FOUNDATIONS FOR ECOLOGICAL RESEARCH WEST OF THE ANTARCTIC PENINSULA
ANTARCTIC RESEARCH SERIES, VOLUME 70, PAGES 219-230

THE DISTRIBUTION OF ANTARCTIC MARINE BENTHIC COMMUNITIES

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The Polar Frontal Zone, although predominantly a surface feature, forms a natural northernmost boundary for defining the Southern Ocean, and relatively few benthic organisms have distributions which cross this boundary. Many Antarctic benthic plants and animals have circumpolar distributions but some broad geographical subdivisions may be made. Detailed studies of community distribution are few in Antarctica, but heterogeneity has been demonstrated on all spatial scales. The Southern Ocean has a rich fauna compared with the much younger Arctic basin, and there is no convincing evidence either for or against a universal latitudinal cline in diversity in the southern hemisphere to match that well described from the northern hemisphere. Shallow water distributions are strongly affected by ice-related processes, and this leads to a strong vertical zonation in the biological assemblages of sublittoral habitats.

1. INTRODUCTION

Although the study of Antarctic benthos has a long and distinguished history as far back as the work of HMS *Challenger* [*Dell*, 1972; *White*, 1984; *Dayton*, 1990; *Fogg*, 1994], until relatively recently most work has been descriptive. The early expeditions were concerned mainly with documenting and describing the new species to be found in polar waters. These early collectors were conscientious and thorough, and although it is clearly rather difficult to estimate the number of species yet to be described, *Winston* [1992] has provided an assessment which suggests that the Southern Ocean benthic fauna is at least as well described as those for many other geographical regions (Table 1). For taxa such as macroalgae, bivalve and gastropod molluscs, and polychaetes the Southern Ocean fauna is now relatively well known; for other taxa there have been significant recent advances in knowledge (for example, bryozoans and nemerteans), and a few groups remain difficult and understudied. Unfortunately the meiofauna remain almost unknown in the Southern Ocean, although same recent collections have been made and at least one detailed study is underway [*Vanhofe et al.*, in press].

In the last two decades or so, Antarctic benthic ecologists have been concerned increasingly with autecological studies, although there have also been a few important studies of processes such as predation, recruitment and population dynamics (for a recent review see *Arntz et al.*, 1994). Unfortunately there have been relatively few studies of the processes regulating the distribution of Antarctic benthic organisms, and so this review will necessarily be an attempt to draw a general picture from rather fragmentary knowledge. Any such attempt inevitably draws attention to Dayton's vouchsafing of the timeless importance of good, fundamental, natural history; such studies are the foundations on which we build our generalizations [*Dayton*, 1990].

In the first part of this review I will discuss such large-scale patterns of distribution as are known from the Southern Ocean. I will then discuss what we know of the processes governing both large-scale and small-scale distribution of Antarctic benthos.

2. LARGE SCALE PATTERNS OF DISTRIBUTION

2.1. *Biogeographic Provinces*

There have been many attempts to describe broad scale patterns of distribution for the Antarctic marine biota. These have been based on oceanographic patterns [*Ekman*, 1953], macroalgae [*Neushul*, 1968; *Lawson*, 1988; *John et al.*, 1994], fish [*Regan*, 1914; *Waite*, 1919; *Norman*, 1938; *Nybelin*, 1947; *Andriashev*, 1965], isopods [*Kusakin*, 1967], ascidians [*Kott*, 1969], molluscs [*Powell*, 1951] or the fauna as a whole [*Knox*, 1960; *Hedgpeth*, 1969]. *Dell* [1972] provides a succinct and balanced discussion of this difficult topic, and proposes a general scheme, itself based essentially on that of *Hedgpeth* [1969a, 1970] and which has largely stood the test of time (Figure 1).

The basic features of the Dell/Hedgpeth scheme are three concentric zones denoting the High Antarctic Region around the Antarctic continent, the Antarctic Region extending to the Polar Front, and the Subantarctic Region north of the

Published in 1996 by the American Geophysical Union.

TABLE 1. Estimates of percentage of selected Antarctic benthic marine taxa that have been described to date, with range of values for seven other geographical areas (east and west coasts of the USA, Caribbean, Indo-Pacific, Great Barrier Reef, east Pacific and Africa). Data are for continental shelf faunas only. From *Winston* [1992].

Taxon	Estimated percentage of fauna known from Antarctica	Range of estimates of known fauna for seven other areas
Algae	80	60-90
Sponges	50	40-80
Corals	90	70-95
Octocorals	50	50-75
Hydroids	90	80-98
Actinians	95	50-90+
Nemerteans	20	20-80
Bryozoans	40-50	40-80
Ascidians	95	25-80
Opisthobranch molluscs	40-50	20-90
Ophiuroids	70	60-90
Echinoids and holothurians	80	80

Polar Frontal Zone. The Antarctic Region largely covers very deep water and is hence essentially concerned with plankton; the benthos of the Antarctic abyssal plain are almost unknown [*Clarke*, this volume]. In recent years, polar oceanographers have tended to divide the surface waters into those permanently ice-covered (roughly, but only roughly, equivalent to the High Antarctic Region proposed by Dell), the vast area of seasonal ice-coverage, and those areas which usually remain ice-free in winter. The latter two zones together overlap Dell's Antarctic region. Within the basic tripartite division, Dell also recognizes a series of smaller districts. These are based largely on islands or island groups, and thus reflect the degree of faunal differentiation between these islands (Figure 1).

The problem with drawing up such large scale patterns is that they are inevitably biassed by the patchy nature of coverage. A distribution map drawn for any species of Antarctic benthos would essentially represent a plot of where expeditions have worked (a problem which is by no means unique to Antarctica). Large sections of the Antarctic continental shelf in particular remain unsampled (or at least unrepresented in the literature), with particularly critical gaps in waters off Marie Byrd Land (between 90° and 150°W) and off much of east Antarctica (between 0° and 150°E).

Nevertheless many Antarctic benthic organisms are known from numerous widely distributed sites around the Antarctic continent (for example the scallop *Adamussium colbecki*). The best overall collation of such information is still *Bushnell and Hedgpeth* [1969] although this compilation necessarily lacks the subsequent contributions to Antarctic marine biogeography by Chilean [e.g., *Gallardo et al.*, 1977], Polish [see *Rakusa-Suszczewski*, 1993] and German [*Voβ*, 1988] biologists and by recent international collaborative studies of benthic ecology in Antarctica [*Wägele and Brito*, 1990; *Galéron et al.*, 1992; *Klöser et al.*, 1994a].

These patterns suggest that there are no major long-term barriers to dispersal for these organisms, and this in turn suggests that further sampling around the Antarctic continent is unlikely to provide evidence for undiscovered major distributional boundaries. In general faunal provinces are mostly clearly defined where large numbers of species reach the edge of their range more or less together. For benthic organisms this is usually related to a wide expanse of deep water, a major land barrier, or a marked change in water characteristics (particularly temperature) [*Angel*, 1994]. With the present state of knowledge it therefore remains a reasonable inference that many Southern Ocean benthic taxa representative of the High Antarctic Region will prove to be circum-Antarctic in distribution.

Distributional patterns are far more complex along the Antarctic Peninsula and between the various islands of the Scotia arc. This reflects, of course, the dynamic nature of dispersal and speciation in this area, and underlies Dell's plea that an understanding of detailed geographical and bathymetrical ranges *'is of far more value... ...than discussions about systems of (biogeographical) provinces'* [*Dell*, 1972]. Thus *Moe and DeLaca* [1976] have shown that there is a distinct cline in the diversity of macroalgae along the Antarctic Peninsula. Although subsequent, more detailed, sampling has added to the floral lists at several sites [*Brouwer et al.*, 1994; *Chung et al.*, 1994; *Klöser et al.*, 1994b], the overall pattern remains valid [*John et al.*, 1994]. What is not yet fully understood is the relative extent to which this pattern can be explained by historical processes (glacial advances and refugia) or the impact of physiological limitations [*Dayton*, 1990; *Clayton*, 1994].

