Fig. 3 are, therefore for an average of 58.33 d. Four specimens exhibited a negative growth rate. This shows the scale of errors involved with remeasuring individuals which have not grown, or have grown very little, in the intervening period. The largest specimens in the experiment grew by ~0.1 mm on average. The accuracy of the vernier callipers was 0.05 mm. The distribution of points in Fig. 3 is wide, and some bivalves grew significantly less than the average. The errors associated with remeasuring specimens combined with the variability of growth rate in *Yoldia eightsi* has produced the spread of data seen here.

By solving the equation relating increment to individual length (Fig. 3), mean daily growth rates of specimens for given sizes were calculated. The rates were 5.1 µm for

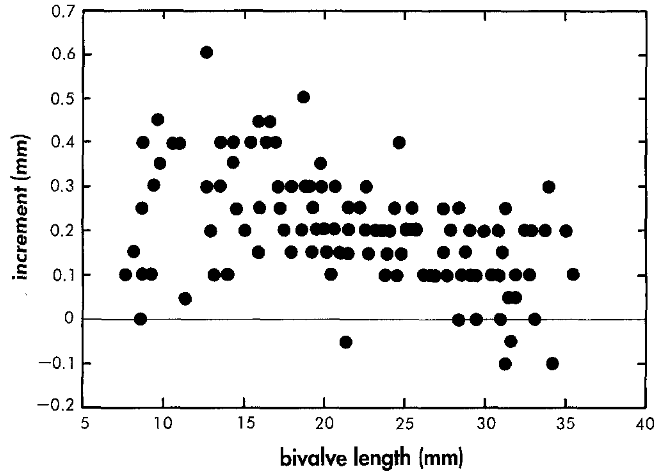

Fig. 3. *Yoldia eightsi.* Growth at Site 1. The 2 mo growth increment (mm) is plotted against bivalve length (mm). The 4 negative values are indicative of errors associated with remeasuring specimens which had either grown very little or not at all. Linear, exponential and logarithmic regressions were fitted to the data, which was logarithmically transformed ($\log_e$) where appropriate; best fit was to a linear model, where increment = 0.381 − 0.00813 length ($r^2 = 0.22$, $F = 37.8$, $P < 0.001$, $n = 130$)

Table 2. *Yoldia eightsi.* Ages (yr) at given lengths, assuming growing seasons of differing duration

Duration of growing season	Bivalve length:		
	20 mm	35 mm	40 mm
4 mo	33	81	113
5 mo	12	65	90
6 mo	10	54	75

a 10 mm-length individual, 3.75 µm for a 20 mm individual, and 2.36 µm for a 30 mm *Yoldia eightsi.* These growth rates should be amongst the fastest of the year, as the period during which the measurements were made encompassed the latter part of the summer. *Y. eightsi* are predominantly deposit feeders (Davenport 1988, 1989), and the period of study was during the months of strongest deposition of organic material from the water column in Factory Cove, Signy Island, as shown by sediment-trap data (Gilbert 1991). If the period of strong growth is known, then the daily growth rate above can be converted into an annual rate. Sediment-trap data near to the experimental sites in this study would suggest that significant deposition usually occurs over a 4 to 6 mo period, generally between December and May (Gilbert 1991, A. Clarke, personal communication). On this basis, ages for individuals of 20, 35 and 40 mm length have been calculated from the data in Fig. 3 extrapolated to seasons of 4, 5 and 6 mo duration (Table 2). The average season should fall somewhere between 4 and 6 mo duration, and hence the largest specimens in this experiment (35 mm in length), which were also the largest *Yoldia eightsi* found at this site, should be between 54 and 81 yr old. Individuals of 20 mm in length should be between 10 and 33 yr of age and 40 mm individuals between 75 and 113 yr.

If the equation relating increment to animal length (Fig. 3) is solved to find the length where there is no more growth (increment = 0), a length of 46.9 mm is obtained. This is the equivalent of the L_∞ length estimate used in the von Bertalannfy growth model. It is much larger than the maximum individual length of 35 mm observed in the population, and was one of the reasons for including 40 mm length individuals in the age calculations.

