BENTHIC MARINE HABITATS IN ANTARCTICA

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Benthic habitats in Antarctica differ from those in other parts of the world in several important characteristics. Most of the Southern Ocean overlies the abyssal plain, where the sediments are primarily siliceous. Ice-rafted debris provides isolated patches of hard substratum but otherwise little is known of the biology of the deep-sea in Antarctica. Shallow water habitats are heavily influenced by ice, with typical intertidal habitats being almost devoid of life. Continental shelves are unusually deep around Antarctica and the sediments are predominantly glacial-marine. Antarctica lacks typical fluvial habitats such as rivers, estuaries and has very few intertidal mudflats, and away from the immediate sublittoral the habitats suffer less physical and biological disturbance than the continental shelves of the Arctic.

1. INTRODUCTION

Antarctica poses severe challenges for the benthic ecologist. Most of the Southern Ocean overlies the abyssal plain, the continental shelves are unusually deep, and access is impeded by floating ice shelves or vast areas of seasonal pack ice. Despite these difficulties there is a long and proud history of benthic investigation in the Antarctic and we know a great deal more about the fauna, at least in shallow water, than is often realized.

The early benthic work largely took place during expeditions concerned primarily with geographic exploration or important physical observations such as geomagnetism or meteorology. Nevertheless the early collectors were remarkably thorough and *Dayton* [1990] laments that these pioneers will never gain the recognition they deserve. *Headland* [1989] provides a comprehensive list of polar exploration (updating an earlier, and largely unpublished, compilation by Roberts), and valuable historical reviews of Antarctic biology are those of *Fogg* [1994] and *El-Sayed* [this volume]. *Dell* [1972], *White* [1984], *Dayton* [1990] and *Arntz et al.* [1994] have all reviewed the history of benthic marine biology in the Southern Ocean. Until relatively recently all benthic work in Antarctica has had to rely on remote, and usually destructive, sampling techniques. Although SCUBA techniques have been used since the late 1950s [*Neushul*, 1959, 1964] and have become increasingly important in the last ten to fifteen years (Figure 1), safety considerations limit these investigations to the shallowest of depths. The history of SCUBA in Antarctic marine biology has been summarized by *White* [in press] and *Dayton* [1990].

The advent of sophisticated remotely-operated vehicles (ROVs) marks a technical advance which looks likely to change the face of Antarctic benthic marine biology; the contrast between the view of a pristine structured benthic community provided by an ROV and an unsorted pile of dead or damaged specimens provided by a bottom trawl is striking indeed. It must be recognized, however, that identification of organisms on photographs or video film still may require access to specimens collected by more conventional means. The importance of new techniques in Antarctic benthic biology has been emphasized by *Arntz et al.* [1994], but these new techniques bring their own challenges. *Bullivant and Dearborn* [1967] pioneered the use of underwater photographic techniques in Southern Ocean benthic research in their study of deep water communities in the Ross Sea. It is only since the work of German benthic ecologists working in the Weddell Sea that significant progress has been made in obtaining quantitative ecological data from photographic or video techniques [*Barthel et al.*, 1991; *Gutt et al.*, 1991; *Gutt and Piepenberg*, 1991; *Ekau and Gutt*, 1991; *Gutt et al.*, 1994].

1.1. Some Definitions

The definition of Antarctica for a benthic ecologist is not straightforward, as *Dell* [1972] has emphasized. Particular difficulties surround the islands of the Scotia arc, South Georgia, and those islands which lie within the Polar Frontal Zone. The definition proposed by *Dell* [1972] has gained general acceptance, and will be followed here. The Antarctic is defined as including the islands of the Scotia arc (South Orkney Islands, South Sandwich Islands and South Georgia) and Bouvetøya, but not Marion Island, Macquarie Island, Îles Crozet or Îles Kerguelen; these are viewed as sub-polar habitats and thereby excluded. The outer edge of the Southern Ocean is taken to be the Polar Frontal Zone. The Southern Ocean thus encompasses roughly 10% of the

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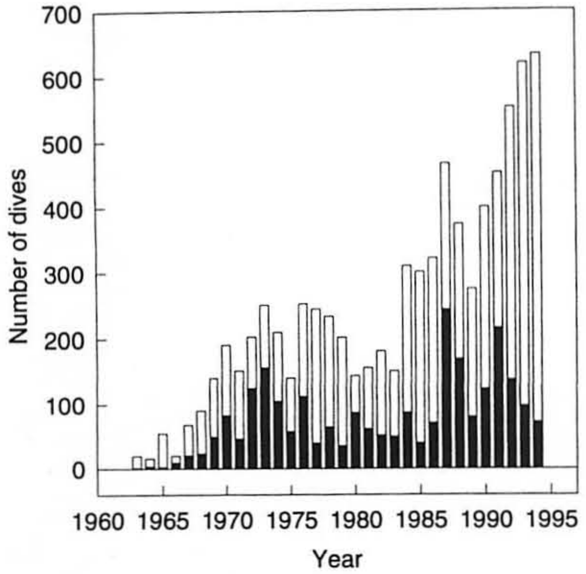

Fig. 1. The number of SCUBA dives undertaken each year at Signy Island by British Antarctic Survey divers. The solid bar shows dives undertaken through winter fast-ice. The increasing reliance on SCUBA techniques for work in Antarctica is clear.

world's oceans and is contiguous with the Pacific, Atlantic and Indian Oceans.

