

ANTARCTIC ZOOBENTHOS*

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Abstract Technical progress in recent years has extended Antarctic benthic research through more sensitive physiological techniques, more sophisticated and reliable measurements of environmental parameters, more efficient sampling gear, and a multitude of statistical and computer based methods. At the same time the high technical standard of modern ice-breaking research vessels has led to a revival of the original discovery phase by increasing access to remote areas under the packice and providing a platform for improved imaging techniques and sophisticated aquarium and experimental facilities. In recent years biodiversity studies, life cycle investigations, modern taxonomy, physiology and biochemistry have been combined to attempt to understand adaptive strategies of the benthic fauna, their functional rôle in the Antarctic ecosystem, and present zoogeographic patterns within the framework of evolutionary history.

Based on recent literature (since 1985) on or related to Antarctic benthic research, but also considering major advances published earlier, an attempt is made to summarize the present stage of knowledge on:

- environmental conditions in the past and present
- evolution and zoogeography
- species richness and biodiversity
- abundance and biomass
- community dynamics and interactions
- physiology and autecology, and
- life history strategies, mainly reproduction, growth and productivity, of the Antarctic benthic fauna.

Two additional sections deal with conservational and methodological aspects related to Antarctic benthic communities.

Furthermore, future perspectives of benthic research in the Antarctic are considered, particularly against the background of global environmental changes and further advances in technology.

Introduction

Over a century ago, the first substantial benthic samples taken in Antarctic waters by the staff of the “Challenger” primarily served the purpose of completing the inventory of the world ocean’s fauna. This first discovery phase, with a strong emphasis on taxonomy, continued during the first half of the 20th century, before Antarctic stations were established

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ashore. Then the focus of research shifted to studies of life history, behaviour, and physiology of the benthic fauna in shallow waters. Occasionally, as for example in McMurdo Sound, a further step was taken towards the study of biological interactions *in situ*.

It is not the purpose of this paper to summarize the history of benthic research in the Antarctic up to the present day, as was done earlier by Dell (1972). We rather attempt to highlight recent progress against the background of research in the past, which has been considered *in extenso* in the majority of reviews to be cited in this paper. The important rôle played by the early explorers has recently been stressed by Davenport & Fogg (1989) and Dayton (1990).

At first glance it seems doubtful whether another review on benthic research in Antarctica could be of any use. In fact, there have been over 20 papers on Antarctic benthos with review character since Hedgpeth (1969, 1971) first called the public attention to the fact that the benthic fauna of the Southern Ocean is of special interest. At least 13 of these reviews have appeared recently, i.e. in or after 1985 (Table 1). We will – quite arbitrarily – try to summarize progress in benthic research from about that year although, of course, important achievements had been made before. In 1982, Lipps & Hickman had published their comparative report on the evolution of the Antarctic and deep sea faunas; in 1983, Clarke finished with the anthropocentric view of the hardships of life in cold water, and in 1984–85 Picken, White and Arnaud published stimulating reviews on more recent results, mainly from shore-based Antarctic stations.

For the present review, we have considered a total of 318 papers on or related to benthic research, 166 of which have been published in 1985 and later. Purely taxonomic work – without a connection to ecological questions – has been excluded. From the 166 recent papers, the following general conclusions can be drawn.

- The bulk of the papers report work done in the Weddell Sea and in the Antarctic Peninsula/Scotia Arc region (Fig. 1). This may reflect recent activities of RV POLARSTERN and shore-based work mainly on King George and Signy Islands. Another important centre has been McMurdo Sound with shore-based work from the North American station. Shipboard sampling has, quite surprisingly, yielded more papers than work from the shore.
- Relatively few papers have been published from areas north of the Antarctic Convergence; nearly all work has been done in the high Antarctic.
- Both deep- and shallow-water sampling have contributed a great deal to recent publications, whereas scuba diving has not become as overwhelmingly important as was anticipated 10 years ago. Laboratory work in cool containers is increasing in importance but still at an initial stage.
- General descriptive biogeographical work and reports on community distribution have been the leading topics during the past six years followed by papers on species interactions (in a wide sense, including benthic-pelagic coupling). Population dynamics and studies on reproduction and life histories have been catching up in importance but still contribute only a minority of the papers. Sadly little work has been done on physiological and biochemical questions related to the Antarctic benthos.

In the following sections we will try to summarize the “state of the art” of different aspects of benthic research. Progress in the individual fields has been made at different pace and in different ways. In some areas the data base has improved considerably, partly due to new facilities and techniques; in others old concepts have been examined critically and stimulating

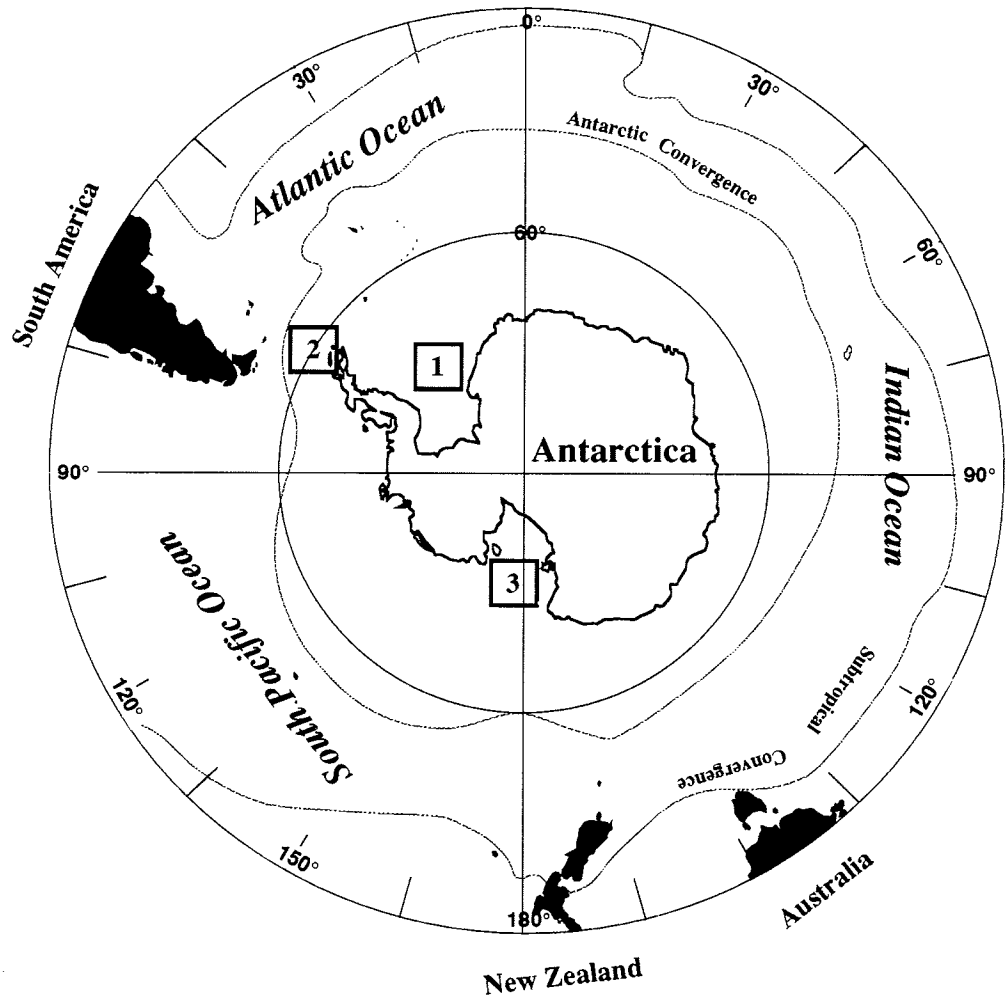


Figure 1 Principal Antarctic investigation areas according to number of publications since 1985 (see Table 1). 1: Weddell Sea; 2: Antarctic Peninsula & Scotia Arc; 3: Ross Sea (mainly McMurdo Sound).

new ideas have been proposed. However, in many cases the available data are not yet sufficient to enable us to accept or reject certain hypotheses, or to produce definite statements as to the future development of certain areas of benthic research in Antarctica. At present, the study of polar benthos, as any other field of polar research, is still a young, developing field of endeavour.