Discussion

Growth rates for *Yoldia eightsi* of 3.06 and 3.60 µm d^{-1} were reported for specimens of 16.05 to 28.00 mm and 19.10 to 32.50 mm length, respectively, by Davenport (1989) from a preliminary mark–recapture study, while Rabarts (1970) found rates of 5.5 µm d^{-1} for 5 mm-length individuals and 4 µm d^{-1} for 11 to 13 mm individuals. These results were all obtained from studies of *Y. eightsi* from Signy Island and compare with rates in this study of 5.1, 3.75 and 2.36 µm d^{-1} for 10, 20 and 30 mm-length specimens, respectively. Recently, Nolan and Clarke (1993) obtained growth rates of 5.9 µm d^{-1} for 12 mm individuals. Thus, growth increments of 5 to 6 µm d^{-1} for specimens around 10 mm in length and 3 to 4 µm d^{-1} for 20 mm *Y. eightsi* seem appropriate. The rates produced by Rabarts and by Nolan and Clarke were calculated using three different techniques. Rabarts used data from analyses of population distributions, while Nolan and Clarke measured the major internal-shell incremental bands and also used ^{45}Ca incorporation to assess instantaneous growth rates. The close agreement between their data and the field measurements quoted here is encouraging. The daily growth rates found for *Y. eightsi* are not dramatically slower than those obtained for related temperate species, but the overall annual rates of growth are less. Much of the reduction in annual growth rates could be accounted for by a shortening of the period of significant phytoplankton productivity at higher latitudes leading to a concomitant reduction in the growing season (Nolan and Clarke 1993).

The ages calculated from the in situ growth rates in this investigation suggest that the largest specimens in Factory Cove are probably ~65 yr old, based on a growing season of 5 mo. Five months would seem appropriate, considering the length of the period when significant amounts of material are sedimenting out of the water column (Gilbert 1991). This was also the period of time used by Nolan and Clarke (1993) and is the same as the length of season deduced by periodic analysis of shell microgrowth bands (Bryer 1993). Problems may arise with enclosure-based investigations, if the enclosures significantly affect the local sediment conditions. The most common effect is a disruption of water flow over the seabed or through the sediment, affecting food supply to the specimens under investigation. Methods of reducing these effects to a minimum include constructing enclosures as large as possible and using a porous mesh with which to make the enclosures, allowing a freer movement of water over the experiment. There must have been some effects due to the enclosures used in the present study, and it was not possible to quantify those effects. However, the close similarity between the daily growth rates found here and the microgrowth increments found by Nolan and Clarke for unrestrained *Yoldia eightsi*, is strong evidence that those effects did not significantly alter the growth rates found in the present experiments.

Many *Yoldia eightsi* >40 mm in length (ranging as high as 43.0 mm) have been collected during deeper-water sampling programmes (50 to 300 m) in the Orwell Bight between Signy and Coronation Island (Rabarts 1970, S. Hain personal communication). Specimens up to 46.5 mm in length were found in the "Discovery" expedition of 1927 around the South Orkneys in 244 to 344 m depth (Rabarts and Whybrow 1979). Many of these deeper-water locations are very close to the present study site, some being within 1 km. It is therefore likely that the food supply regimes will be similar. Thus, the ages of the 40 mm individuals in Table 2 may be appropriate for some of these deeper-water individuals. If this calculation is extrapolated to larger specimens, individuals of 43 mm length are 117 yr old, on the basis of a 5 mo season, while those of 45 mm are 150 yr old.

The size distributions at the two sites differed markedly. However, at both sites there was a dearth of specimens in the middle of the size range, with many more bivalves present <10 mm and >20 mm in length than in between. This type of distribution pattern, showing the presence of some small individuals combined with an accumulation of specimens in the larger size categories, but very small numbers of individuals of intermediate size, has also been reported for *Yoldia eightsi* from sites near those studied here by Rabarts (1970) and Nolan and Clarke (1993). Dumbell-shaped size distributions were found by Gage and Tyler (1982, 1991) and Gage (1990) in deep-sea populations of the brittle star *Ophiomusium lymani* from the Rockall Trough. They used computer models to dissect out the possible causes of such distributions, and concluded that there was relatively low mortality in large adults, culminating in a build up and merging of individuals from different age classes in the large size ranges. This could explain the peak in large-sized specimens in the distributions found here for *Y. eightsi*.