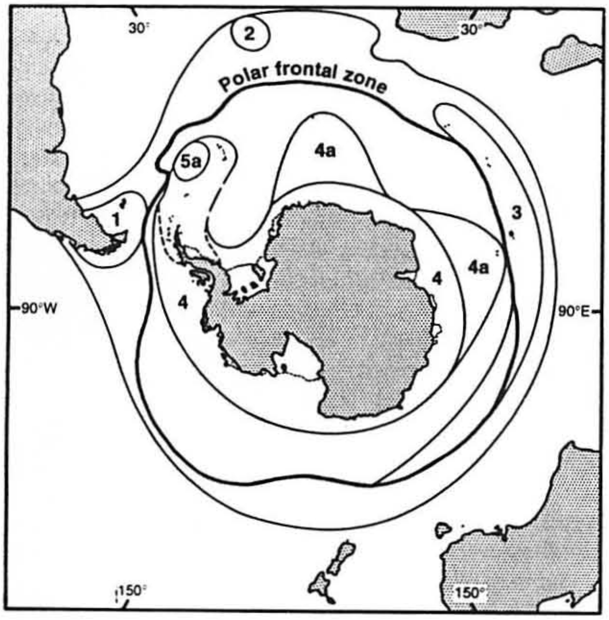

Fig. 1. Biogeographic provinces proposed for Southern Ocean benthos by *Hedgpeth* [1969] and *Dell* [1972]. Outside (north of) the Polar Frontal Zone, the subpolar region contains a number of districts, centered on islands (Falkland Islands, Tristan da Cunha, and a larger district encompassing Prince Edward Island, Îsles Kerguelen and Macquarie Island). Inside the Polar Frontal Zone, there is also a distinct district centered on South Georgia.

Unfortunately we currently lack similarly detailed information for almost all animal taxa. Further detailed distributional work along the Scotia arc will be especially important in helping to unravel the evolutionary history of the Antarctic benthic fauna.

2.2. *The Influence of the Polar Frontal Zone*

The Polar Frontal Zone (called the Antarctic Convergence in earlier literature) marks the traditional northern boundary of the Southern Ocean [*Dell*, 1972]. This is a distinct oceanographic feature which fulfills many of the criteria for the boundary of a faunal province. It is, however, predominantly a surface feature and although the distribution of few Antarctic zooplankton extends across the Polar Frontal Zone into subpolar waters [*Mackintosh*, 1960], this is not necessarily true of either mesopelagic or benthic species.

Many of the species of mesopelagic zooplankton and midwater fish known from the Southern Ocean are widely distributed in other waters [*Iwasaki and Nemoto*, 1986; *Clarke and Holmes*, 1987; *Kock*, 1992], and the Warm Deep Water of the Southern Ocean may be regarded as part of a continuous faunal zone which extends into the Antarctic beneath the Polar Frontal Zone. The Warm Deep Water cools as it approaches the Antarctic continent, and this will presumably influence the distribution of midwater animals, but little is known of the detailed distribution of the mesopelagic fauna in the Southern Ocean.

For the benthos, however, distribution is influenced a number of factors including depth, habitat, bottom topography and oceanography. While the Polar Frontal Zone may influence the dispersal of larvae or rafted adults, the distribution of shallow water benthos will also be affected by large expanses of deep water. The continental shelf around Antarctica is bounded almost completely by deep abyssal plains which isolate the fauna very effectively from the continental shelves of Africa, India or Australasia. The only significant connection is with the continental shelf fauna of South America, along the Antarctic Peninsula and through the now fragmented chain of islands forming the Scotia arc. When taken with the geological and glaciological history of Antarctica, these two factors explain the dominant broad scale features of the biogeography of Southern Ocean benthos, namely the high degree of endemism in many taxa, the distribution of many species in both Antarctica and South America, the patterns of faunal exchange along the Scotia arc, the concentration of many taxa at the edge of the continental shelf, and the role deep-sea refugia in the evolutionary history of isopods and amphipods [*Dell*, 1972; *White*, 1984; *Dayton*, 1990; *Clarke and Crame*, 1989, 1992; *Brandt*, 1992].

2.3. *Endemism*

Many authors have commented on the high degree of endemism of the Antarctic benthic fauna [summaries are given by *Dell*, 1972; *White*, 1984; *Picken*, 1985; and *Dayton*, 1990]. The extent of endemism does of course, depend critically on the definition of the area being considered but the Southern Ocean forms a naturally discrete entity and the high degree of endemism remains a genuine feature of the polar benthos. *Dayton* [1990] lists benthic taxa with the percentage of endemic species in the Southern Ocean fauna ranging from >50% (polychaetes, holothurians, bryozoans) to 90% or more (amphipods, pycnogonids). The precise figures will vary depending on recent taxonomic work but the high endemism of Southern Ocean benthos established by the early systematists remains a key biogeographic and evolutionary feature. Nevertheless, many groups do contain taxa that extend into South America, and Antarctica also contains several species which are almost universally distributed across the globe (for example the apparently ubiquitous polychaete *Capitella capitata*).

2.4. *Comparison With the Arctic*

The fauna of an area such as the Southern Ocean cannot be viewed in isolation, and it is pertinent to ask how the present Antarctic benthic fauna is related to faunas elsewhere. The strongest contrast is probably with the benthic fauna of the Arctic, which unlike the Antarctic is strikingly low in species [*Arnaud*, 1977; *Curtis*, 1975; *Clarke and Crame*, in press]. The explanation for the low species richness of the Arctic fauna is likely to be a combination of extreme disturbance from both physical (ice scour, heavy riverine input, salinity fluctuations) and biological (marine mammal activity) factors [*Oliver and Slattery*, 1985; *Dayton*, 1990], together with the relative youth of the system [*Dunton*, 1992]. This striking difference between the Arctic and Antarctic benthic faunas thus reflects at least in part the difference in their evolutionary histories, thereby emphasising the importance of historical processes in understanding the patterns we observe today.

2.5. The Latitudinal Diversity Cline

Many groups of benthic marine organisms have a peak in diversity (species richness) in the tropics, with increasingly fewer species at lower latitudes. This latitudinal diversity cline is particularly clear in molluscs but also appears to characterize foraminifera and some other groups [*Stehli et al.*, 1967; *Clarke*, 1992; *Clarke and Crame*, in press]. The cline is particularly marked in the northern hemisphere, in part as a result of the depauperate Arctic fauna and the intense species-richness of the Indo-West Pacific.

It is not currently clear the extent to which a similar cline is to be found in the less well sampled southern hemisphere, or whether it is a general feature of all marine taxa [*Clarke*, 1992; *Clarke and Crame*, in press]. What is clear, however, is that the fauna of the Southern Ocean is far more diverse than that of the Arctic, primarily as a result of a long evolutionary history *in situ* [*Lipps and Hickman*, 1982; *Clarke and Crame*, 1989, 1992]. The diversity of the Antarctic marine benthos has recently been summarized by *Arntz et al.* [in press] and is discussed elsewhere [*Clarke*, this volume]; the diversity and distribution of Antarctic macroalgae has recently been summarized by *John et al.* [1994] (see section 2.1 above).

3. SMALL SCALE PATTERNS OF DISTRIBUTION

There have been relatively few studies of the smaller scale distribution of Antarctic benthos. Studies published to date have been concerned primarily with either the geographical distribution of selected assemblages, or vertical zonation in relation to physical disturbance.

3.1. Distribution of Benthic Assemblages

Detailed studies of the distribution of benthic assemblages require repeated sampling, and so such studies have generally been undertaken from shore stations. This sort of work has rather gone out of fashion in Antarctic biology of late, but important early studies were those of *Gallardo et al.* [1977] in Chile Bay, Greenwich Island, and the studies of Arthur Harbour, Anvers Island by *Lowry* [1969], *Richardson* [1972; 1976] and *Richardson and Hedgpeth* [1977].

Chile Bay is approximately 3.5 km wide and 5.5 km long, with an irregular bottom topography. Much of the bottom is greater than 50 m deep, and the depth increases to over 200 m at the mouth of the bay. The sediments are mostly very fine sands, with variable amounts of silt and macroalgal fragments on the surface. Analysis of the bottom faunal assemblages from grab samples indicated that, as is typical of Antarctic soft bottoms, the fauna was dominated, both numerically and in biomass terms, by polychaetes (61% and 47% respectively). The other important contributors to biomass were molluscs (16%), echinoderms (15%) and ascidians (10%); crustaceans were important numerically (15% of all individuals) but contributed only 2% of the total biomass. The benthic assemblage in Chile Bay was species-rich, with 149 species identified. Although data for many taxa were incomplete (a situation typical for benthic work in Antarctica) it was clear that amphipods, polychaetes and bryozoans were particularly diverse [*Gallardo et al.*, 1977].