2. LARGE SCALE DISTRIBUTION OF BENTHIC HABITATS

2.1. The Deep Sea

Even a casual glance at a bathymetric of the Southern Ocean reveals vast areas of seabed at abyssal depths (Figure 2). In contrast, a careful search of the literature on Antarctic benthic marine biology will fail to uncover much data on these areas; we know almost nothing of the biology of the deep sea in Antarctica. Most of what we have learned has come as the by-product of geological and geophysical sampling programs, the most notable exception to this being the International Weddell Sea Oceanographic Expedition in 1968 and 1969 [*Rankin et al.*, 1969].

Many of the early expeditions to Antarctica took samples of the seabed [*Pirie*, 1913; *Wüst*, 1933; *Douglas and Campbell-Smith*, 1930], and 142 samples were taken by RRS *Discovery* and RRS *William Scoresby* as part of the *Discovery* Investigations [*Neaverson*, 1934]. Further data have been obtained by more recent geological and geophysical expeditions and are discussed by *Domack and McClennen* [this volume].

Like the abyssal plains elsewhere, those around Antarctica are composed primarily of soft sediments. They differ from sediments in most other deep-sea areas in two ways: the low temperatures of the surface waters mean that these sediments are siliceous rather than the carbonates typical of lower latitudes, and there is a strong influence of glacial processes.

Close to the Antarctic continent the sediments contain an abundant silt fraction comprised of rock flour with coarse poorly-sorted debris, and containing little calcite or biogenic material. These types of sediment were termed *glacial-marine* by the Deutsche Südpolar-Expedition [*Philippi*, 19-10], and they form a wide circumpolar band around Antarctica (Figure 3). *Goodell et al.* [1973] have proposed a more rigorous definition of glacial-marine sediments and have distinguished four more or less concentric zones distinguished on textural grounds. In general there is a decrease in the proportion of coarse material with increasing distance from the continent, and the outermost of the four zones proposed corresponds to the pelagic clays of the abyssal plain. The northernmost limit of glacial-marine sediments is related to the surface 0°C isotherm, which influences the rate of iceberg melting. The distribution of these sediments also depends upon the location of sites of iceberg calving, the preferred paths of these icebergs and storm tracks.

In Antarctica icebergs are the major route for ice-rafted sediment transport. Unlike the Arctic, sea-ice is of relatively little importance for moving terrigenous material, largely because the extensive development of ice-shelves essentially precludes the capture of sediments by sea-ice. Ice-shelves also greatly reduce the importance of riverine and aeolian (wind-driven) input to the marine system of Antarctica compared with the Arctic. *Lisitzin* [1972] has estimated that icebergs in Antarctica transport between 35 and 50 x 10^9 tons of sediment each year; more recently *Knox* [1994] estimated a figure of 0.5 x 10^9 tons per year.

Beyond the limits of significant ice-rafted input, the glacial-marine sediments merge gradually into biogenic oozes. The overall character of a biogenic ooze is controlled by the balance between four main processes: supply of biogenic material from the surface layer, dissolution of that material during flux to the seabed, dilution by non-biogenic material and diagenetic alteration after deposition. The low temperatures of surface waters in the Southern Ocean mean that coccolithophorids are absent, and primary production is dominated by diatoms. Since dilution by non-biogenic material is almost non-existent, and the low temperature and depth of the abyssal plain tend to induce dissolution of carbonates, the biogenic oozes of the Southern Ocean are almost exclusively siliceous. The boundary between siliceous oozes and the carbonate oozes formed in warmer subpolar surface waters is dictated largely by the position of the Polar Frontal Zone, and previous positions of the Polar Front can be determined from the switch between siliceous and carbonate sediments in cores.

The lack of substantial riverine or aeolian input means that rates of abyssal sediment accumulation around Antarctica can be very slow, often less than 0.01 m per 10^3 years [*Osmond et al.*, 1971]. High rates of silica accumulation