Environmental background in the past

Ever since the paper by Lipps & Hickman (1982) was published, the importance of climatic events in the past for the evolution of the present Antarctic fauna has been evident to the

biologists working in the Southern Ocean. The questions whether there was an ice shield on the continent, whether icebergs drifted and scoured in nearshore waters, whether the shelf was covered by or free of ice, whether there was an important runoff from rivers, whether the environment was relatively constant or strongly fluctuating, and what the absolute sea-water temperatures were, have been discussed for quite some time, but only in the past few years has there been a decisive improvement of our knowledge. This improvement was based on more and much deeper drill holes in different parts of the continent. Unfortunately, it is sometimes difficult to reconcile recent knowledge from these drill holes with the record from marine sediments which has been available for some time. Furthermore, the findings at different Antarctic sites do not always yield the same results, and the same is true for Australian data referring to the time when this continent was still linked to Antarctica.

Most authors agree that during most of the Cretaceous (~135–66 Ma ago) Antarctica had a mild, humid climate, with temperatures above or around 15°C at the beginning, and around 10°C at the end of this period (Emiliani 1961, Pirrie & Marshall 1990). Antarctica and Australia were still closely connected by that time, and no major circulation existed between them (Lipps & Hickman 1982). However, material possibly rafted by ice in Australia in early Cretaceous (Frakes & Francis 1988) has yet to be reconciled with the evidence of a warm climate with abundant vegetation on the Antarctic Peninsula (Spicer 1990). In early Palaeocene, as in late Cretaceous, cooler surface water conditions prevailed. In late Palaeocene (~62–58 Ma) and at the beginning of the Eocene (~58–52 Ma), the surface sea-water temperatures increased to about 17–18°C before they dropped again to 6–8°C towards late Eocene (~38 Ma) around the Antarctic continent because of the separation of Australia. At that time, bottom water temperatures may have been around 5°C. This is at least what the marine record indicates which has been derived from stable oxygen isotope data (Kennett 1985, Kennett & Stott 1990, Stott et al. 1990, Barrera & Huber 1991, Mackensen & Ehrmann 1992). The marine record shows that diverse calcareous planktonic assemblages, which reflect the relative warmth of surficial waters off Antarctica from the late Cretaceous, persisted throughout the Eocene. During late Eocene, the diversity of these assemblages began to decrease. Near the northern Antarctic Peninsula, a diverse middle to late Eocene palynoflora indicates the presence of forests dominated by *Nothofagus* with an undergrowth containing ferns (Kennett & Barker 1990). The Eocene temperature decrease "... produced glacial conditions throughout Antarctica and ice formation in adjacent seas, but as yet no ice cap" (Lipps & Hickman 1982). However, there are indications that the mountains were glaciated, and that in some valleys the glaciers were reaching the Antarctic coast. This is indicated by isolated Eocene gravel and terrigenous sand grains pointing to ice rafting, and by glaciomarine deposits on King George Island (Birkenmajer 1988, 1992, Wei 1992, Ehrmann & Mackensen 1992).

Most of the Antarctic continent, however, remained ice free, and the climate was temperate and humid. It should be mentioned, however, that a few studies of oxygen isotopes indicate the existence of large ice masses in Antarctica at that time (Matthews & Poore 1980, Prentice & Matthews 1988, 1991).

In early Oligocene sediments with an age of ~36 Ma, a strengthening of glacial conditions and the onset of continental east Antarctic glaciation is recorded. All major sediment parameters, such as ice rafted debris, clay mineralogy and bulk mineralogy, as well as stable oxygen isotopes document this event. At the same time a further cooling of the Southern Ocean waters occurred (Hambrey et al. 1990, 1991, Ehrmann & Mackensen 1992, Zachos et al. 1992).

The question is to what extent this ice sheet may have lasted into subsequent geological epochs or whether it was only temporary. From recent drilling it seems that the ice never totally disappeared from the Antarctic continent once the ice sheet had become established over East Antarctica in earliest Oligocene time. However, a great number of major advances and retreats of the ice have occurred since that time (e.g. Hambrey et al. 1991, Ehrmann et al. 1992).

During the remaining Oligocene (~37–24 Ma) East Antarctica was almost totally covered by ice. In West Antarctica the highest regions remained glaciated, and some valley glaciers continued to reach the sea, as can be deduced from the Polonez Cove Formation and the Legru Bay Group (Birkenmajer 1988, 1992, Porebski & Gradzinski 1987, Gazdzicki 1989).

Whether a Transantarctic Strait existed between East and West Antarctica, is uncertain; its existence is supported by the deep-sea benthic fauna (Webb 1981, Barrett et al. 1989), but not by planktonic diatom assemblages in the Oligocene (Barrett et al. 1989). However, continent-wide glaciation of ice-sheet proportions seems to have been a major feature of that time in Antarctica if data from the CIROS-I drill hole in the Ross Sea, from Prydz Bay and from the South Shetland Islands are combined. The CIROS-I data show strong erosion by ice streams coming down from the Transantarctic mountains which by early Oligocene had reached about half their present height. Glaciers were calving at sea level most of the time, but there seems to have been little or no sea ice. The ice shield is supposed to have been "temperate" (similar to the conditions of Patagonian glaciers today) but it may have been voluminous. Cool temperate *Nothofagus* forests grew on the foothills and along the river mouths and persisted through several glacial cycles (Barrett et al. 1989).

The final separation of South America from Antarctica (~29 Ma ago) resulted in the opening of the Drake Passage. Although shallow water may have passed at that time, a deep gap and the Antarctic Circum-polar Current (ACC) probably did not develop before 23.5 ± 2.5 Ma (Barker & Burrell 1982). A fortuitous arrangement of continental fragments and island areas may have restricted ACC transport until about 16 Ma (Barker & Burrell 1982).

A slight warming (~17.5–15 Ma) during the beginning of Miocene (~24–5 Ma) was followed by another temperature decrease between 15 and 12 Ma (Shackleton & Kennett 1975, Miller et al. 1987, Mackensen et al. 1992). The Antarctic continent, according to the isotope data, was then surrounded by packice but not by permanent ice shelves (Lipps & Hickman 1982). From middle Miocene time onwards all geological records agree that extensive ice existed on the continent, according to the Prydz Bay data possibly more ice than today (Hambrey et al. 1991). The CIROS-I data indicate erosion by glaciers between mid-Miocene and early Pliocene as a consequence of the growing West Antarctic ice sheet (Barrett et al. 1989). Already in late Miocene ice shelves had developed in East Antarctica and, for the first time, also in West Antarctica (Ciesielski et al. 1982, Kennett & Barker 1990). Towards the end of the Miocene and during the earliest Pliocene, marine siliceous biogenic sediments which replace the calcareous remainders of the former warm water assemblages reveal a rapid northward movement (~300km) of the Antarctic Convergence and cold Antarctic surface waters, which were supposedly related to a major expansion of the Antarctic ice cap at that time. The Ross ice shelf then extended much beyond its present-day limits (Kennett 1985, Kennett & Barker 1990).

By the beginning of the Pliocene (5.3–1.6 Ma) the circumpolar current had definitely developed, the whole of Antarctica had become glaciated, and an isolated distinctly Antarctic ecosystem had evolved. However, contrary to earlier proposals, Antarctica had significant intervals during this period when it was warmer and less glaciated than now, with

vegetation growing in certain places (Webb et al. 1984, Quilty 1990). Kennett (1985) from oxygen and carbon isotope data concludes, e.g. that the period between 5 and 3.5 Ma was one of these "warm" periods, with a sea level that was 75–100m higher than today (Haq et al. 1987). At the end of the period the ice volume increased on a global scale.

During the Pleistocene (1.6–0.01 Ma), Antarctica was predominantly glaciated, but not even during this ice age were there constant conditions. Oxygen isotope data reveal several "Milankovich cycles", with slow expansion and relatively fast collapse of ice caps, over the last 750000 years. The last glacial maximum was reached 18–25000 years ago, causing fully glacial conditions not only in Antarctica but also in southern South America (Quilty 1990). Glacial episodes during the Quaternary are marked by finer sediments with lower siliceous biogenic components due to increased seasonal ice cover, reduced diatom productivity and weaker bottom water flow. The converse is true for interglacial episodes (Kennett & Barker 1990, Grobe & Mackensen 1992). In the Holocene, warmest temperatures prevailed some 9000 years ago; after their decrease they varied only moderately until present (Heusser 1989).

Summarizing, recent drilling data indicate that there seems to have been a volume of ice on the Antarctic continent during the past 36 million years, i.e. at least from early Oligocene times, that was by no means less extensive than that of today. Furthermore, changes in the past, including variation in the extension of ice caps, advances and retreats of ice shelves, occurrence of icebergs and packice, and much warmer periods in between with vegetation growing in river valleys, occurred more commonly than was anticipated hitherto. Particularly during the Pliocene, Antarctica was considerably warmer at times than presently.