The most distinctive feature of the benthic assemblage of Chile Bay was the difference in faunal assemblages in shallower and deeper water, with the boundary at about 100 m. The deeper regions were characterized by very high densities of the polychaete *Maldane sarsi*, with densities up to 6000 m^{-2} (Figure 2); amphipods, cumaceans and bivalve molluscs were also important in the deeper water samples. At depths shallower than 100 m *Maldane sarsi* was still present, but at much lower densities, and the benthic assemblage was characterized by ascidians, gastropod molluscs, the typical shallow water Antarctic bivalve *Yoldia eightsi* and the cumacean *Eudorella gracilor*. Superimposed on these broad trends were smaller scale differences between samples, reflecting fine scale heterogeneity in the habitat and associated fauna.

The soft-bottomed benthic fauna of Arthur Harbour, Anvers Island has been studied in detail by American biologists working from Palmer Station [*Lowry*, 1975; *Richardson*, 1976; *Richardson and Hedgpeth*, 1977; *Hyland et al.*, 1994]. During January and February 1971 five replicate grab samples were taken from 12 stations in Arthur Harbour, with eight grabs taken from deeper water nearby. These samples yielded 167,853 individuals, of which just under half (77,332) were retained by a 1 mm mesh screen. These were separated into 282 taxa, of which polychaetes were the dominant group (108 species, 54% of all individuals). Also important were arthropods (117 species, 30%) and molluscs (35 species, 11%), although again not all taxa could be resolved to the species level. Of the polychaetes, for example, only just over half (58 species) could be satisfactorily identified and in some particularly difficult groups (for example, capitellids) it was not even clear how many species were involved.

The 12 stations within Arthur Harbour could be classified into five assemblages, with a sixth assemblage in deeper water (and a seventh pseudo-assemblage linking two replicate samples dominated by decaying macroalgae). Four of the

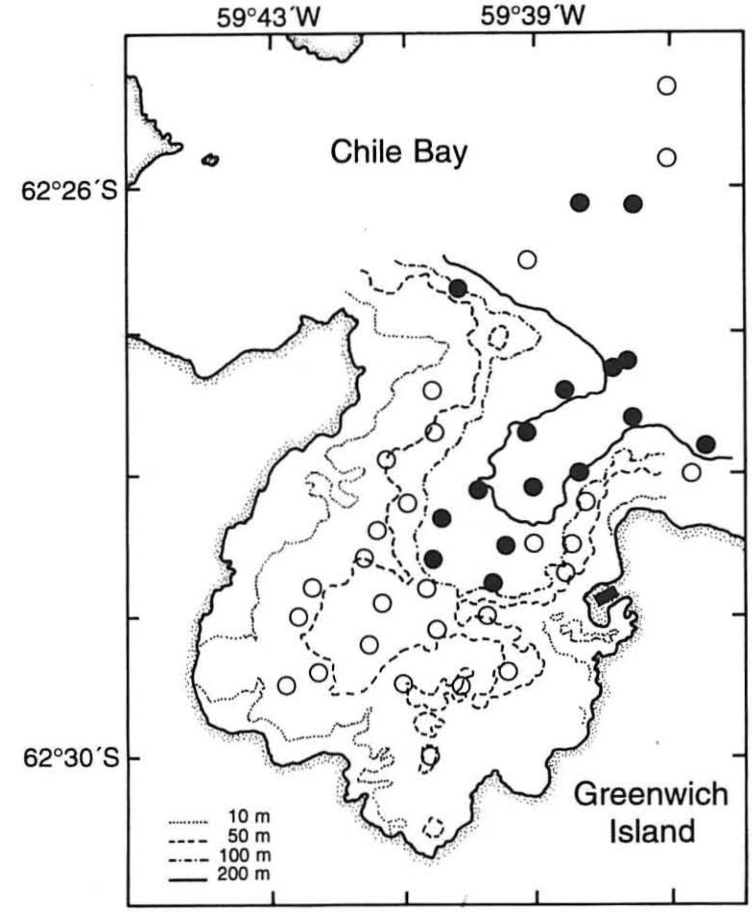

Fig. 2. Distribution of the polychaete *Maldane sarsi* in Chile Bay. Open circles show samples with low densities, filled circles show samples dominated by *Maldane*. Redrawn from *Gallardo et al.* [1977].

five assemblages from within Arthur Harbour appeared to represent a depth continuum, and it is likely that the turnover of species with depth is influenced by a complex suite of environmental factors including temperature and salinity fluctuations, macroalgal debris, ice scour and glacial input.

Two of these stations were re-examined in March and April 1989 by *Hyland et al.* [1994]. At the shallower of these two sites, the biological assemblage was found to have changed considerably in the intervening 18 years. There had been a shift to a more species-rich and abundant macrofauna, similar to that characteristic of the deeper and more physically stable parts of Arthur Harbour. The most likely explanation for this change is that the nearby glacier front has retreated by about 250 m, thereby reducing the level of inorganic sediment input to this part of the bay.

The only recent detailed study of benthic assemblages in Antarctica has been that of the eastern Weddell Sea shelf undertaken in the last decade by German scientists working from R/V *Polarstern*. *Voβ* [1988] has shown that the benthic fauna of the eastern Weddell Sea Shelf may be grouped into three main assemblages (Figure 3). This classification is based primarily on material collected by Agassiz trawl, and hence any one sample may have mixed organisms from a variety of different communities or habitats. *Galéron et al.* [1992] showed that within these main assemblages there were spatial differences associated with, for example, distance from the ice shelf. More recent work using underwater photography of organisms *in situ* has demonstrated a high degree of spatial heterogeneity in the distribution of both individual species and assemblages [*Barthel et al.*, 1991; *Gutt et al.*, 1991]. This indicates that the classification of broad communities by *Voβ* [1988] necessarily obscures much finer detail.

The cost of mounting large scale oceanographic work in the Southern Ocean means that this remains the only recent detailed large-scale study of the distribution of benthic communities in Antarctica. Most recent work, particularly that from shore stations, has concentrated instead on faunal and floral inventory, autecology or the finer scale distribution of particular species or higher level taxa.

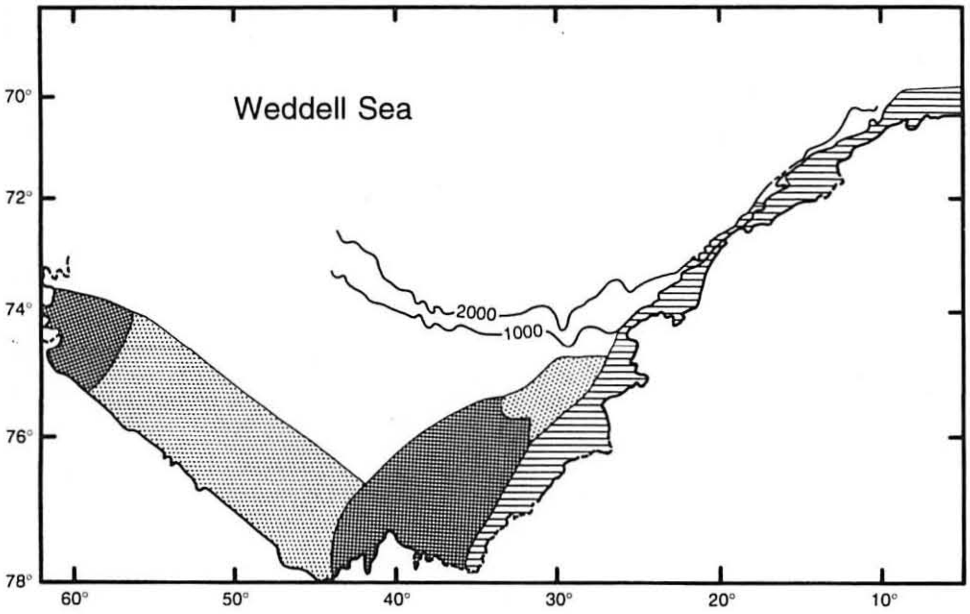

Fig. 3. Benthic assemblages on the continental shelf of the eastern Weddell Sea. Horizontal hatching: Eastern Shelf Community, Pale stippling: Southern Shelf Community, Dark stippling: Southern Trench Community. Redrawn from *Voβ* [1988].