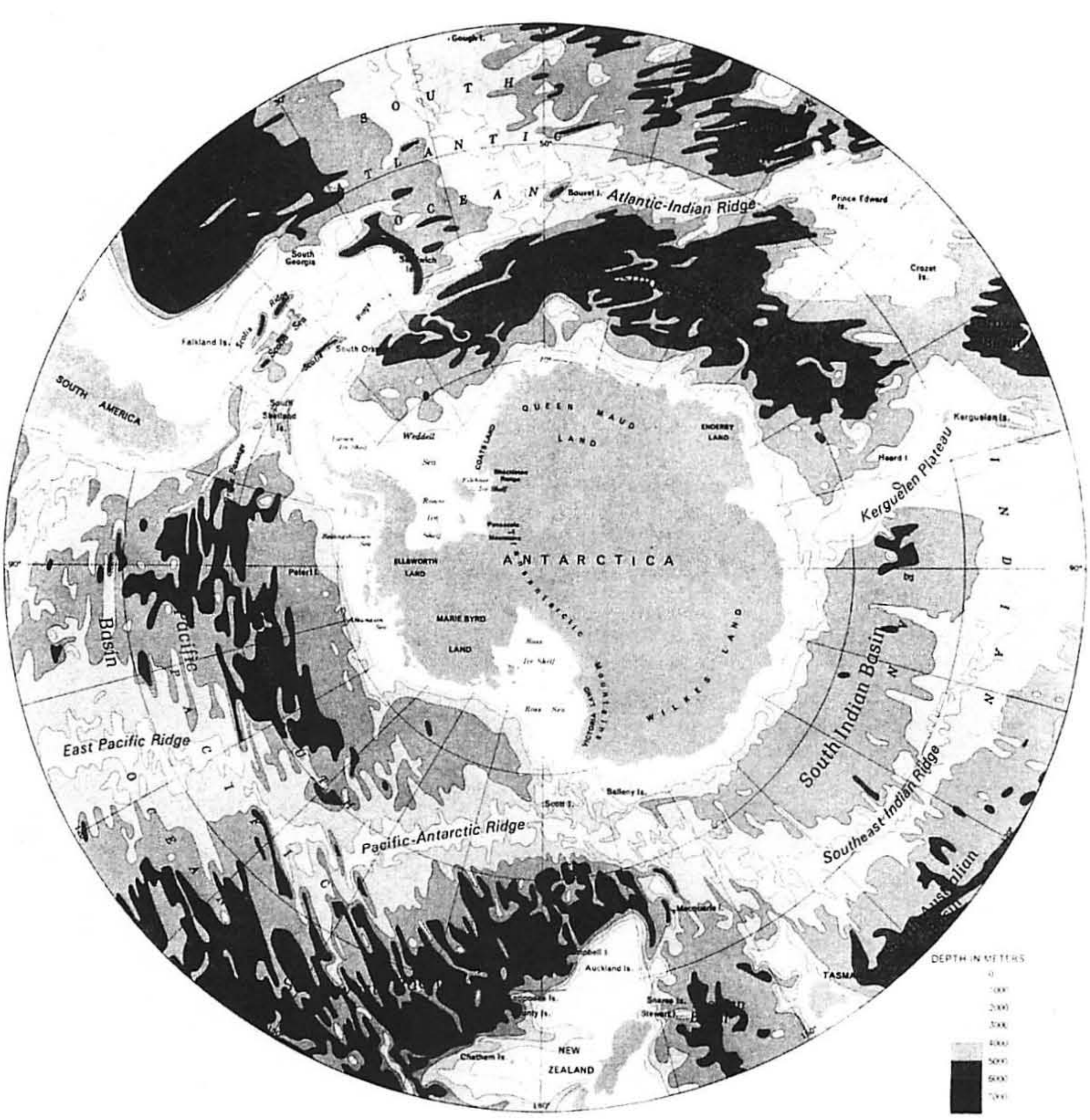

Fig. 2. A map showing the major bathymetric contours around Antarctica. The depth scale is in eight shades of grey, and covers the range from 0-1000 m (palest) to 7-8000 m (darkest). Note the extensive areas of deep water within the Southern Ocean. Reproduced from *Goodell et al.* [1973].

have been reported on the continental shelf of the Ross Sea, and it has been speculated that deposition in the Ross Sea as a whole may be equivalent to the total riverine input of silica to the world's ocean [*Ledford-Hoffman et al.*, 1986]. The Southern Ocean dominates the global oceanic silica cycle, and it has been estimated that over 75% of the current accumulation of biogenic silica in marine sediments takes place south of the Polar Frontal Zone [*Ledford-Hoffman et al.*, 1986; *Jones et al.*, 1990]. In the north-central Weddell Sea *Fischer et al.* [1988] found that vertical silica flux increased rapidly once open water conditions had arrived over the sediment trap site; they also found significant differences in the peak flux rate between years. *Honjo* [1990] and *Domack and McClennen* [this volume] provide a review of the present glacial marine sedimentation in Antarctica.