This increased knowledge of the environmental history of the Southern Ocean is of utmost importance from an evolutionary point of view, since both persistence of conditions (long-term "stability", see e.g. Sanders 1969) and frequency of disturbance or stress (see e.g. Dayton & Hessler 1972, Richardson & Hedgpeth 1977, Barrett and Rosenberg 1981, and Bayne 1985) have been invoked when talking about faunal evolution in marine ecosystems (Lipps & Hickman 1982).

Present effects of physical factors on the benthos

The older (Lipps & Hickman 1982) (and some recent – Dayton 1990) literature generally stresses the relative constancy – not "stability" although this term has often been used! – of physical conditions in the South Polar Sea (except light which varies strongly seasonally but in a predictable manner). In recent years some literature has accumulated to check to what extent this is true. Biotic factors will be considered later.

Compared to other marine ecosystems, relatively constant conditions are:

Low but stable temperatures. Perhaps the extreme case is McMurdo Sound where at 585 m depth the annual temperature range is $\pm 0.07^\circ\text{C}$ around an average of -1.89°C (Picken 1984); another published value is $-1.8^\circ\text{C} \pm 0.2^\circ\text{C}$ (Littlepage 1965 *vide* Clarke 1988). Both the mean annual temperature and the extent of annual variation are supposed to increase from the Antarctic continent out towards the Antarctic Convergence (Clarke 1988) but there are exceptions due to the inflow of Warm Deep Water (Dunbar et al. 1985, Bathmann et al. 1991, Arntz et al. 1992) or Cold Deep Water (Dayton 1990) moving up on the shelf. At Signy Island (S. Orkney I.) temperatures vary by 0.5°C (Clarke 1988) whereas at 17 m

in Arthur Harbor they vary between -1.8°C in winter and $+1.0^{\circ}\text{C}$ in summer (Ayala & Valentine 1978). In Admiralty Bay (King George I.) summer temperatures are around $+1.76^{\circ}\text{C}$ (max. $+3.4^{\circ}\text{C}$) at the surface and around -0.18°C at 500m depth. The minimum winter value at the surface is -1.6°C (Wägele & Brito 1990 with refs.).

Low fluctuations in salinity. The normal range in the benthic realm is 34.6–34.9‰ (Lipps & Hickman 1982, Clarke et al. 1988). Exceptions are shallow water and intertidal areas where melt water inflow, tides and currents can cause substantial variations in salinity (e.g. Barry 1988).

Less input from terrestrial sediments than in the Arctic. In contrast to the Arctic, where meltwater streams supply large amounts of sediment to the coastal zone, modern sediment input by meltwater is considered to be minimal in the Antarctic (Dunbar et al. 1985). Under present ice shelf conditions this is true especially for fine sediment, but dropstones are an important substratum for hard-bottom fauna (pers. obs.).

Isolation by deep sea, circumantarctic current systems, and Antarctic Convergence. They all contribute to the constancy of conditions in the South Polar Sea (White 1984).

On the other hand, certain conditions fluctuate intensely.

Light regime. This is highly seasonal. As a consequence, primary production is also seasonal. Major fresh food input, and the vertical flux as a whole are restricted or limited to certain times of the year (see pp. 264).

Sea ice cover. This is variable except in some areas (e.g. east coast of the Antarctic Peninsula where it is \pm permanent). Sea ice at Signy is present for an average of 140 days yr^{-1} but with great year-to-year variation (Clarke et al. 1988). The importance of sea ice which is obvious for life in the water column and for seasonal changes of phytoplankton (Spindler 1990, Spindler & Dieckmann 1991, Scharek 1991) is generally hypothesized for the benthos underneath (e.g. Picken 1984, Arnaud 1985) but has rarely been measured quantitatively (Leventer & Dunbar 1987 *vide* Dayton 1990). Sediment resuspension during winter has been observed at various localities by different authors using sediment traps (Berkman et al. 1986, Bathmann et al. 1991, Wefer & Fischer 1991, Arntz et al. 1992), however, the food value of resuspended material is doubtful (which would give even more importance to the input from melting ice and the water column). Resuspended sediments may, however, contain viable algal material (Berkman et al. 1986).

Anchor ice. This is a major source of physical variation in shallow water communities and, to some extent, responsible for the zonation of the fauna down to about 30m (Dayton et al. 1970, 1974). It does not normally occur at depths $> 33\text{m}$ except in cases where Deep Cold Water moves up the shelf (Dayton 1990). In McMurdo Sound, anchor ice has been found to be responsible for the population fluctuations of *Homaxinella* sponges and it is of general importance both for sponges and their asteroid predator populations (Dayton 1989). Anchor ice can encase plants and animals, tear them off the substrate, and is capable of lifting up to 25kg (Picken 1984).

Iceberg scours. Fresh scours have been found to be very common close to the southeastern Weddell Sea ice edge (Lien et al. 1989, Galéron et al. 1992). Plough marks with a relief

of about 10m and a width of about 300m have been recorded in the study area off the Rijser Larsen ice shelf; undisturbed conditions were found in very shallow bays and in water depths > 330–340m. Most of the plough marks were relatively narrow with widths in the order of 30–70m (Lien et al. 1989). Older scours have been found down to > 400m in the Weddell Sea and may date from glacial periods when the water level was lower than today (Picken 1984). However, icebergs of considerable draft (> 400m) have been reported in other areas (Keys 1984 *vide* Lien et al. 1989).

Ice shelves. These seem to suppress the benthic fauna underneath and create unpredictable conditions due to temporary extension and the calving of icebergs. Most of the coastline and nearshore region of these areas is covered by floating or grounded glacier ice, so beaches and true littoral areas are uncommon (Dunbar et al. 1985). Local primary productivity from algae was found to be impossible under the Ross ice shelf, but bacterial densities and organic carbon were equivalent to deep-sea values. No benthic infauna was collected, but a motile faunal element (mostly crustaceans and several fish) under the ice shelf was found as much as 430km away from the ice edge, under 420m of ice and at a water depth of about 600m (Lipps et al. 1979, Bruchhausen et al. 1979, Dayton 1990). The fish beneath the ice shelf may have fed on the abundant *Orchomene* amphipods (Bruchhausen et al. 1979) whereas a food source for the amphipods was less obvious. Their stomachs contained sediment, bacteria and small crustaceans (Stockton 1982). As scavengers they may be dependent on occasional carcasses getting caught under the ice. This is substantiated by the fact that baited traps attracted several hundred of them (Stockton 1982).

Contrary to the depauperate fauna in shelf ice covered areas at a large distance from the ice edge, benthic life in the vicinity of the ice edge in the Ross Sea turned out to be rich and varied, with species which are also common in areas with annual sea ice (Oliver et al. 1976, Oliver & Slattery 1985). Samples taken in the southern Weddell Sea shortly after the calving of three large ice isles in 1988 by D. Gerdes & J. Gutt (unpubl.) in an area formerly covered by the Filchner ice shelf revealed the existence of motile (amphipods, ophiuroids) and sessile elements (tunicates, hydrozoans); the latter, however in low numbers.

Stations outside but close to the ice edge generally yield a reduced taxa richness in the southeastern Weddell Sea which may be explained by the more frequent disturbance in this area from iceberg scouring and the shorter time of existence of the community. For some groups, however, such as molluscs, higher species richness was found close to the shelf ice edges. Sites at the same depth but at a greater distance from the ice edge revealed a similar fauna (Galéron et al. 1992). This is interesting considering the historical advances and retreats of the ice shelf (Grobe 1986). A “replicate” of the fauna at a site more distant from the shelf ice, serving as a refuge, may have favoured recolonization in the past, similar to refuges of the eurybathic fauna on the continental slope (Klages 1991, Galéron et al. 1992).

Variation of currents and circulation patterns. Bottom current intensity determines the grain size of sediments, and sediment textural and compositional data can be used as a proxy record to derive past current intensity, direction and information about biological composition and productivity in surface waters (Dunbar et al. 1985). Coarser sediments are indicative of resuspending detritus, whereas on the soft bottoms of the trenches the slow currents do not resuspend particles, resulting in a meagre food supply via resuspension for the epifauna (Voß 1988). On the other hand, in the Fildes Strait (King George Island) turbulent tidal currents with velocities up to $2.5\text{m}\cdot\text{s}^{-1}$, causing continuous lateral food advection, seem to be favourable for a greater number of species as compared to the adjacent

Maxwell Bay which is characterized by quiet water. For example, 103 amphipod species have been registered from the Fildes Strait whereas only 55 species have been found in Maxwell Bay (Rauschert 1991).