4. FINE SCALE DISTRIBUTION PATTERNS IN ANTARCTIC BENTHIC COMMUNITIES

The benthic organism whose distribution has been studied more thoroughly in the Southern Ocean than perhaps any other is the Antarctic limpet, *Nacella concinna*. This is a very common species in sublittoral habitats of the maritime Antarctic, with maximum densities being attained at 4-5 m below mean low water (MLW) on the study site at Signy Island [*Picken*, 1980] and at similar depths near Palmer Station [*Hedgpeth*, 1969; *Shabica*, 1971, 1972, 1976]. Over the depth range of the study at Signy Island (2-12 m below MLW) the mean density was 124 individuals m^{-2}, and the limpets ranged freely over all types of hard substratum, though they largely avoided extensive areas of soft bottom. In all of the 21 monthly collections the variance in density exceeded the mean, indicating a highly contagious distribution. *Nacella concinna* is not a homing species and this distribution is likely to be the result of a number of interacting factors, including seasonal aggregation for spawning [*Picken and Allan*, 1983], and predation by starfish [*Shabica*, 1971] and the large common nemertean *Parborlasia corrugatus*.

In the littoral zone, *Nacella concinna* is restricted to sheltered crevices and vertical rock surfaces [*Walker*, 1972; *Shabica*, 1976]. This is partly because of predation by birds [*Hedgpeth*, 1969; *Shabica*, 1976; *Castilla and Rozbaczylo*, 1985; *Nolan*, 1991] but also to aid resistance to heat stress and desiccation [*Davenport*, 1988]. The presence of limpets in the intertidal zone is highly seasonal, for this habitat is encased in solid ice during the winter, forcing the limpets migrate into deeper water [*Walker*, 1972]. The seasonal migration into the intertidal, although exposing the limpets to enhanced predation by birds allows them to take advantage of the rich seasonal microbial film.

Picken [1979] undertook a detailed study of the prosoranch gastropod fauna of a shallow water area at Signy Isand. The bottom was of mixed gravel and sand and suported a dense growth of macroalgae dominated by *Himanothallus grandifolius, Desmarestia anceps* and *Ascoseira mirabilis* [*Richardson*, 1979]. A total of 31 species of gastropod were collected, only eleven of which were previously known from the South Orkney Islands. For all of these species, the variance of the ten monthly samples always exceeded the mean, indicating a contagious (overdispersed) distribution. In most cases the species were closely associated with macroalgae, which explained their distribution, for the macroalgae were themselves so distributed [*Picken*, 1979].

Such detailed studies of distribution emphasize the fine scale heterogeneity in the distribution of marine organisms. This heterogeneity is the result of underlying habitat hetergeneity, as well as biological processes such as ice abrasion, spatial variations in recruitment, and predation. The impact of such heterogeneity on ecosystem function is unclear, but of particular interest in a polar context is how spatial heterogeneity influences the population dynamics and gene flow of rare species without a dispersing larval stage. Unfortunately, almost nothing is known of this at present.

5. VERTICAL ZONATION

Perhaps the most striking distributional feature of marine organisms, and one which has been studied in all areas of the globe, is that of vertical zonation. The obvious and striking influence of ice on the vertical distribution of polar marine benthos has meant that studies of vertical zonation also had a long history in Antarctica.

5.1. Intertidal Zone

The lack of a significant littoral or intertidal flora and fauna in much of Antarctica has been remarked upon since the earliest expeditions, but the first attempt to put the results of these earlier workers into a wider ecological context was that of *Knox* [1960]. Knox remarked that in Antarctica a littoral flora and fauna is '*generally absent*'; where algae are found they exist in sheltered nooks and do not form the bands so characteristic of cold-temperate and Subantarctic areas. The sessile marine invertebrates found widely in the intertidal zone elsewhere, such as mussels and balanoid barnacles, are completely absent, although some molluscs can be found in summer (for example the limpet *Nacella concinna,* and a variety of small gastropods and bivalves). Since Knox's review there has been considerable work on the shallow water fauna of Antarctica, particularly at various sites on the Antarctic Peninsula and in the maritime Antarctic. This has extended significantly our understanding of the patterns of vertical zonation in the upper reaches of the shore, but has left the basic picture discussed by *Knox* [1960] essentially untouched.

The intertidal zone near Palmer Station was examined by a number of biologists in the late 1960s and early 1970s [*Hedgpeth,* 1969b; *McCain and Stout,* 1969; *Stout and Shabica,* 1970; *Shabica,* 1971, 1972; *Stockton,* 1973; *Moe and DeLaca,* 1976]. During the summer months there develops a well-defined band of filamentous green algae, including species of *Entromorpha, Ulothrix, Urospora* and *Cladophora*; *Stockton* [1973, 1990] recorded *Urospora* sp. as the principal intertidal species. In more sheltered cracks and crevices there are small thalli of red algae including *Leptosomia simplex, Curdiea racowitzae* and *Iridaea obovata.* During the winter, all of these disappear [*Shabica,* 1972] and the flora must recruit afresh to the intertidal next season.

The fauna in the intertidal is sparse, but by no means nonexistent. The most conspicuous animal is the Antarctic limpet *Nacella concinna* (formerly *Patinigera polaris*) but there are also bivalves (*Lasaea rubra, Kidderia bicolor*), as well as several gastropods, polychaetes, hydroids, nemerteans and amphipods. In some areas there are conspicuous patches of the crustose red alga *Hildenbrandia,* the upper limit of which can form a straight line, probably marking the lowest extent of the tide [*Hedgpeth,* 1969b; *Stockton,* 1990]. *Hedgpeth* [1969b] reported that intertidal life at Palmer Station was limited essentially to the lowest 0.3 meters. The mean annual tidal range between a high tide and the subsequent low tide is 0.65 meters, with a maximum value of 1.65 meters, and a maximum range between extreme highs and extreme lows of 2.19 meters [*Amos,* 1993].

Rocky shores are highly variable habitats, with the degree of exposure to wave action as a principle environmental variable. The description above, largely based on the work of *Hedgpeth* [1969] and subsequent workers at Palmer Station, is probably typical of the maritime Antarctic in sloping areas relatively protected from wave action but exposed to brash ice [*Stockton,* 1990].

Most of the work on the intertidal zone of the maritime Antarctic has been carried out during the austral summer once the winter ice has melted, and algal growth is conspicuous. A recent study of vertical rock faces at Signy Island involved year-round observation, and has demonstrated the importance of the winter ice-foot to the dynamics of the intertidal community [*Barnes,* 1995]. In many polar areas the formation of winter sea-ice, together with the subsequent tidal movement of this ice, leads to the build up of a massive encasement of ice in the intertidal zone; this is often referred to as the ice-foot (Figure 4; *Kotlyakov and Smolyarova,* 1990). At Signy Island the tidal range is approximately 2.5 meters during spring tides and about 1.5 meters during neap tides; the ice-foot usually extends over a depth range slightly greater than the maximum tidal range and may thicken extensively during the winter.

For obvious reasons it is very difficult to sample beneath the ice-foot in winter, but it is likely that no intertidal life survives its formation, and the habitat is colonized *de novo* each season once the ice melts. In these areas there is virtually no intertidal life apart from the sparse summer colonizing flora and fauna, down to about 2 meters; abundant life does not start until about 4 meters [*Barnes,* 1995]. A similar pattern has been described at King George Island [*Rauschert,* 1991].

Where the intertidal has a shallower slope the ice-foot may develop less extensively. Here some longer-lived sessile organisms (for example, small bivalves) may survive in sheltered crevices. How these organisms overcome the effects of freezing when exposed to low winter air temperatures is not at all clear, although there is some evidence that some species may be able to survive freezing of extracellular water [*Kanwisher,* 1955]. Despite its obvious importance to understanding the distribution and ecology of polar and cold-temperate intertidal organisms, very little work has been undertaken on how these organisms withstand the low air temperatures to which they may be regularly exposed.