Large ice-rafted boulders (drop-stones) are important in providing isolated patches of hard substratum on the otherwise soft abyssal plain of the Southern Ocean. The concentration of these drop-stones is likely to decline with distance from the calving ice-front and their distribution will influence the colonization dynamics of some encrusting taxa in the Southern Ocean. Unfortunately very little is known of

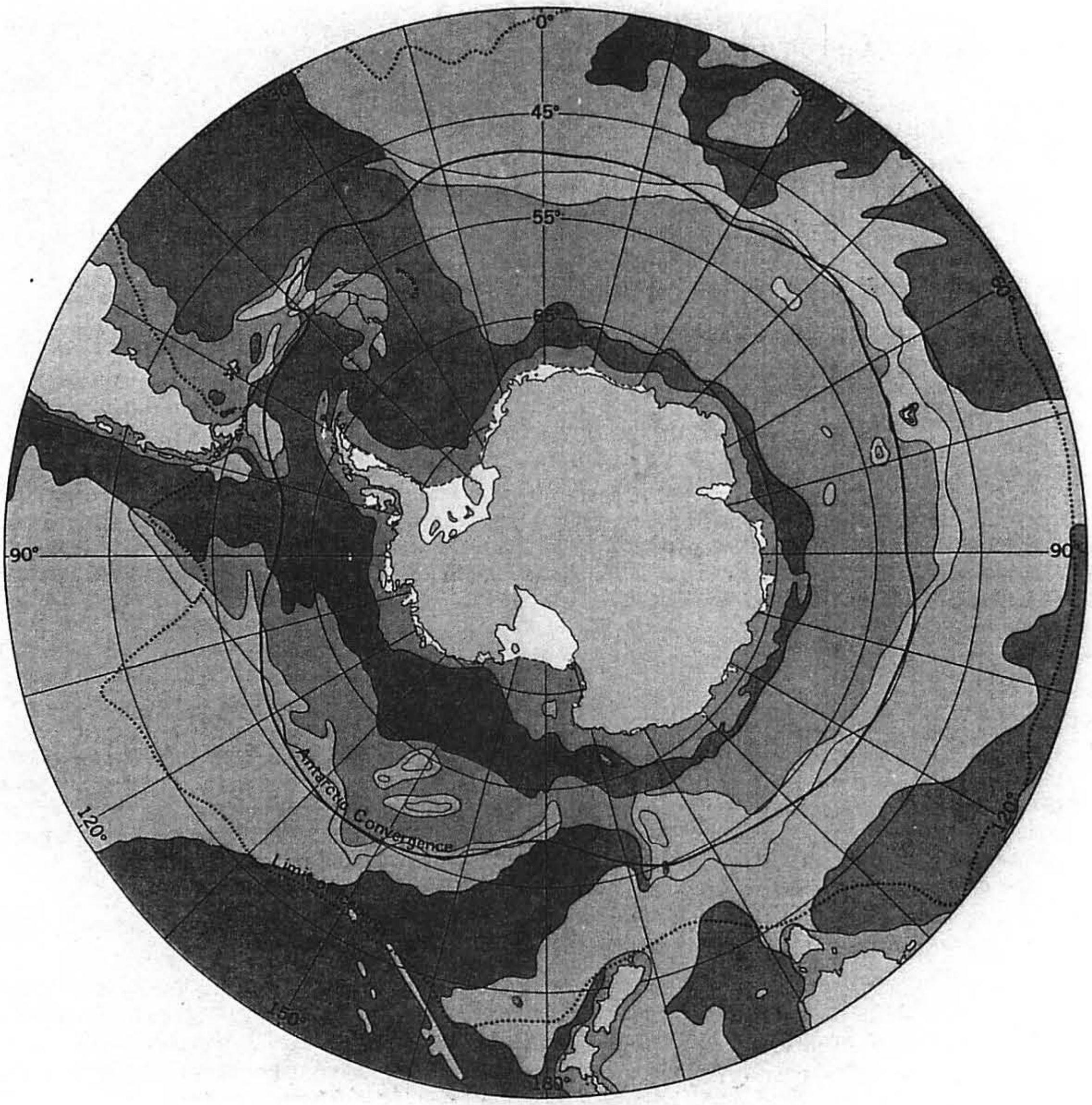

Fig. 3. A map showing the main sediment types around Antarctica. Note the distribution of the major sediments in broad swathes around Antarctica. Closest to the continent are submarine tills and glacial marine sediments; outside this (and also dominating the western South Atlantic) is a narrow band of clay-silt (dark grey), and surrounding this a broad band of siliceous ooze (pale gray). Reproduced from *Goodell et al.*, [1973].

either the distribution or fauna of these drop-stones.

One habitat that was unknown before the mid-1970s and which is currently the subject of intense investigation is that of hydrothermal vent fields [*Gage and Tyler*, 1991]. The tectonic history of the Southern Ocean suggests that hydrothermal vent fields may well exist there (for example in the eastern Scotia Sea), but as yet none are known.

The deep-sea floor thus remains as the largest single benthic habitat in Antarctica, but the least studied. Knowledge of the Southern Ocean abyssal plain is, however, critical to our understanding of the population dynamics of many taxa and of the history of the high latitude marine fauna.