Circulation patterns are also responsible for dramatic differences in productivity in eastern McMurdo Sound as compared to the West. The western sound receives water from beneath the Ross ice shelf which has a lower phytoplankton standing stock, more sluggish current speeds and more persistent ice cover; in contrast, the currents along the eastern side flow southward from a much more productive area (Barry & Dayton 1988, Barry 1988). The oligotrophic-to-eutrophic shift is accompanied by marked differences in density of the benthic faunal communities (Dayton & Oliver 1977, Dayton 1990, see p. 258).

Long-term/large scale modification of circulation patterns. Barry & Dayton (1988) discuss that the 1982–83 El Niño Southern Oscillation (ENSO) event may have modified the circulation patterns within McMurdo Sound. This may have finally caused heavy ice formation after a decade of low ice conditions (Dayton 1989).

Volcanic eruptions. Local benthic mortality caused by volcanic eruptions in 1967, 1969 and 1970 off Deception Island (Antarctic Peninsula) has been observed by Gallardo et al. (1977) and Gallardo (1987a). The infauna in this area suffers recurrent and drastic alterations which result in an altered composition and scarcity of taxa (Gallardo et al. 1977).

Summarizing, the Antarctic benthic environment – similar to what has been found in the deep sea – is exposed to more physical variability and disturbance, both on a geological (see p. 247) and a recent time scale, than was thought in the past. It has never been a “stable”, unchanging environment, as was already stated by Lipps & Hickman 1982, and it is not one today. Nevertheless, compared to other benthic marine ecosystems, it has some remarkably constant physical properties, and it is certainly less affected by stress than most other ecosystems in the world (areas influenced frequently by iceberg scour, such as King George Island, may be an exception). Indeed Oliver & Slattery (1985) speculate that precisely the lack of physical disturbance is one of the most important factors maintaining the dense macrobenthic assembly they studied at McMurdo Sound.

Zoogeography and the evolution of the benthic fauna

Factors potentially responsible for shaping the Antarctic benthos

The Antarctic benthos in its present composition and diversity has evolved as a consequence of the long- and short-term abiotic environmental conditions in the past (pp. 244ff) and of biotic interactions (pp. 264ff). The distribution of most of the Antarctic fauna is circum-polar (Hedgpeth 1971, Knox & Lowry 1977, Richardson & Hedgpeth 1977, Voß 1988) which is, of course, due to the similarity of conditions in the sea around the continent and the circumantarctic current systems. The Antarctic Convergence working as a barrier (White 1984) has contributed to an isolation of the present fauna and to its being different from that of the surrounding continents, and this barrier may have become even more

effective because of the limited dispersal abilities of many forms (see p. 277), thus producing a reduced gene flow from outside the Antarctic ecosystem (Clarke 1990a, Clarke & Crame 1992). The comparatively low similarity between the Scotia Arc Fauna and that of the Lazarev Sea (cruise ANT IX/3, pers. obs.), despite the existence of the Weddell Gyre as a transport system, seems to indicate, however, that exchange within the large circumantarctic current systems and eddies is not equally efficient everywhere. The question of genetic variability of individual species is beyond the scope of this review; the reader is referred to the papers by Grassle & Grassle (1977), Ayala & Valentine (1978) and Patarnello et al. (1990).

Numerous other factors have been discussed in relation to the evolution of the benthic fauna, including long-term stability, frequency of disturbance, low temperatures, temperature decrease, extreme seasonality of food supply, impact of various types of ice, and (lack of) terrestrial input. We will refer to these factors in various sections of this review. Any of them may have played an important part in the evolution of the Antarctic benthos. There have been some recent arguments, however, that may facilitate the discussion:

- The Antarctic environment as a polar environment is older than anticipated and has not been as constant as scientists used to think (see pp. 244ff). This means, a marked temperature gradient from the tropics to the pole developed earlier than anticipated, and the present polar fauna had more time to evolve under gradually changing conditions. Lipps and Hickman (1982) pointed out that long geologic periods are not required for speciation; however, is this true for the slow generation sequences in the Antarctic (see pp. 263 and 280)?
- Disturbance has been (and is) more frequent in the benthic environment than has been thought formerly (see pp. 247 and 250). However, there has been a major discussion to what extent disturbance is rather favourable (Dayton & Hessler 1972) or unfavourable (Oliver & Slattery 1985) for the development of a diverse fauna.
- Low temperatures *per se* do not seem to present an insuperable problem for the evolution of a rich fauna (see p. 272), and speciation may proceed as effectively in cool as in warm waters (Clarke 1990a). (Again, the question is to what extent slow generation times may influence speciation!). Changes in temperature may have caused extinction on a geological time scale, but temperature decrease in Antarctica was slow and should have caused emigration rather than extinction (Clarke 1990a).
- Ice conditions and the advection of terrestrial material by ice and rivers have apparently been very variable in Antarctic history. Particularly, the advance and retreat of the ice cap on the continental shelf and above the upper slope (Grobe 1986) may have been detrimental for some shelf species although many survived (Brandt 1991). The resultant up-and-down movement may explain the high degree of eurybathy in the Antarctic benthic fauna (Klages 1991). On the other hand, obligate shallow benthic organisms such as macroalgae certainly were affected (Dayton 1990).
- The extremely seasonal input of food from the sea ice and the water column is increasingly considered to be of great importance (Clarke 1988, 1990a; Clarke et al. 1988). Episodic availability of food requires particular adaptive responses which impose specific constraints on the types of organisms able to exploit such resources (Pearson & Rosenberg 1987). In the course of evolution this factor should have selected for organisms that sustain long starvation periods or live on food resources other than primary production and material sedimenting from the pelagic (see pp. 264ff). Examples for those organisms can be found among cirripedes, pantopods, amphipods (Klages pers. comm.) and isopods (Wägele 1990).

Antiquity and origin of the present fauna

Contrary to the view some 30–40 years ago that the Antarctic fauna should not be very old, evidence has been accumulating in recent years that most of the Southern Ocean shallow water marine fauna evolved *in situ* since the Cretaceous or even earlier when the continents were still connected (Clarke & Crame 1989) and the fauna was still strikingly similar (Menzies et al. 1973). More recent publications that support this view include the gastropods (Clarke 1990a; Clarke & Crame 1989) and the isopod families Serolidae and Arcturidae (Brandt 1991, Wägele & Brandt 1992). However, various other alternatives have also been discussed, e.g. immigration from the deep sea facilitated by similar conditions in that environment, or immigration from South America via the Scotia Arc (Watling & Thurston 1989). Particularly controversial has been the question whether (part of) the deep-sea fauna originated from the Antarctic or vice versa (Sieg 1988). On the other hand, the tanaidacean fauna of the Antarctic shelf is represented exclusively by “phylogenetically young” taxa (Sieg 1988, 1992) which, however, may also have an age of ~30 million yr. Almost the entire Antarctic Tanaidacean fauna seems to have become extinct when temperatures dropped in the Eocene, and cold-stenothermic eurybathic species then colonized the Antarctic shelf. Later this fauna was modified by Magellanian elements (Sieg 1988).

Some groups are absent from the Antarctic fauna nowadays although they were common in former times; the case recently best investigated is that of the decapods (esp. Reptantia) which were found to be rich in fossils in the Cretaceous (Pirrie 1989) and in the Eocene, with no rupture across the Cretaceous-Tertiary boundary (Feldmann & Tshudy 1989, and citations therein). Today there are almost no reptants in the high Antarctic but the few natant species that have made it are often very abundant (Arntz & Gorny 1991). Shallow-water balanomorph cirripedes, on the other hand, became almost extinct only recently, perhaps due to ice scour (Dayton 1990). A parallel case for deep water regions is that of the scallop *Adamussium colbecki* of which only dead shells have been found in the Weddell Sea (Hain 1990, Hain & Melles 1994).

Other groups show a particular separation into closely related species which are almost certainly the product of radiation *in situ* (Clarke & Crame 1989 who give examples among pycnogonids, gastropods, echinoderms and ascidians). In the Serolidae and Arcturidae it is precisely the original genera which have radiated in the Antarctic (Brandt 1991, Wägele & Brandt). However, most of the actual radiation is restricted to relatively few groups (White 1984, Dayton 1990). The ecological consequences of this fact have been pointed out by Watling & Thurston (1989) and Dayton (1990).