Where appropriate topography occurs, tide pools can be found. At Palmer Station these pools become blanketed by

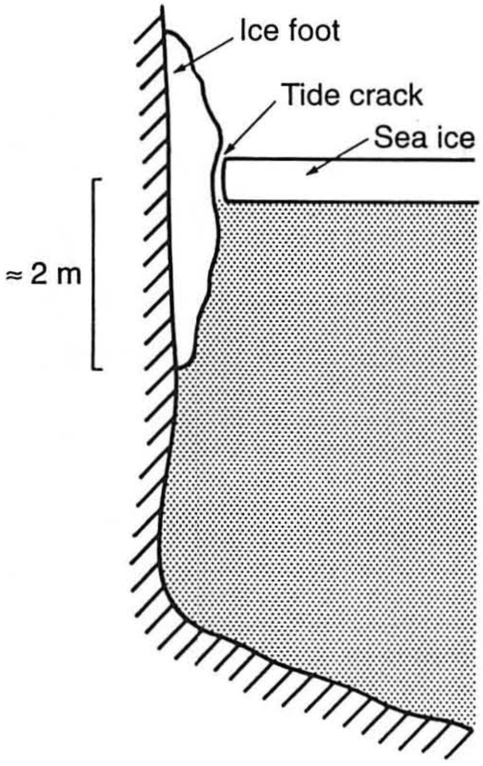

Fig. 4. A diagrammatic representation of the winter ice-foot in the maritime Antarctic. Also shown is the tide-crack which separates the surface fast-ice from the ice-foot. Reproduced, with permission, from *Barnes* [1995a].

almost 2 meters of snow and shore ice in winter, but they can remain open to the subtidal water through tunnels originating at their seaward edge [*Shabica*, 1972]. These tunnels allow seawater to circulate at high tide, and their temperature thus never fall below -1.97°C despite ambient air temperatures below -20°C. During winter there was a marked reduction in the size and number of algae, although fructification of *Iridaea* sp. was noted throughout the winter [*Shabica*, 1972]. Where they are found, tide pools may therefore be an important factor in allowing some species to overwinter within the intertidal habitat. Tide pools have also been described from Robert Island, also in the South Shetland Islands [*Castilla and Rozbaczylo*, 1985]. Here the surrounding flora included *Porphyra endirifolium, Urospora penicilliformis, Enteromorpha bulbosa, Iridaea obvata* and *Adenocystis utrincularis*. The bottom of the tide pools was encrusted with lithothamnioid algae and *Hildenbrandria*, and the fauna included the abundant small gastropod *Laevilittorina antarctica*.

5.2. Intertidal Soft Sediments

There are very few areas of tidal mud in the Antarctic, and where these do occur (for example, at several sites in the South Orkney Islands and the northern Antarctic Peninsula) they have been little studied, and much of what work has been done unfortunately languishes unpublished. Although these areas are covered by snow and ice in winter, the shallow slope predicates against the formation of a damaging ice-foot. The flora and fauna is more extensive than in the rocky intertidal, and where glacial debris provides scattered rocks as substrata, a relatively rich biota can develop.

Typically in areas of sheltered water (for example, where moraine debris affords protection from swell and brash ice) there can be a rich development of diatoms, microbial films, filamentous green algae and red macroalgae. The dominant grazers appear to be the ubiquitous *Nacella concinna*, but also characteristic are the smaller *Laevilittorina* species, which are very common on the underside of rocks. In these areas suspension feeders can exist in the intertidal, and typical representatives include serpulid polychaetes, hydroids and bryozoans [*Barnes*, 1995; *Barnes et al.*, in press], and the bivalves, *Lasaea rubra, Lissarca miliaris* and *Kidderia bicolor*. Predators include the nemertean *Tetrastemmis*, nepthtyid polychaetes, amphipods and at least one very common planarian. The sediments themselves, at least when sufficiently removed from the immediate impact of glacial input, support a varied infauna which includes capitellid and maldanid polychaetes, amphipods, bivalves, sipunculids and the infaunal anemone *Edwardsia*. *Rauschert* [1991] has reported a large priapulid from the intertidal of the Fildes Peninsula. Although intertidal mud and mixed substrata are a rare habitat in Antarctica, they deserve attention for the insights they may provide for the impact of physical factors on the development of infaunal communities.

5.3. Subtidal Zonation

A strong vertical zonation in subtidal benthic communities has been described for many areas of the Southern Ocean and is probably a universal feature of Antarctica. Vertical zonation has been reported for high Antarctic sites around the continent, including McMurdo Sound [*Dayton et al.*, 1970], Haswell Islands [*Gruzov et al.*, 1977], Terra Nova Bay [*Gambi et al.*, 1994], Terre Adelie [*Arnaud*, 1974] and Ellis Fjord [*Kirkwood and Burton*, 1988].

At McMurdo the primary agent causing the strong vertical zonation is the formation of anchor ice. Anchor ice forms when undercooled water produced during the formation of surface ice sinks and encounters suitable nucleating sites, which are often sessile marine organisms. The ice then grows, encasing and killing the benthos, until its buoyancy is sufficient for it to tear free of the seabed, lifting the entrapped organisms to the surface. In high latitudes such as McMurdo anchor ice may form as deep as 30 meters [*Day-*

ton et al., 1969; *Zamorano*, 1983] and can result in a severe depletion of benthic flora and fauna to that depth. Generally the shallower depths are populated by mobile grazing or scavenging fauna such as limpets, echinoids and starfish; sessile invertebrates are usually few.

In the maritime Antarctic and the northern Antarctic Peninsula the incidence of anchor ice is less frequent, and its impact generally only reaches depths of a few meters [*Shabica*, 1972; *Rauschert*, 1991; *Barnes*, 1995]. Furthermore, anchor ice at these more northerly locations is often less consolidated and consequently less damaging to the fauna [*Shabica*, 1972]. Other forms of ice, notably brash ice and small bergs, do however exert an impact on benthic communities in the shallower waters.

Most studies of zonation have been qualitative, but a recent detailed photographic study of vertical zonation at Signy Island has provided valuable quantitative data on the vertical zonation of the benthos [*Barnes*, 1995a, 1995b]. On exposed vertical faces, the effect of the winter ice-foot renders the rock essentially bare down to 1.5 meters below mean tide level. From 2 to about 3.5 meters the biota is dominated by various forms of coralline algae (*Hildenbrandia, Lithothaminion*) and macroalgae; animal taxa include serpulid polychaetes, cnidarians, ascidians and the characteristic early colonizing bryozoans *Celleporella bougainvillei, Inversiula nutrix* and *Escharoides tridens*. The deeper zone from 4 to about 5.5 meters is characterized by bryozoans (especially *Baenia erecta* and *Arachnopusia inchoata*) and sponges. A representative profile for a vertical face at Signy Island is shown in Figure 5.

The interesting feature of these profiles on steep rock faces is the predominance of bryozoans. On stable substrata bryozoans are almost always competitively inferior to other encrusting fauna, particularly sponges and ascidians. The predominance of bryozoans at shallow depths at Signy Island, and the importance of characteristic early successional species such as *Baenia erecta*, suggests a biota subject to frequent and massive disturbance by ice-scour. Once an area has been cleared of fauna, then early colonizing species such as bryozoans and serpulid polychaetes are able to dominate until they are either outcompeted by other taxa, or the community is again eradicated. That sponges and ascidians are rarely dominant at shallow depths at Signy Island indicates a high frequency of ice-scour and recolonization relative to the rate of establishment of a competitively dominant sponge/ascidian assemblage [*Barnes*, 1995a].

Zonation was also examined on transects comprising vertical profiles extending to 40 m at two sites at Signy Island [*Barnes*, 1995b]. Hard substratum extended to either 25 m (Powell Rock) or 35 m depth (Outer Island), before merging into soft bottom (Figure 6). At shallow depths, where ice scour may be severe, large areas where dominated by encrusting calcareous algae, and to a lesser extent macroalgae. Only where an increase in slope afforded some measure of protection from ice impact (for example, at 8 m at Powell Rock or at 12 m at Outer Island) were encrusting bryozoans to be found. Indeed it is a common observation in the maritime Antarctic that the densest and most diverse assemblages of sessile benthos are to be found wherever local topography offers a modicum of protection from abrasion by ice. Where the substratum switched to soft-bottom then the proportion of area utilized by encrusting flora or fauna decreased markedly (Figure 6).