2.2. The Continental Shelves

The continental shelves around Antarctica are unusual in being deep, typically as much as 800 m in places. This is primarily the result of the isostatic depression of the continent as a whole resulting from the mass of the polar ice cap. In the past the ice-shelves and glaciers have extended further towards the edge of the continental shelves than they do now. In some cases the ice extended right to the edge of the shelf, presumably obliterating all life. What is not yet clear is whether there was a time when all shelves were so covered simultaneously; this would have resulted in the complete loss of all continental shelf faunas [see discussion in *Clarke and Crame*, 1989, 1992].

The extension of glaciers and ice shelves has eroded deep canyons in some areas of continental shelves, and also resulted in a tendency for the inner shelves in some areas to be deeper than further out at the shelf-break. Unlike most continental shelves, including those in the Arctic, those surrounding Antarctica do not receive any substantial fluvial (riverine) input; there are few mudflats and essentially no large riverine deltas in Antarctica. Antarctic continental shelves do, however, receive large amounts of ice-rafted debris and also a substantial input of sediment carried by glacial meltwater.

It is now clear that the rate of ice-rafted sedimentation in polar regions is primarily controlled by four factors:

- The rate of continental erosion
- The thermal structure of glaciers and ice-shelves (since this influences their erosional and melting behavior)
- The size of ice-shelves
- Seawater temperature

The balance between these factors is not yet fully understood and is likely to vary from place to place. Thus an ice shelf with a frozen base would usually result in slower melting of icebergs and hence deposition of sediment further offshore, whereas icebergs calved from an ice-shelf with a liquid base would deposit their sedimentary load very close to shore. Where such ice-shelves are floating the bulk of deposition would take place beneath the ice-shelf itself. Spatial variation in deposition will also reflect the dynamics of iceberg calving and transport.

In general, sediments on the continental shelf closest to the continent consist of undifferentiated glacial till, gravels, sands and biogenic deposits. The tills are largely unaffected by marine processes and occupy the inner third of the continental shelves; the larger fragments are angular, faceted and striated. This sediment type (facies) forms the innermost zone of the four-fold classification of *Goodell et al.* [1973]. Further out towards the edge of the continental shelf are the glacial-marine sand-silts of the outer continental shelf, and the sediments of the outer continental slope.

Little detailed work appears to have been undertaken on bottom sediments in the area of the Antarctic Peninsula. It is to be presumed that the present depositional regime is affected by the relatively low incidence of calving glaciers and the relatively high incidence of meltwater and aeolain deposition from exposed ground, compared with continental shelves close to the ice-bound continent.

3. SEDIMENTATION, HYDROGRAPHY AND ICE

3.1. Sedimentation Rates on Continental Shelves

Sedimentation rates have been estimated at two sites on the Antarctic continental shelf. *Dunbar et al.* [1989] found that vertical flux rates varied substantially between the eastern and western sides of McMurdo Sound, and these differences could be related to oceanographic patterns. This applied to measurements of diatoms, biogenic silica and lithogenic material [*Dunbar et al.*, 1985, 1989; *Dunbar and Leventer*, 1986]. These studies also showed that resuspension and lateral advection were important processes in the benthic environment, transporting biogenic material from shallow sites to deeper basins on the continental shelf. These processes can also move macroalgal debris from shallower waters, where production takes place, to deeper waters. Such macroalgal debris can form an important contribution to deep-water carbon flux and incorporation into sediments [*Liebezeit and von Bodungen*, 1987; *Reichardt*, 1987].

Significant vertical fluxes of faecal pellets associated with krill grazing can dominate sediment trap samples in Bransfield Strait [*von Bodungen et al.*, 1988; *Wefer et al.*, 1982, 1988], whereas on other occasions the flux may be dominated by diatom resting spores [*Karl et al.*, 1991; *Leventer*, 1991] or amorphous debris [*Schnack*, 1985]. These results indicate an important role for zooplankton grazing in mediating the flux of diatoms to the seabed and also demonstrate significant spatial and temporal variation in flux rates [*Bathmann et al.*, 1991a, 1991b; *Karl et al.*, 1991].

3.2. Hydrography

The vertical flux of organic matter from surface waters to the seabed links benthic habitats to processes in the overlying water column. Critical to this pelagic-benthic coupling is the local hydrography [*Grebmeier and Barry*, 1991]; unfortunately there have been few studies of hydrography of direct relevance to benthic habitats in Antarctica. Two key exceptions, however, have been oceanographic studies at two high latitude sites, McMurdo Sound [*Barry*, 1988; *Barry and Dayton*, 1988] and Ellis Fjord [*Gallagher and Burton*, 1988], and at King George Island on the Antarctic Peninsula [*Klöser et al.*, 1994].