Radiation is always connected with a high level of endemism, which has been discussed by several authors (Knox & Lowry 1977, White 1984, Picken 1984, Clarke & Crame 1989, Dayton 1990). Species endemism typically ranges between 57 and 95% whereas at the genus level it is much lower (White 1984). Recent new data include isopods (87% endemic species of a total of 302, 21% endemic genera of a total of 121, Brandt (1991), and amphipods (about 95% endemic species of a total of > 600, Jazdzewski et al. 1991). On the other hand, endemism of molluscs in the Weddell Sea is very low. Only two monoplacophorans, six gastropod and no bivalve species have been found exclusively in this area (Hain 1990).

Other possible consequences of isolation and a long existence of relatively constant conditions, gigantism and dwarfism, have been discussed by Broyer (1977), Gutt (1991a) and Klages (1993). There is apparently no common pattern for all benthic groups.

Zoogeographic affinities

The older literature has been summarized, and the general value and the robustness of Hedgpeth's (1971) biogeographical conclusions have been supported, by Dell (1972) and White (1984). The main feature is the circumantarctic occurrence of many species plus smaller provinces or regions (Dayton 1990). A more recent division of areas based on amphipods and polychaetes by Sicinski (1986) coincides in part with the regional division by Knox & Lowry (1977) but separates the Magellanic area and subdivides four Antarctic islands.

High affinities restricted to the high Antarctic (Davis Sea, Ross Sea, Adelie coast) have recently been shown for Weddell Sea gammaridean amphipods (Klages 1991) and gastropods (Hain 1990) whereas most Weddell Sea bivalves have a circumantarctic distribution which includes the South Shetlands, South Orkneys and Kerguelen (Hain 1990). For echinoderms the Weddell Sea may act partially as a link between the Scotia subregion and East Antarctica (Voß 1988, Gutt 1991a).

Where there are – still or again – links with other continents, they are strongest with South America, e.g. for sponges (with the Magellanic region) (Sarà 1992), isopods (Brandt 1991, Wägele & Brandt 1992), bivalves and gastropods (Clarke & Crame 1989), but in most cases the palaeontological record is not good enough to decide whether immigration occurred in the one or other direction (Clarke & Crame 1989). Particularly low affinities have been encountered between Subantarctic amphipods and those of the Weddell Sea (only 18 of 101 spp. in common; Klages 1991).

For sublittoral benthic habitats on the shelf and on the slope the availability of data has somewhat improved since the pioneering work of Bullivant & Dearborn (1967). This is especially true for the Weddell Sea (Voß 1988, Hain 1990, Klages 1991), but the deep sea remains almost totally unstudied everywhere. In some cases a deep-sea connection has been established (tanaidaceans: Sieg 1992; molluscs: Arnaud & Bandel 1976 *vide* Clarke & Crame 1989, Dell 1972, Hain 1990 with earlier citations; a few isopod species: Hessler & Thistle 1975; amphipods: Watling & Thurston 1989, both latter citations *vide* Clarke & Crame 1989). Regionally the white spot Weddell Sea has largely disappeared but others remain (Bellingshausen and Amundsen Seas, East Antarctica, Davis Sea excluding the Vestfold Hill area; see e.g. Arnaud 1992).

Distribution and zonation*General aspects*

Patterns of Antarctic benthic distribution were first studied in the Ross Sea (Bullivant & Dearborn 1967). Since then types and zonation patterns of most Antarctic epifaunal assemblages have been described as essentially circumpolar (Hedgpeth 1971, Knox & Lowry 1977, Richardson & Hedgpeth 1977, Voß 1988) although the existence of comparable assemblages has been doubted by others (White 1984). Picken (1984), Gallardo (1987a) and Dayton (1990) reviewed the subject in more detail, and recently Arnaud (1992) has summarized a series of characteristics of Antarctic benthos including: scarce fauna in intertidal and upper sublittoral zones due to ice; eurybathy; patchy distribution likely to be caused by

sediment variation; occasional high dominance of individual species but generally low numbers.

Where there are ice shelves, the macrobenthos underneath is poor. There is no local primary production from algae, but bacterial densities and organic carbon are equivalent to deep-sea values. No benthic infauna has been collected whereas motile epifauna (crustaceans and fish) was found several hundred kilometres from the ice edge (Lipps et al. 1979, Bruchhausen et al. 1979). Life under the ice shelf in the vicinity of the edge is rich and varied in the Ross Sea (Oliver et al. 1976, Dayton et al. 1984, Oliver & Slattery 1985) but sessile elements are scarce in the Weddell Sea in an area formerly covered by the ice shelf (D. Gerdes & M. Klages pers. comm.).

In areas where there are no ice shelves, shallow water benthic life is less rich due to the impact of anchor ice and iceberg scour. Looking at zonation, a scarcity of faunal elements in very shallow water (≤ 30 m) and an increase of biomass and diversity to intermediate depths have been stressed (Zamorano 1983 and references therein). Off King George Island (South Shetland Islands) a strong negative impact of ice was found only to a depth of 4 m; below this depth, faunal richness increased (Rauschert 1991). However, very large priapulids (*Priapulus tuberculatospinosus*) were found in the intertidal of the Fildes Peninsula (Rauschert 1986), and locally extensive macrophyte vegetation and dominance of herbivorous species depending on the algae may occur (Everitt et al. 1980, Arnaud 1987). Zonal patterns have been reported by many workers, especially on hard and cobble substrata (Dayton et al. 1974, Smith & Simpson 1985, Dayton 1990 and others). Where there are zonal patterns in soft-bottom benthos, they appear to be less conspicuous than local species assemblages and the mechanisms by which these are maintained (Gallardo 1987a, Dayton 1990). Polychaete species distribution in soft bottoms of Chile Bay (South Shetland Islands) indicated a predominance of suspension feeders, particularly Cirratulidae, *Tharyx* sp. and Spionidae, in the shallower parts, and of sediment feeders (mainly Maldanidae) in the deeper parts (Gallardo et al. 1977, 1988). Similar results were published by Jazdzewski et al. (1986) for Admiralty Bay (King George Island). Further recent distributional work has been done in McMurdo Sound: Dayton (1989), Terra Nova Bay: Gambi & Mazzella (1992); Fildes Peninsula: Baoling et al. (1989).

General zonation patterns in the Davis Sea are known to some extent. Distribution of the characteristic epifaunal species off Davis Station was determined by substrate type whereas the infaunal amphipods and tanaidaceans were relatively similar between sites (Tucker 1988). In an extensive study of the macrobenthic assemblages of Ellis Fjord (Vestfold Hills), Kirkwood and Burton (1988) found substratum type to be the factor most strongly associated with changes in the distribution and abundance of macrobenthic species. Other important factors were depth, distance from the fjord mouth, bottom slope, shoreline characteristics, current speed, and the presence of low-salinity water at shallow depths during the summer melt. The four major substrata in Ellis Fjord were sand, rock, *Serpula narconensis* reefs and the thalli of *Phyllophora antarctica*. The *Serpula* colonies supported the most species whereas sand bottoms supported the least. Anchor ice is absent in the fjord. This factor may be responsible for the greater proportion of filter-feeding species in Ellis Fjord than at other sites off the Vestfold Hills, together with the high level of organic but low level of inorganic input to the benthic system (Kirkwood & Burton 1988).

The zone immediately below 30 m depth has been very little studied. Most of the conspicuous species in McMurdo Sound between 33 and 60 m are sponges and their asteroid and molluscan predators (Dayton et al. 1974). Infauna seems to play a minor rôle, and data on infaunal benthos are comparatively scarce, also from deeper water. No zonation by depth was detected for benthic infauna in the Bransfield Strait (Mühlenhardt-Siegel 1989). The early view

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that lower sublittoral and bathyal assemblages consist predominantly of suspension feeders which will tolerate only a narrow temperature range, but are found over a wide depth range (Picken 1984), has not essentially changed, however some more data – mainly from the Weddell Sea – have been created to substantiate this statement both on the community and the individual species level. On the other hand the assertion that the greatest faunal and physical break should lie at the edge of the continental shelf with a \pm uniform deep sea below (Lipps & Hickman 1982) has not been confirmed by Weddell Sea data (see e.g. Klages 1991, Arnaud & Hain 1992).

Community level macrobenthos studies in the Weddell Sea

Voß (1988) first studied the benthic communities on the shelf and upper slope of the eastern and southern Weddell Sea. He distinguished three major macrobenthic assemblages (for species composition consult Voß 1988), which were confirmed by Galéron et al. 1992 (Fig. 2).