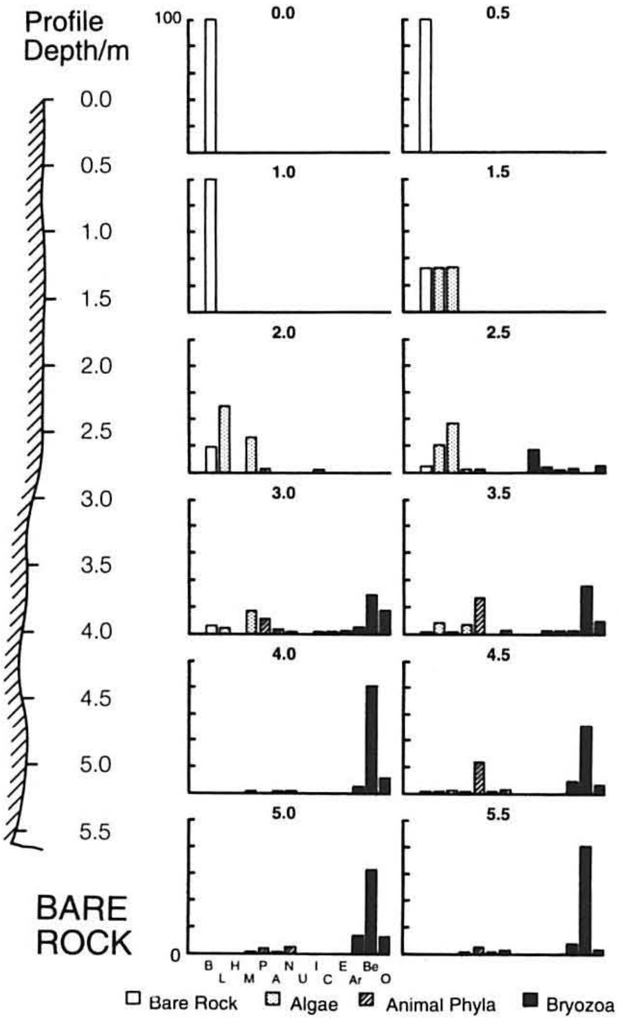

Fig. 5. Vertical zonation of subtidal shallow water (0-5.5 m) encrusting fauna at Bare Rock, Signy Island, South Orkney Islands. Reproduced, with permission, from *Barnes* [1995a].

These studies of benthic zonation at Signy Island [*Barnes*, 1995a, 1995b] are the most detailed and comprehensive yet undertaken in Antarctica. They do, however, agree broadly with the earlier studies undertaken both at sites in the maritime Antarctic [*Shabica*, 1972; *Zomorano*, 1983; *Rauschert*, 1991] and in the high Antarctic [*Dayton et al.* 1970; *Arnaud*, 1974; *Gruzov*, 1977; *Kirkwood and Burton*, 1988; *Gambi et al.*, 1994]. At shallower depths the primary controls on as-

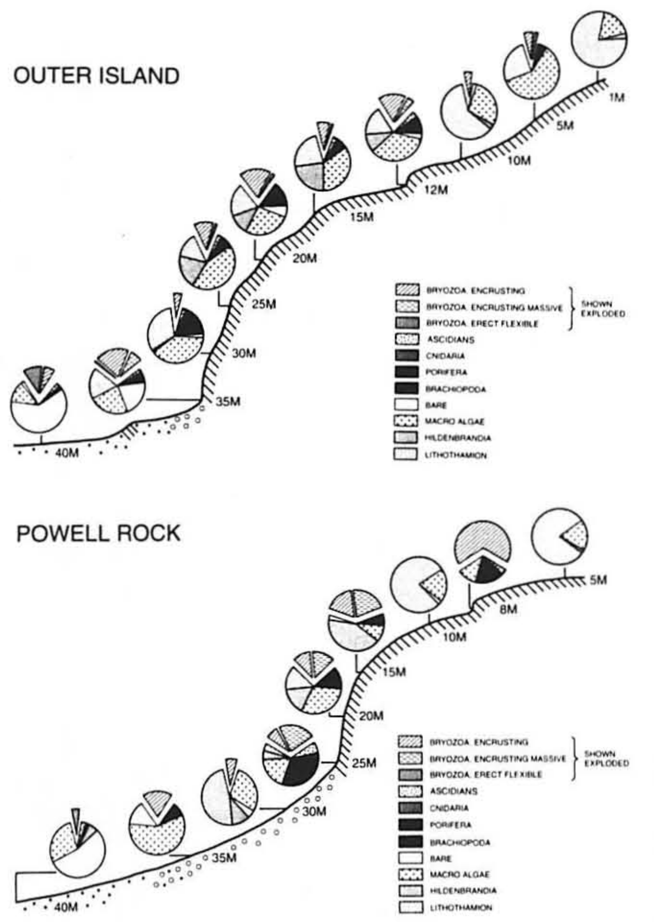

Fig. 6. Vertical zonation of encrusting fauna down to 40 m at two sites (Outer Island, Powell Rock) at Signy Island, South Orkney Islands. Reproduced, with permission, from *Barnes* [1995b].

semblage composition are those of aspect, substratum and ice impact; it is only in deeper waters that ecological interactions come to be the dominant factor [*Dayton et al.*, 1974]. The interaction between pattern and process is discussed elsewhere [*Clarke*, this volume].

Acknowledgements. Work on the ecology of benthic marine invertebrates at Signy Island forms part of the Nearshore Marine Biology program of the British Antarctic Survey. Thanks are due to the many biologists, assistants and diving officers who have sustained this program from 1962 until its closure in 1995. From 1996 the program will be based at Rothera Station and will form a contribution to the SCAR EASIZ (Ecology of the Antarctic Sea-Ice Zone) program. I thank Martin White and two referees for helpful comments on the manuscript.

REFERENCES

Amos, A.F., RACER: the tides at Palmer Station, *Antarct. J. U.S., 28(5)*, 162-164, 1993.

Andriashev, A.P., A general review of the Antarctic fish fauna, in *Biogeography and Ecology of Antarctica*, edited by J. van Mieghem and P. van Oye, pp. 491-550, The Hague, Junk, 1965.

Angel, M.V., Spatial distribution of marine organisms: patterns and processes, in *Large-Scale Ecology and Conservation Biology*, edited by P.J. Edwards, R.M. May, and N.R. Webb, pp. 59-109, Blackwell, Oxford, 1994.

Arnaud, P.M., Contribution à la bionomie marine benthique des régions antarctiques et subantarctiques, *Téthys, 6*, 465-656, 1974.

Arnaud, P.M., Adaptations within the Antarctic marine benthic ecosystem, in *Adaptations within Antarctic Ecosystems*, edited by G.A. Llano, pp. 135-157, The Smithsonian Institution, Washington, D.C., 1977.

Arnaud, P.M., The state of the art in Antarctic benthic research, in *Actas del Seminario Internacional 'Oceanografia in Antartide'*, edited by O. Ferretti, V.A. Gallardo, and H.I. Moyano, pp. 341-436, Centro EULA, Universidad de Concepçion, Chile, 1992.

Arntz, W.E., T. Brey, and V.A. Gallardo, Antarctic zoobenthos, *Oceanogr. Mar. Biol. Ann Rev., 32*, 241-304, 1994.

Arntz, W.E., J. Gutt, and M. Klages, Antarctic marine biodiversity, in *Antarctic Communities: Species, Structure and Survival*, edited by B. Battaglia, J. Valencia, and D.W.H. Walton, Cambridge University Press, in press.

Barnes, D.K.A., Sublittoral epifaunal communities at Signy Island, Antarctica: I. The ice foot zone, *Mar. Biol, 121*, 555-563, 1995a.

Barnes, D.K.A., Sublittoral epifaunal communities at Signy Island, Antarctica: II. Below the ice foot zone, *Mar. Biol, 121*, 565-572, 1995b.