These studies have shown that there are complex interactions between wind forcing, circulation and meltwater. Such interactions can impact benthic assemblages through resuspension of sediment, flux of glacial material or the advection of particulate food [*Klöser et al.*, 1994]. In McMurdo Sound there are striking differences in the benthic standing crop biomass between either side of the fjord, which can be related to larger scale patterns of current flow [*Dayton and Oliver*, 1977; *Barry*, 1988; *Barry and Dayton*, 1988]. Benthic assemblages dependent upon the advection of primary production are rich and diverse where currents

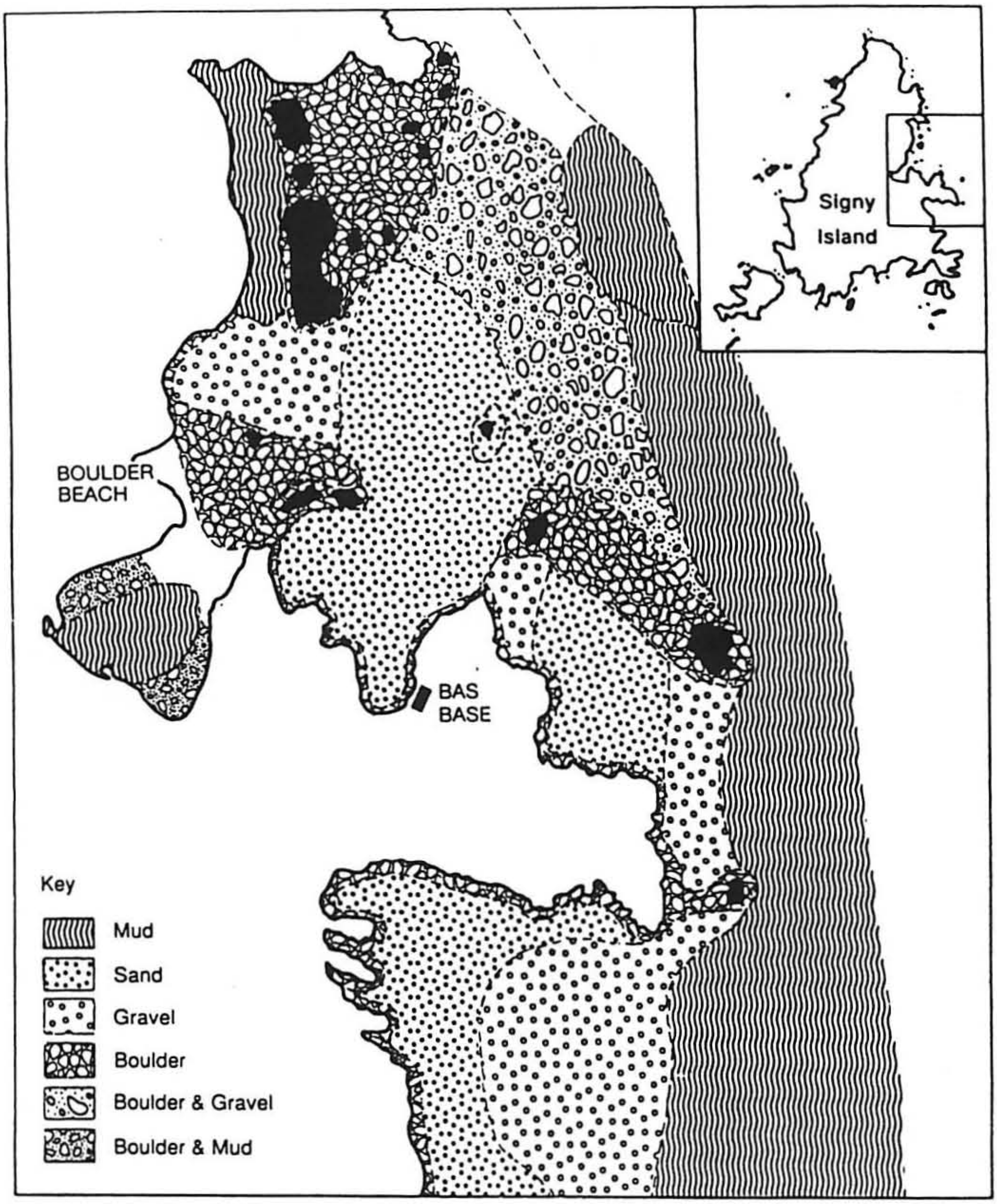

Fig. 4. A map of the main bottom sediment types in Borge Bay, Signy Island. From work by British Antarctic Survey scientists between 1970 and 1982; map compiled by N.S. Gilbert.

bring phytoplankton from the Ross Sea. In contrast, currents from beneath the Ross Ice Shelf advect very little particulate material and the associated benthic communities are sparse.

3.3. Disturbance By Ice

In shallower waters close to land, the benthic fauna can be subject to iceberg impact. The grounding of a large berg can cause extensive gouging of the seafloor, and it will eradicate all benthic life in the area of impact. Surveys of the deeper areas of the inner Weddell Sea shelf by ROV have, however, revealed extensive areas of undisturbed complex assemblages. This indicates that, in direct contrast to much of the Arctic, the benthic communities of the deeper continental shelves around Antarctica are subject to only infrequent physical disturbance by ice-rafted debris. Much of the continental shelf is too deep for direct impact by all but the largest icebergs, and the Antarctic marine ecosystem also lacks the biological agents of disturbance, such as benthic feeding whales, walruses, large crabs and flat-fish, so characteristic of the Arctic marine system [*Oliver and Slattery*, 1985; *Dayton*, 1990].