(a) The Eastern Shelf Community, within the confines of the Antarctic Coastal Current in the east, on unsorted sediments at depths between 204 and 445 m. It is dominated

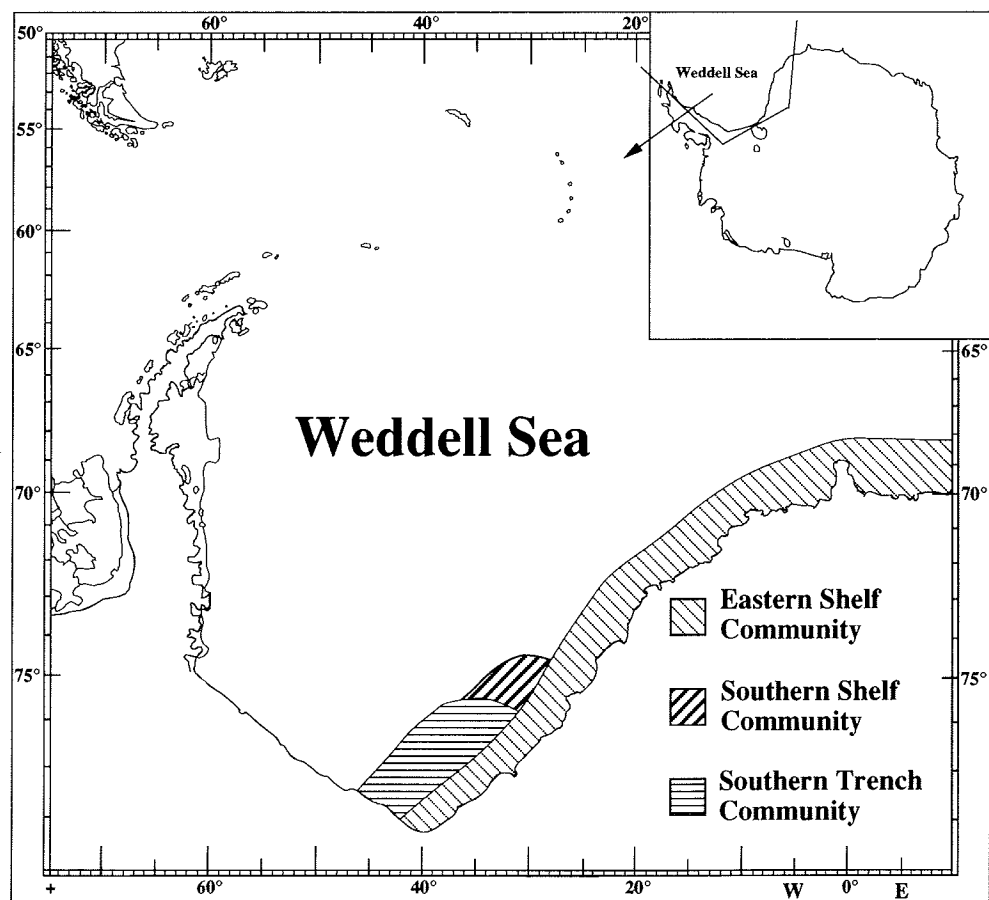


Figure 2 Major macrobenthic assemblages on the eastern and southern Weddell Sea shelf and slope. (After Voß 1988 and Galéron et al. 1992).

by suspension feeders such as sponges and bryozoans. Species number, diversity and evenness are high.

- (b) The Southern Trench Community, on soft bottoms with erratic boulders and stones in the Filchner Trench and in the depression close to the Antarctic Peninsula, at depths between 622 to 1176 m. Suspension feeders are almost absent whereas motile deposit feeders, esp. holothurians, are numerous (Gutt & Piepenburg 1991). Species number and diversity are low and evenness is on a medium level.
- (c) The Southern Shelf Community, on sandy and soft bottoms strewn with stones, in front of the Filchner-Rønne ice shelf and off Halley Bay at depths between 220 and 531 m. Suspension feeders, especially bryozoans, are dominant. Species number is very high, evenness is on a medium level, but diversity is low.

During the European Polarstern study (EPOS), Voß's (1988) separation of an Eastern and a Southern Shelf Community was confirmed. High sedimentation rates, indicating a high primary productivity (Bathmann et al. 1991) in the Eastern Shelf Community, may explain the dominance of suspension feeders in this area whereas the poorer Southern Shelf Community off Halley Bay reveals a higher trophic diversity (Galéron et al. 1992). The investigations were extended by transects perpendicular to the ice shelf to account for the bathymetric range of Voß's communities. Stations close to the ice edge in the southeastern Weddell Sea are grouped by cluster analysis due to reduced taxa richness and low abundance of bryozoans, peracarids and echinoderms. Off Halley Bay stations close to the ice edge have "replicates" in similar depths at some distance from the edge (the shelf deepens in the onshore direction) (Galéron et al. 1992, see p. 249).

New data on individual macrobenthic species and groups, mainly from the Weddell Sea

Most recent data are from the Weddell Sea where the ice shelves cover almost all areas shallower than 200 m; data from other areas (e.g. King George Island: Arnaud et al. 1986) are scarce. Former studies had shown that some degree of eurybathy may also be found in typical shallow water species such as *Nacella concinna* which has a depth range of 0–110 m (Powell 1973 *vide* Picken 1980a). The bivalve *Yoldia eightsii* which has a circumpolar distribution in Antarctic and Subantarctica waters, occurs over a wide range of depths, from about 5 m at Signy Island to at least 728 m near South Georgia (Davenport 1988).

Among the shelled molluscs in the eastern Weddell Sea, 36 gastropod and 27 bivalve species have a bathymetric distribution wider than 500 m. *Turritelopsis gratissima* and *Cyclopecten gaussianus* are untypical in that they are restricted to depths between 380 and 500 m. Bivalve assemblages in the area of the Scotia Arc (South Orkneys—South Shetland—Elephant Island—SW Peninsula) did not reveal a depth dependency in the depth range 20–850 m (Mühlenhardt-Siegel 1989). Most bivalves from the Weddell Sea are epibenthic or epizoic; endobenthic (> 5 cm) bivalves are missing although they can provide a large biomass in littoral areas of the Antarctic Peninsula (see Jazdzewsky et al. 1986, Zamorano et al. 1986) and off Subantarctic islands (Hain 1990).

A caridean decapod zonation of the order *Chorismus*–*Notocrangon*–*Nematocarcinus* was observed from shallower (~200 m) to deep (~2000 m) waters in the southeastern Weddell Sea, however with widely overlapping ranges. *C. antarcticus* was found from 155 to 782 m, *N. antarcticus* from 227 to 831 m, and *N. lanceopes* from 595 to 2031 m. The three species were dominant in subsequent depth ranges (Arntz & Gorny 1991, Gutt et al. 1991).

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Of 186 gammaridean amphipod species of the southeastern Weddell Sea 74 have a depth range of > 500m (Klages 1991). Some arcturid isopods from the Peninsula region and the southeastern Weddell Seas are similarly eurybathic; *Antarcturus spinosus* and *A. furcatus* range over 2500m of depth (Wägele 1987b, where further literature is cited concerning this subject).

Three sponge associations on the eastern Weddell Sea shelf and slope are mainly connected to different substrata; most species of this group are eurybathic, too. Spatial extension of the associations was found to be between several hundred metres and about 2km. Within single stations most species were found to be patchily distributed (Barthel & Gutt 1992).

Two groups of holothurians with distinct distributions were found in the Weddell Sea. The first group, with the majority of species belonging to the Aspidochirotida and the Elaspodida, lives on soft bottoms whereas the second group – mainly Dendrochirotida – lives on sand, hard bottoms, and biogenic structures (Gutt 1991a). The Dendrochirotida, commonly regarded as shallow-water forms, occurred on the shelf down to 600m and deeper. Most of the deep-sea holothurians, on the other hand, were also present on the shelf (Gutt 1991c).

The circumantarctic distributed sea urchins *Sterechinus neumayeri* and *S. antarcticus* have a depth range from 100 to 850m and 100 to at least 1200m, respectively, in the south-eastern Weddell Sea (> 1200m not investigated, Fig. 3).

Meiobenthic studies

While Antarctic macrobenthos is relatively well known to a few hundred metres depth but still poorly studied at greater depths, knowledge of Antarctic meiobenthos is very limited at any depth (Arnaud 1992).