There were also large differences between the densities at the two sites (Fig. 2), with 5 to 10 times as many small specimens present at Site 2 than at Site 1. Adult densities at Site 2 were lower than at Site 1, and this suggests that high adult densities inhibit recruitment and/or survival of young stages. This could be achieved by the adults either consuming larvae as they begin to settle, or eating recently settled individuals along with the sediment they normally ingest (Davenport 1988). Density-dependent control of recruitment is a phenomenon which has been documented in the past, especially in soft-sediment communities. It can either facilitate larval settlement and survival (Gallagher et al. 1983, Crowe et al. 1987) or inhibit it (Woodin 1974, Petersen 1982, Elmgren et al. 1986, Olafsson 1989). This type of control in association with relatively low mortality of adults has also been invoked to explain population distributions in gastropod molluscs which are dominated by large individuals (Peck and Culley 1990).

The fact that the largest individuals in the Factory Cove population studied here were growing at a significant rate (Fig. 3), combined with the calculation of an L_∞ of 46.9 mm, and the fact that specimens well in excess of 40 mm in length are found in deeper water close by, all indicate that maximum size is being limited below that normally attainable. The respective size distributions are also evidence of a greater disturbance at Site 2, which is the more exposed of the two sites. This would suggest that iceberg scour may be the factor limiting maximum size in the *Yoldia eightsi* population in Factory Cove. The importance of trampling and scour effects was demonstrated during our study: the growth-study enclosures set out at the outer site were destroyed by an iceberg within 2 wk of deployment. A similar destruction of experimental equipment designed to assess growth in *Y. eightsi* at another nearby site in Factory Cove was reported by Davenport (1989), and grounded icebergs are frequently noted in this area, especially in the more exposed locality at Site 2. The ages calculated from the growth experiment would lead to the expectation that all areas within Factory Cove experience iceberg scour approximately every 50 to 75 yr. Clearly there are areas which are scoured more often than others, however, as the *Y. eightsi* are mobile within the sediment, the removal of individuals from the population must be viewed as a highly stochastic event. The rate of recovery of scoured sites will depend on the movement of large individuals back into the denuded area as well as settlement of larvae, although recently scoured sections of seabed will be better for larval settlement than those without recent disturbance.

Ice has been noted in the past as being a major parameter in determining and limiting benthic habitats for colonisation in Polar waters. Dayton et al. (1969, 1970) reported that anchor ice in McMurdo Sound, Antarctica, played a major role in determining the zonation patterns of benthic species and that anchor ice was detectable to depths of 33 m. Ice scour is known to enhance conditions for ephemeral macroalgae by providing freshly cleaned sites for colonisation and by removing herbivores (Hooper and Whittick 1990). Icebergs of over 400 m draft have been documented in Antarctic waters (Keys 1984), and iceberg scouring has been documented from both Arctic and Antarctic continental shelves, down to depths beyond 300 m (Lien 1983, Barnes et al. 1984, Goodwin et al. 1985). In a study of seabed characteristics on the continental shelf of the eastern Weddell Sea, Antarctica, Lien et al. (1989) found that features related to iceberg grounding covered all of their study area except the protected slopes of submarine troughs. Their investigation was carried out on seabed between 250 and 400 m depth. This would suggest that the deeper-water populations of *Yoldia eightsi* may be subject to iceberg activity and that the upper sizes in those localities may also be limited by the frequency of scouring in the deeper habitats, as appears to be the case for the shallower population. If this were the case, then a soft-bottom environment around Signy Island should be scoured by icebergs every 120 to 150 yr, based on the sizes of individuals found in those habitats. On evolutionary timescales, iceberg scouring effects will have been a powerful influence affecting populations of benthic invertebrates over large areas of the world's oceans. This is emphasised by the fact that, during the last ice age, between 10000 and 30000 years ago, icebergs ranged as far south as 41 °N (Bond et al. 1992), which is a southern European latitude. Thus, the present population characteristics of many infaunal cold-water and continental shelf species may have been partly shaped by iceberg activity.

In conclusion two major opposing factors appear to control recruitment in the *Yoldia eightsi* populations in Factory Cove, Signy Island. These are the inhibition of settlement or survival of newly settled individuals by high densities of adults and the clearance of areas for settlement by icebergs. Iceberg scour appears to limit the upper sizes and ages attainable by the bivalves in this population and these effects may also be present in deeper water, although at much lower levels. Overlaid on this are the seasonal factors of intensity and duration of food material sedimenting out of the water column which affect growth rates an a yearly basis.

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