In contrast to the Arctic, there appear to have been few quantitative studies of the incidence of iceberg gouging. Several anecdotal studies by SCUBA divers of iceberg scours have, however, indicated the extensive damage to both habitat structure and benthic communities [*Shabica*, 1972; *Kauffman*, 1974]. Similar studies at Borge Bay, Signy Island have revealed extensive initial damage, but fairly rapid recolonization by meiofauna and some mobile macrofauna (L.S. Peck and S. Vanhofe, personal communication, 1995).

4. FINE SCALE DISTRIBUTION OF BENTHIC HABITATS: THE NEARSHORE ENVIRONMENT

Two important features distinguish the shallow nearshore marine system around Antarctica from those elsewhere in the world. The first is the impact of ice, and the second is the lack of typical fluvial habitats such as estuaries, deltas or mudflats.

4.1. Shallow Subtidal Nearshore Habitats

With the exception of the absence of typical riverine habitats, any SCUBA diver entering the shallow waters around Antarctica would be confronted with the range of substrata familiar from elsewhere. These include smooth hard substrata, boulder fields, cobbles, pebbles, and soft substrata ranging from coarse sands to fine silts and muds (Figure 4). Soft substrata may show similar grain-size distributions to those from lower latitudes [*Gilbert*, 1991a], but for the coarser sediments the lack of riverine transport and the input from glacial melt or ice-rafted debris means that the grains are often more angular and less polished than at lower latitudes. It is likely that this, combined with the generally low sorting, will affect their packing and pore size distribution with consequent impacts on diffusion processes, microbial pathways and the ecology of the meiofauna. Apart from anecdotal and unpublished reports, however, relatively little is known of this aspect of nearshore marine ecology in Antarctica.

Marine habitats exhibit spatial heterogenity on small scales similar to that familiar from terrestrial habitats. Unfortunately because of difficulty of access, there have been few studies of such small-scale heterogeneity, despite its undoubted importance for population dynamics and local faunal diversity. *Richardson* [1979] has documented the detailed distribution of benthic substratum and macroalgae in Borge Bay, Signy Island, South Orkneys (Figure 5). This study covers a small part of the area shown in Figure 4 and shows that heterogeneity is maintained at the smaller scale. There is also marked heterogeneity in the distribution of the two dominant species of macroalgae in the area, *Himantothallus grandifolius* and *Desmarestia anceps*. These two species have a contagious (overdispersed) distribution, which in turn carries through to the distribution of their epifauna [*Picken*, 1979]. Although these examples come from the South Orkney Islands, they illustrate general principles which will apply throughout the maritime Antarctic.

4.2. Intertidal Habitats

Perhaps the most striking feature of the Antarctic marine ecosystem for a visitor familiar with temperate or tropical regions is the almost complete absence of an intertidal flora and fauna. This is the result of the direct impact of ice: in winter the entire habitat is encased in solid ice, and in summer those areas which do melt out are subject to severe scouring by brash ice, the impact of small bergs, and intermittent freezing. Tidal pools do exist in some areas, and these can be flushed at each tidal cycle beneath an overlying cover of snow [*Hedgpeth*, 1971]. The overall impact of ice in the intertidal zone is, however, to limit the fauna to a few mobile forms which migrate from deeper water in summer (for example, gastropods such as the Antarctic limpet *Nacella concinna*, the nemertean *Tetrastemmis* sp., and many amphipods) and a small number of species which live in crevices or under boulders; these can include planarians, polychaetes, gastropods, bivalves, amphipods and hydroids. The flora of the intertidal is dominated by calcareous algae and microbial assemblages which colonize the habitat afresh each season once the ice has melted, although small thalli of red algae can be found in sheltered crevices.

Although the impact of ice is most immediately obvious in the intertidal area, this impact is felt throughout the shallow water marine ecosystem in Antarctica. It is perhaps the single most important physical variable influencing the ecology of the benthic flora and fauna in these habitats.

4.3. The Influence of Ice

The influence of ice is all-pervasive in the nearshore marine ecosystem of Antarctica, and its affects can be both direct and indirect. In shallow waters ice has a major direct impact by scouring, which results in the local eradication of the benthic fauna with a frequency that is related to depth. As a result there is a distinct zonation to the benthic assemblages found in shallow water assemblages around Antarctica. Zonation is a well-described feature of all intertidal and immediately subtidal assemblages around the world, where it is primarily a response to physical variables or processes which vary along the gradient, although the reponse of the biota may be modified by biological interactions. What makes the polar regions so distinctive is the dominant role played by ice in structuring this zonation (for further details see *Clarke*, this volume).