Barnes, D.K.A., P. Rothery, and A. Clarke, Colonisation and development in encrusting communities from the Antarctic intertidal and sublittoral, *J. Exp. Mar. Biol. Ecol.*, in press.

Barthel, D., J. Gutt, and O.S. Tendal, New information on the biology of Antarctic deep-water sponges derived from underwater photography, *Mar. Ecol. Progr. Ser., 69*, 303-307, 1991.

Brandt, A., Origin of Antarctic Isopoda (Crustacea, Malacostraca), *Mar. Biol., 113*, 415-423, 1992.

Brouwer, P.E.M., E.F.M. Geilen, N.J.M. Gremmen, and F. van Lent, Biomass, cover and zonation patterns of sublittoral macroalgae at Signy Island, South Orkney Islands, Antarctica, *Bot. Mar., 38*, 259-270, 1995.

Bullivant, J.S., and J.H. Dearborn (Eds.), The fauna of the Ross Sea, *New Zealand Dept. Sci. Industr. Res. Bull., 176*, 1-76, 1967.

Bushnell, V.C., and J.W. Hedgpeth (Eds.), *Antarctic Map Folio Series*, New York, American Geographical Society, 1969.

Castilla, J.C., and N. Rozbaczylo, Rocky intertidal assemblages and predation on the gastropod *Nacella (Patinigera) Concinna* at Robert Island, South Shetlands, Antarctica, *Inst. Antarct. Chileno Ser. Cient., 32*, 65-74, 1985.

Chung, H., Y.S. Oh, I.K. Lee, and D.-Y. Kim, Macroalgal vegetation of Maxwell Bay in King George Island, Antarctica, *Korean J. Phycol., 9*, 47-58, 1994.

Clarke, A., Is there a latitudinal diversity cline in the sea?, *Trends Ecol. Evol., 7*, 286-287, 1992.

Clarke, A., Marine Benthic Populations in Antarctica: Patterns and Processes, this volume.

Clarke, A., and J.A. Crame, The origin of the Southern Ocean marine fauna, in *Origins and Evolution of the Antarctic Biota*, edited by J.A. Crame, pp. 253-268, Geological Society Special Publication No. 47, The Geological Society, London, 1989.

Clarke, A., and J.A. Crame, The Southern Ocean benthic fauna and climate change: an historical perspective, *Phil. Trans. Roy. Soc. Lond. B, 338*, 299-309, 1992.

Clarke, A., and J.A. Crame, Diversity, latitude and time: patterns in the shallow sea, in *Marine Biodiversity: Causes and Consequences*, edited by R.F.G. Ormond and J. Gage, Cambridge University Press, in press.

Clarke, A., and L.J. Holmes, Notes on the biology and distribution of *Pasiphaea* species from the Southern Ocean, *Bull. Br. Antarct. Surv., 74*, 17-30, 1987.

Clayton, M.N., Evolution of the Antarctic marine benthic algal flora, *J. Phycol., 30*, 897-904, 1994.

Curtis, M.A., The marine benthos of Arctic and subarctic continental shelves, *Polar Rec., 17*, 595-626, 1975.

Davenport, J., The tenacity of the Antarctic limpet *Nacella concinna*, *J. Mollusc. Stud., 54*, 355-356, 1988.

Dayton, P.K., Polar benthos, in *Polar Oceanography, Part B: Chemistry, Biology and Geology*, edited by W.O. Smith, pp. 631-685, Academic Press, London, 1990.

Dayton, P.K., G.A. Robilliard, and A.L. DeVries, Anchor ice formation in McMurdo Sound, Antarctica, and its biological significance, *Science, 163*, 273-275, 1969.

Dayton, P.K., G.A. Robilliard, and R.T. Paine, Benthic faunal zonation as a result of anchor ice formation at McMurdo Sound, Antarctica, in *Antarctic Ecology, Volume 1*, edited by M.W. Holdgate, pp. 244-258, London, Academic Press, 1970.

Dayton, P.K., G.A. Robilliard, R.T. Paine, and L.B. Dayton, Biological accommodation in the benthic community at McMurdo Sound, Antarctica, *Ecol. Monogr., 44*, 105-128, 1974.

Dell, R.K., Antarctic benthos, *Adv. Mar. Biol., 10*, 1-216, 1972.

Dunton, K., Arctic biogeography: the paradox of the marine benthic fauna and flora, *Trends Ecol. Evol., 7*, 183-189, 1992.

Ekman,V.K., *Zoogeography of the Sea*, London, Sidgwick and Jackson, 1953.

Fogg, G.E., *A History of Antarctic Science*, 483 pp., Cambridge University Press, 1994.

Galéron, J., R.L. Herman, P.M. Arnaud, W.E. Arntz, S. Hain, and M. Klages, Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica, *Polar Biol., 12*, 283-290, 1992.

Gallardo, V.A., J.G. Castillo, M.A. Retamal, Y. Yáñez, H.I. Moyano, and J.G. Hermosilla, Quantitative studies on the soft-bottom macrobenthic animal communities of shallow Antarctic bays, in *Adaptations Within Antarctic Ecosystems*, edited by G.A. Llano, pp. 361-387, The Smithsonian Institution, Washington D.C., 1977.

Gambi, M.C., M. Lorenti, G.F. Russo, and M.B. Scipione, Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: zonation, biomass and population structure, *Ant. Sci., 6*, 449-462, 1994.

Gruzov, E.N., Seasonal alterations in coastal communities in the Davis Sea, in *Adaptations Within Antarctic Ecosystems*, edited by G.A. Llano, pp. 263-278, The Smithsonian Institution, Washington, D.C., 1977.

Gutt, J., M. Gorny, and W.E Arntz, Spatial distribution of Antarctic shrimps (Crustacea: Decapoda) by underwater photography, *Ant. Sci., 3*, 363-369, 1991.

Hedgpeth, J.W., Introduction to Antarctic zoogeography, *Antarctic Map Folio Series*, pp. 1-9. New York, American Geographical Society, 1969a.

Hedgpeth, J.W., Preliminary observations of life between tidemarks at Palmer Station, 64°45'S, 64°05'W, *Antarct. J. U.S., 4*, 106-107, 1969b.

Hedgpeth, J.W., Marine biogeography of the Antarctic regions, in *Antarctic Ecology, Volume 1*, edited by M.W. Holdgate, pp. 97-104, London, Academic Press, 1970.

Hedgpeth, J.W., Perspectives of benthic ecology in Antarctica, in *Research in the Antarctic*, edited by L.O. Quam, pp. 93-136, Washington D.C., American Association for the Advancement of Science, 1971.

Hyland, J., D. Laur, J. Jones, J. Shrake, D. Cadian, and L. Harris, Effects of an oil spill on the soft-bottom macrofauna of Arthur Harbour, Antarctica compared with long-term natural change, *Ant. Sci., 6*, 37-44, 1994.

Iwasaki, N., and T. Nemoto, Distribution of pelagic shrimps in the Australian Southern Ocean (abstract), *Mem. Nat. Inst. Polar. Res., 40*, 247-248, 1986.

John, D.M., I. Tittley, G.W. Lawson, and P.J.A. Pugh, Distribution of seaweed floras in the Southern Ocean, *Bot. Mar., 27*, 235-239, 1994.

Kanwisher, J., Freezing in intertidal animals, *Biol. Bull., 109*, 56-63, 1955.

Kauffman, T.A., Seasonality and disturbance in benthic communities, Arthur Harbour, Antarctic Peninsula, *Antarct. J. U.S., 9(6)*, 307-310, 1974.

Kirkwood, J.M., and H.R. Burton, Macrobenthic species assemblages in Ellis Fjord, Vestfold Hills, Antarctic, *Mar. Biol., 97*, 445-457, 1984.

Klöser, H., G. Ferreyra, I. Schloss, G. Mercuri, F. Laturnus, and A. Curtosi, Hydrography of Potter Cove, a small fjord-like inlet on King George Island (South Shetlands), *Est. Coast. Shelf Sci., 38*, 523-537, 1994a.

Klöser, H., G. Mercuri, F. Laturnus, M.L. Quartino, and C. Wiencke, On the competitive balance of macroalgae at Potter Cove (King George Island, South Shetlands), *Polar Biol., 14*, 11-16, 1994b.