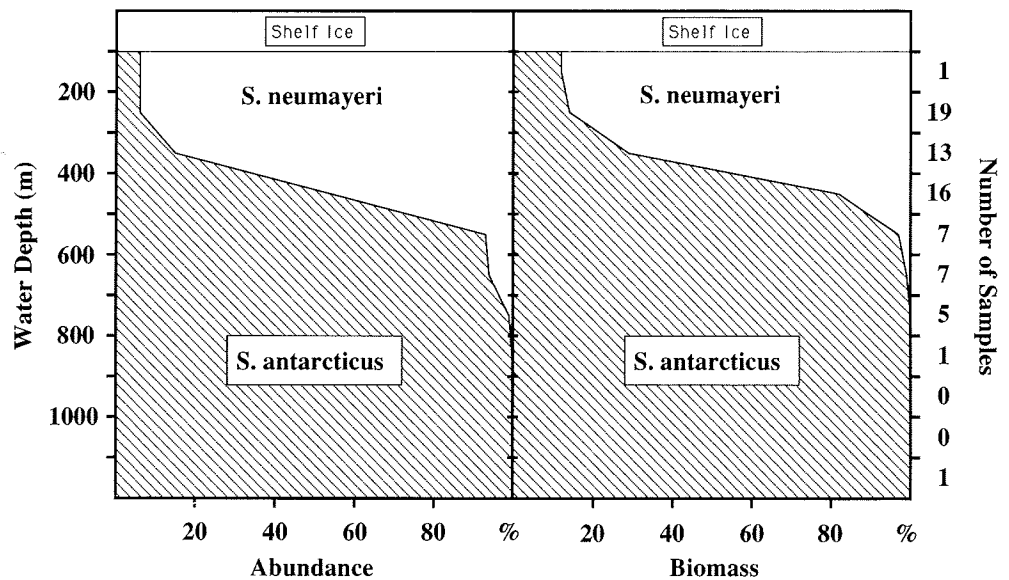


Figure 3 Depth distribution of abundance and biomass of the echinoids *Sterechinus neumayeri* and *S. antarcticus* between 100m and 1200m water depth on the Weddell Sea shelf and slope. (From Brey & Gutt 1991).

During the EPOS expedition, meiofauna communities were identified along a depth transect from about 500 to 2000 m off Halley Bay. Nematodes, harpacticoids, ostracods, polychaetes and bivalves were present at all sampling sites. Multivariate analysis discriminated between three communities which are correlated with depth and sediment characteristics: a near shelf ice, a slope and a deep-sea community (Herman & Dahms, 1992).

Density and biomass

The organic carbon content of Antarctic sediments tends to be rather low (Dayton 1990) despite the fact that sedimentation pulses from surface phytoplankton blooms can be important in summer (Bathmann et al. 1991, POLARSTERN ANT IX/Bathmann pers. comm.). This suggests that the benthic community may be an important sink (Dayton 1990).

A traditional view is that hard and soft bottoms in Antarctica support a high biomass and a large number of benthic individuals (White 1984, Clarke & Crame 1989 plus citations p. 260, Clarke 1990a plus citations p. 13).

Early investigations around the Antarctic Peninsula revealed, for example, relatively high abundance values (6000–8000 ind. · m⁻²) at Arthur Harbor (Palmer Archipelago; Lowry 1975), similar values in Chile Bay (3000–6000 ind. · m⁻²) and much lower ones in Discovery Bay, Greenwich Island (Gallardo & Castillo 1969). Mean biomass in Chile Bay was 160–180 g wet mass · m⁻². More recently, Mühlenhardt-Siegel (1988, 1989) has presented abundance and biomass data of zoobenthic communities in the Antarctic Peninsula and Scotia Arc areas. Abundance on the southwestern shelf of the Antarctic Peninsula (median: 2505 ind. · m⁻²) was significantly lower than around the Scotia Arc islands (median: 8642 ind. · m⁻²). The corresponding median biomass was 9.06 g wet mass · m⁻² and between 16.98 and 57.13 g · m⁻². Macrozoobenthos off South Georgia, Elephant Island and the Antarctic Peninsula was found to be dominated by polychaetes, molluscs and crustaceans in terms of abundance, and by echinoderms and polychaetes in biomass (Mühlenhardt-Siegel 1988, 1989). Abundance values for the southeastern Weddell Sea ranged from 131 to 12846 ind. · m⁻², biomass from 0.12 g to 1644.2 g wet mass · m⁻² (Gerdes et al. 1992).

A comparison of summer and winter benthic data of shelf infauna in the Bransfield Strait did not reveal any seasonal differences in abundance and biomass (Mühlenhardt-Siegel 1989). Further literature data have been summarized in this study and by Gerdes et al. (1992); most of these values are 1–2 orders of magnitude lower than the legendary densities between 118712 and 155572 ind. · m⁻² found in McMurdo East Sound by Dayton & Oliver (1977). These authors registered lower, but still appreciable densities in the “oligotrophic” West Sound between 1960 and 10036 ind. · m⁻² (plus one station with 45294 ind. · m⁻²). What makes comparisons difficult is the use of different screens, mostly 0.5 vs. 1.0 mm (cf. Dayton 1990). Nowhere in the Arctic have as high values been found as in McMurdo East Sound, and nowhere in Antarctica values as low as at some Arctic stations (Dayton 1990), but again the general use of a 1.0 mm mesh in the Arctic has influenced the results to some degree.

More recent data mostly refer to densities of individual taxa rather than to total faunal communities. Shallow-water (to ≈ 30 m) densities of epi- and endofauna in Admiralty Bay were found to be low (Wägele & Brito 1990), also for the limpet *Nacella concinna* of which mean values of 124 ind. · m⁻² and a mean biomass (dry tissue mass) of 13.7 g · m⁻² had been reported for the sublittoral off Signy Island (Picken 1980b). The scallop *Adamussium*

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colbecki has been found with densities up to $65 \text{ ind.} \cdot \text{m}^{-2}$ and a biomass (wet mass) approaching $2 \text{ kg} \cdot \text{m}^{-2}$ in the southwestern Ross Sea (Berkman 1990). Conversely, the biomass of shelled molluscs in the eastern Weddell Sea has been found to be very low (Hain 1990). Hain provides three possible explanations for this: species populations are small and patchy in distribution; 55% of all species are smaller than 10mm; all species excluding *Chlanificula thielei* have brittle shells. Although locally maximum densities of 26 and $32 \text{ ind.} \cdot \text{m}^{-2}$ have been found for the holothurians *Achlyonice* sp. and *Elphida glacialis*, respectively (Gutt 1988), in the "Southern Trench Community", median photographically determined densities in this area were only 6 and $17 \text{ ind.} \cdot \text{m}^{-2}$ (based on two stations, Gutt & Piepenburg 1991). Densities of *Sterechinus* spp., the most common echinoid genus in Antarctic waters, estimated from trawl samples and from photos in the southeastern Weddell Sea, were extremely low ($0.107 \cdot \text{m}^{-2}$), as were the biomasses ($0.010 \text{ g AFDM} \cdot \text{m}^{-2}$) of the two species (Brey & Gutt 1991). Already Dayton et al. (1974) had reported very low asteroid predator abundances in McMurdo Sound, the most common species being *Odontaster validus* with a density of $2.7 \cdot \text{m}^{-2}$. Sponge densities vary strongly within clusters and between geographically close stations (Barthel & Gutt 1992). Among the crustaceans, amphipods revealed relatively low mean density but locally dense patches and high biomasses, e.g. $479\text{--}17401 \text{ ind.} \cdot \text{m}^{-2}$ and $421\text{--}14600 \text{ g AFDM} \cdot \text{m}^{-2}$ in Admiralty Bay (Jazdzewski et al. 1991), and $10\text{--}1209 \text{ ind.} \cdot \text{m}^{-2}$ and $0.9\text{--}440 \text{ mg AFDM} \cdot \text{m}^{-2}$ at stations between 200 and 2000m depth in the southeastern Weddell Sea (Klages 1991). Although dense patches of about $100 \text{ ind.} \cdot 100 \text{ m}^{-2}$ were found for the shrimp species *Notocrangon antarcticus* and *Nematocarcinus lanceopes* on the continental shelf (200–600m) and slope (800–1000m) of the eastern Weddell Sea, mean values were much lower ($6.4 \text{ ind.} \cdot 100 \text{ m}^{-2}$ and $3.8 \text{ ind.} \cdot 100 \text{ m}^{-2}$, Gutt et al. 1991).

Infauna is quite poor both in density and biomass at most sites of the high Antarctic (continental) Weddell Sea, but the exceptional values in McMurdo East Sound demonstrate that this is not necessarily a common pattern for very high southern latitudes. Infauna around the Peninsula and in the Scotia Arc region is more important than in the southeastern Weddell Sea (Mühlenhardt-Siegel 1988). Epifaunal biomass values appear higher than they are due to the fact that much of the "biomass" is in fact calcimass or silicimass. Density values of epifauna seem to be higher than in the Arctic.