In the very shallowest waters the impact of ice is largely by direct scour or winter freezing. In slightly deeper wa-

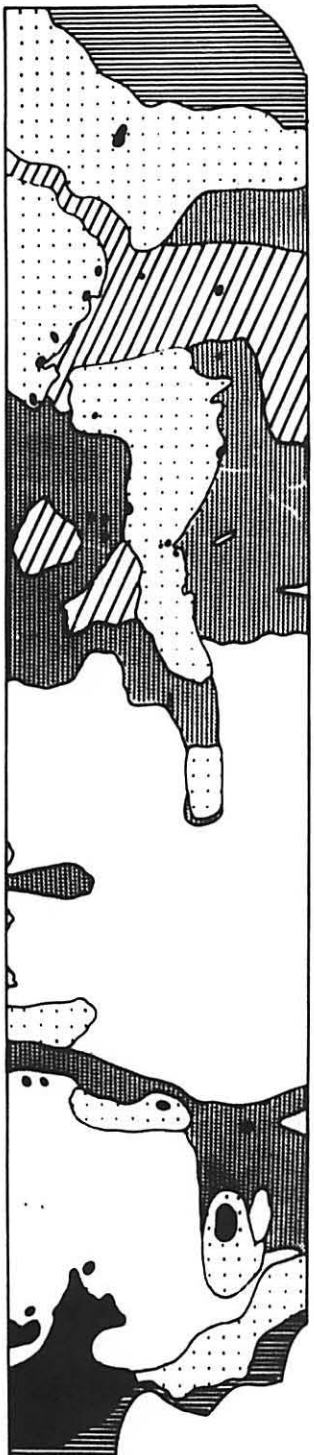

Fig. 5*a*. Distribution of bottom substrata at Borge Bay, Signy Island, Antarctica. The bottom types are rock (black), boulder (stipple), pebble (fine vertical hatching), sand (cross-hatching), and silt (blank). The horizontal hatching at the bottom and top represents shoreline. Reproduced, with permission, from *Richardson* [1979].

Fig. 5*b*. Distribution of macroalgae in the same area as shown in Fig. 5*a*. Areas of decaying macroalgal material are outlined and clear, areas of macroalgae (principally *Himantothallus grandifolius* and *Desmarestia* species) are shown in black. Reproduced, with permission, from *Richardson* [1979].

ters, however, the formation of anchor ice is an important process. Anchor ice forms on the bottom when undercooled water freezes, often around sessile benthic organisms which act as nucleating sites. As the anchor ice grows *in situ*, it encases nearby organisms, killing them. Eventually the ice lifts off the bottom, clearing the substratum of benthos as it does so. Anchor ice forms down to depths of over 30 m at very high latitudes such as McMurdo Sound, where long-term variations in the intensity of its formation, perhaps driven by wider scale oceanographic processes operating over similar time scales, may have significant impact on the population dynamics of some benthos [*Dayton et al.*, 1970]. In the maritime Antarctic, anchor ice formation is less frequent and is generally at shallower depths.

In deeper waters, the direct impact of ice is by iceberg scour. The frequency of this impact will depend on a number of factors, including depth, proximity to actively calving ice-shelves, and local oceanography. Although there are areas of the Antarctic continental shelf where iceberg impact is frequent, the great depth of much of the shelf means that the benthos is not generally subject to the intensity of scouring that characterizes much of the Arctic shelf.

The indirect effects of ice include those of glacial run-off and the impact of surface sea-ice in winter. The meltwater emanating from glaciers and grounded ice-shelves can carry substantial quantities of immature sediment of a wide range of grain sizes. Close to glaciers or ice-fronts, the rate of sedimentation can be very high, leading to the eradication of all but those species tolerant of such high inorganic loads. The impact of this sedimentation decreases with distance from the ice-front, to deeper water where the sediment becomes dominated by biological material. Where the position of a glacier front changes, this can lead to a change in the depositional regime in the nearby benthic habitats, with consequent change in the biological assemblages (see for example, *Hyland et al.*, 1994).

The formation of surface sea-ice in winter also has a number of significant impacts on the benthos beneath. In particular it stabilizes the water column by isolating this from the effects of wind-induced turnover. As a result much particulate matter, both inorganic and biological, sediments out of the water column. The consequent increase in water clarity is important in promoting the early spring benthic microalgal bloom, before the main water column bloom takes off [*Gilbert*, 1991b]. The low concentrations of particulate matter in winter mean that for some (but not all) benthic suspension feeders winter food availability may be very low [*Barnes and Clarke*, 1994, 1995].

Sea-ice is an important habitat for microbial communities, and these can reach a substantial biomass in early spring. When the ice melts, all of this material is released into the water column, and some may sediment directly to the seafloor, where it provides an important carbon source for macrobenthos, meiofauna and microfauna [*Nedwell et al.*, 1993]. Sea-ice (and especially the amount of superficial snow cover) is also important in regulating the amount of light reaching the seabed. This in turn influences primary production by macroalgae and benthic microalgae [*Gilbert*, 1991b], and hence benthic invertebrate biomass and productivity [*Dayton et al.*, 1986].

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