Knox, G.A., Littoral ecology and biogeography of the southern oceans, *Proc. Roy. Soc. Lond. B., 152*, 577-624, 1960.

Kock, K.-H., *Antarctic Fish and Fisheries*, 359 pp., Cambridge University Press, 1992.

Kotlyakov, V.M., and N.A. Smolyarova, *Dictionary of Glaciology*, p. 133, Elsevier, Amsterdam, 1990.

Kott, P., Antarctic Ascinidacea, *Ant. Res. Ser., 13*, American Geophysical Union, Washington, D.C., 1-239, 1969.

Kusakin, O.G., Fauna of Isopoda and Tanaidacea in the coastal zones of the Antarctic and Subantarctic waters (In Russian), *Issled. Fauny Morei, 4 (12)*, 1967. [English Translation: *Biological Reports of the Soviet Antarctic Expedition (1955-1958), 3*, 220-389, Jerusalem, 1968].

Lawson, G.W., Seaweed distribution patterns as revealed by ordination with reference to the Atlantic and Southern Oceans, *Helg. Meeresunters., 42*, 187-197, 1988.

Lipps, J.H., and C.S. Hickman, Origin, age and evolution of Antarctic and deep-sea faunas, in *Environment of the Deep Sea, Volume 2*, edited by W.G. Ernst and J.G. Morin, pp. 324-356, Prentice-Hall, Englewood Cliffs, New Jersey, 1982.

Lowry, J.K., Soft bottom macrobenthic community of Arthur Harbour, Antarctica, *Ant. Res. Ser., 23*, American Geophysical Union, Washington, D.C., 1-19, 1975.

Mackintosh, N.A., The pattern of distribution of the Antarctic fauna, *Proc. Roy. Soc. Lond., B, 152*, 624-631, 1960.

McCain, J.C., and W.E. Stout, Benthic zonation on submarine cliffs in the vicinity of Arthur Harbour, Antarctica, *Antarct. J. U.S. 4*, 105-106, 1969.

Moe, R.L., and T.E. DeLaca, Occurrence of macroscopic algae along the Antarctic Peninsula, *Antarct. J. U.S., 11(5)*, 20-24, 1976.

Neushul, M., Benthic marine algae, *Antarct. Map Folio Ser., 10,* 9-10, 1968.

Nolan, C.P., Size, shape and shell morphology in the Antarctic limpet *Nacella concinna* at Signy Island, South Orkney Islands, *J. Mollusc. Stud., 57,* 225-238, 1991.

Norman, J.R., Coast fishes. Part 3: The Antarctic regions, *'Discovery' Rep. 18,* 1-105, 1938.

Nybelin, O., Antarctic fishes, *Sci. Res. Norweg. Antarct. Exp., 1927-28, 26,* 1-76, 1947.

Oliver, J.S., and P.N. Slattery, Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound, Antarctica, *Ophelia,* 24, 155-175, 1985.

Picken, G.B., Growth, production and biomass of the Antarctic gastropod *Laevilacunaria antarctica* Martens 1885, *J. Exp. Mar. Biol. Ecol., 40,* 71-79, 1979.

Picken, G.B., The distribution, growth, and reproduction of the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1980), *J. Exp. Mar. Biol. Ecol., 42,* 71-85, 1980.

Picken, G.B., Marine habitats: benthos, in *Key Environments: Antarctica,* edited by W.N. Bonner and D.W.H. Walton, pp. 154-172, Oxford, Pergamon Press, 1985.

Picken, G.B., and D. Allan, Unique spawning behaviour by the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908), *J. Exp. Mar. Biol. Ecol., 71,* 283-287, 1983.

Powell, A.W.B., Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda, *Discovery Rep., 26,* 47-196, 1951.

Rakusa-Suszczewski, S. (Ed.), *The maritime Antarctic coastal ecosystem of Admiralty Bay,* 216 pp., Department of Antarctic Biology, Polish Academy of Sciences, Warsaw, 1993.

Rauschert, M., Zum Vorkommen von Priapuulus tuberculatospinosus (Priapulida) in der marinen Fauna von King George, Süd-Shetland-Inseln, Antarktis, *Mitt. Zoologisch. Mus. Berlin, 62,* 333-336, 1985.

Rauschert, M., Ergebrisse der faunistischen Arbeiten im Benthal von King George Island (Südshetlandinseln, Antarctis), *Ber. Polarforsch., 76,* 1-75, 1991.

Regan, C.T., The Antarctic fishes of the Scottish National Antarctic Expedition, *Trans. Roy. Soc. Edinb., 49,* 229-292, 1913.

Richardson, M.D., Benthic studies in the Antarctic, *Antarct. J. U.S., 7,* 185-186, 1972.

Richardson, M.D., The classification and structure of macrobenthic assemblages of Arthur Harbour, Anvers Island, Antarctica, Ph.D. thesis, Oregon State University, 1976.

Richardson, M.D., and J.W. Hedgpeth, Antarctic soft-bottom, macrobenthic community adaptations to a cold, highly productive, glacially affected environment, in *Adaptations Within Antarctic Ecosystems,* edited by G.A. Llano, pp. 181-195, The Smithsonian Institution, Washington, D.C., 1977.

Richardson, M.G., The distribution of Antarctic marine macroalgae related to depth and substrate, *Bull. Br. Antarct. Surv., 49,* 1-13, 1979.

Shabica, S.V., The general ecology of the Antarctic limpet, *Patinigera polaris, Antarct. J. U.S., 6,* 160-162, 1971.

Shabica, S.V., Tidal zone ecology at Palmer Station, *Antarct. J. U.S., 7(5),* 184-185, 1972.

Shabica, S.V., The natural history of the Antarctic limpet *Patinigera polaris* (Holmbron and Jacquinot), Ph.D. thesis, University of Oregon, 1976.

Stehli, F.G., A.L. McAlester, and C.E. Helsley, Taxonomic diversity gradients of recent bivalves and some implications for geology, *Bull. Geol. Soc. Amer., 78,* 455-466, 1967.

Stockton, W.L., An intertidal assemblage at Palmer Station, *Antarct. J. U.S., 8,* 305-307, 1973.

Stockton, W., The intertidal zone at Palmer Station, Anvers Island, Antarctic Peninsula, in the wake of the *Bahia Paraiso* spill, *Antarct. J. U.S., (1990 review),* 203 (only), 1990.

Stout, W.E., and S.V. Shabica, Marine ecological studies at Palmer Station and vicinity, *Antarct. J. U.S. 5(4),* 134-135, 1970.

Vanhofe, S., J. Wittoeck, G. Desmet, B. Van den Berghe, R.L. Herman, R.P.M. Bak, G. Nieuwland, J.H. Vosjan, A. Boldrin, S. Rabitti, and M. Vincx, Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment, *Mar. Ecol. Prog. Ser.,* in press.

Voβ, J., Zoogeographic und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres (Antarktis), *Ber. Polarforsch., 45,* 1-145, 1988.

Wägele, J.W., and T.A.S. Brito, Die sublitorale Fauna der maritimen Antarktis. Erste Unterwasserbeobachtungen in der Admiralitatsbucht, *natur und Museum, 120,* 269-282, 1990.

Waite, E.R., Fishes, *Scient. Rep. Australas. Antarctic Exped. 1911-1914, C, III (I),* 1-92, 1916.

Walker, A.J.M., Introduction to the ecology of the Antarctic limpet *Patinigera polaris* (Holmbron and Jacquinot) at Signy Island, South Orkney Islands, *Bull. Brit. Antarct. Surv., 28,* 49-71, 1972.

White, M.G., Marine benthos, in *Antarctic Ecology, Volume 2,* edited by R.M. Laws, pp. 421-461, Academic Press, London, 1984.

Winston, J.E., Systematics and marine conservation, in *Systematics, Ecology and the Biodiversity Crisis,* edited by N. Eldredge, pp. 144-168, Columbia University Press, New York, 1992.

Zamorano, J.H., Zonación y biomasa de la macrofauna bentónica en Bahía South, Archipiélago de Palmer, *Ser. Cient. Inst. Antárct. Chileno, 30,* 27-38, 1983.

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(Received September 5, 1995; accepted October 25, 1995.)