Biomass values have been summarized by White (1984), Dayton (1990), who also compares them with data from Arctic benthic environments, and Brey & Clarke (1993) who compare them with data from boreal and subtropical regions (Fig. 4).

As in other oceans, biomass generally decreases from shallow to deeper waters (Uschakov 1963 *vide* Clarke & Crame 1989, Brey & Clarke 1993) but there are some peculiarities.

- Compared to boreal and subtropical regions, the fauna in very shallow water is comparatively scarce or even absent. The regular heavy ice impact prevents the development of the rich flora and fauna usually found both on hard and soft bottoms in other regions.
- Despite the great variations referred to above, macrobenthos biomass on the Antarctic shelf and slope in general is distinctly higher than in boreal and subtropical areas of equal depth (Fig. 4). According to Brey & Clarke (1993) high standing stocks in this zone may be the result of adaptations to low and oscillating food levels and particularly to the low maintenance energy requirement associated with the low ambient temperature.
- Towards the deep sea (below 1000m) Antarctic and non-Antarctic biomass levels do not seem to differ much, indicating that deep sea conditions in the Antarctic are much the same as elsewhere in the world (Fig. 4).

Benthic meiofauna has been studied very little both in terms of density and biomass

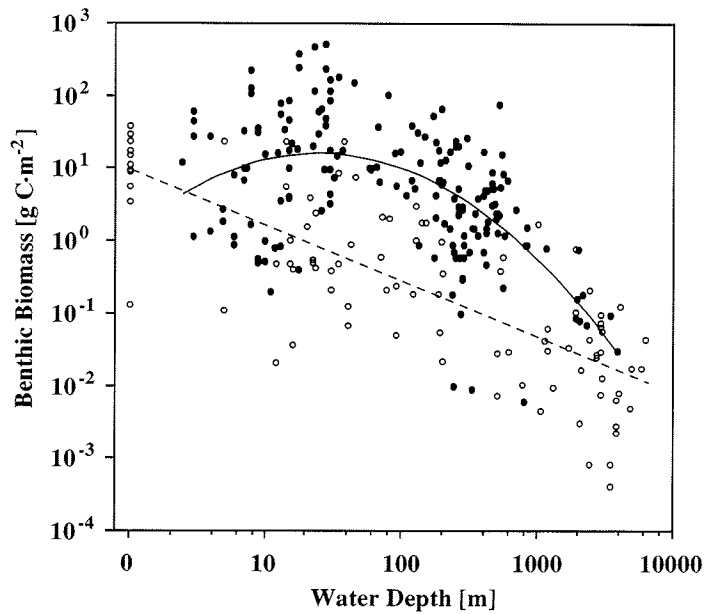


Figure 4 Variation of macrobenthic community biomass (B) with depth (D) in Antarctic (dots) as well as boreal and subtropical regions (circles). Zero depth indicates intertidal data. (From Brey & Clarke 1993).
 Antarctic: $\log(B) = 0.112 + 1.583 \cdot \log(D) - 0.568 \cdot (\log(D))^2$
 $R = 0.582, N = 175$
 Boreal & Subtropical: $\log(B) = 0.986 - 0.903 \cdot \log(D)$
 $r = 0.763, N = 94.$

in Antarctic waters. Density of meiofauna at Kerguelen Islands was between 21 and 4873 ind. · 10cm⁻², with nematodes making up between 85 and 97.3% and copepods 6% (Soyer & de Bovée 1977). In Halley Bay the range was narrower (790–3720 ind. · 10cm⁻²) (Herman & Dahms 1992). These values are not exceptional, if compared with data from temperate latitudes. However, the rôle of meiofauna (and protozoans!) in the Antarctic benthos remains to be quantified based on a much larger material.

Species richness, diversity, equitability

Species richness, diversity and evenness are rather difficult topics to deal with in any marine ecosystem and especially in the Antarctic, because the basic requirements for comparison – use of the same samplers, screen sizes and area extensions – are seldom met. Moreover, taxonomic breakdown to the species level continues to be a major problem for areas such as the Weddell Sea, which until recently were a “white spot” on the map.

Certainly the number of species in the Southern Ocean, similar to what occurred in the investigation of the deep sea, is higher than most people expected (starting, however, from the anthropocentric view that extremely cold waters, covered by ice most of the year and supplied with fresh primary production only during a short period in spring and summer,

should be detrimental to the development of a varied fauna). However, early epifaunal studies (Dearborn 1968, Dell 1972) revealed high species richness and diversity. Following Lowry (1975), and also Richardson & Hedgpeth (1977), Antarctic infauna is generally considered rich and diverse, with some areas such as Arthur Harbor (Anvers Island) coming close to maximum diversity values whereas others such as Chile Bay (South Shetland Islands) were much less spectacular (Gallardo & Castillo 1969). As for the deep sea, several alternative hypotheses were put forward to explain the apparent predominance of high-diversity sites, including environmental constancy and predictability, biological disturbance, spatial heterogeneity and the nature of trophic regimes (Lipps & Hickman 1982). Spatial heterogeneity may in fact be responsible for the high species number and diversity of epibenthos in the Eastern Shelf Community as compared to other assemblages in the south-eastern Weddell Sea (Voß 1988). Densely populated biogenic sediments are derived from sponge or bryozoan debris forming thick mats, which may locally be over 1 m thick (Dayton 1990). Also large sponges provide a further substratum on the bottom which is utilized by numerous epizoic animals (Voß 1988, Gutt 1991a, Kunzmann 1992).

While confirming a tendency towards high overall species richness and diversity in Antarctic waters, some more recent reviewers have cautioned against over-generalization (White 1984, Clarke & Crame 1989, Clarke 1990a, Gutt 1991c). Several groups, among them sessile suspension feeders (sponges, bryozoans), motile epibenthos (amphipods) and taxa which cover a wide range in terms of motility or trophic function (polychaetes), are rich in species; others seem to occupy an intermediate level (bivalves, gastropods, isopods); and a few groups are either missing altogether (stomatopods) or restricted to a few representatives, such as cirripedes and natant decapods (reptants are almost totally absent from the high Antarctic). Clarke (1990a) points out that the decapod fauna (and the fish which are not subject of this review) were quite rich around the fragments of Gondwana in Cretaceous and early Tertiary times, and that they were possibly eliminated by glacial advances in the past, the isolating barrier of the Polar Front making recolonization difficult. The question remains, however, why this should have concerned just the more motile elements such as decapods and fish.

Extraordinarily high numbers of species usually refer to the whole Antarctic (Table 2). What makes these figures outstanding is rather the extremely wide circumpolar distribution of many species than their absolute numbers, which compare quite well to those of other continents.

Within-taxon diversity is quite variable (Table 2); some families or genera have radiated enormously whereas others have not. Among isopods, three families account for at least one-half of the Antarctic species (White 1984) which now total 346 (Brandt 1990). In the genus *Serolis*, 20 of the 64 known species are endemic to the Antarctic (Luxmoore 1985). Despite the fact that on a latitudinal scale Antarctic bivalves and gastropods show a low within-site diversity due to problems of calcification (Clarke & Crame 1989), a recent study on the eastern Weddell Sea shelled gastropods and bivalves (Hain 1990) revealed a remarkably high taxonomic diversity: the 145 gastropod species belong to at least 26 families and 69 genera, while the 43 bivalve species belong to 17 families and 25 genera (Table 2). Many genera and some families are represented by only one species. High species numbers occur only in three families (Buccinidae, Turridae, Philobryidae). Some, elsewhere very successful, groups are missing in the South Polar Sea altogether: Caridoidea, Veneroidea, Tellinoidea, and Mactroidea. Some groups such as periwinkles (Littorinoidea), limpets (Patellogastropoda) and scallops (*Adamussium colbecki*), which are common in other parts of the Antarctic, are lacking in the eastern Weddell Sea for bathymetric or

Table 2 Species richness and taxonomic diversity of better known groups of the Antarctic benthos; — = no data.

Order	Families	Genera	Species	Area	Source
Gastropoda	26	69	145	Weddell Sea	Hain 1990 & pers. comm.
Gastropoda Prosobranchia	—	—	98	Davis Sea	Egorova 1982
Gastropoda	—	—	97	Enderby Land — Ross Sea	Powell 1958
Bivalvia	17	25	43	Weddell Sea	Hain 1990 & pers. comm.
Bivalvia	—	—	50	Davis Sea	Egorova 1982
Bivalvia	—	—	33	Ross Sea	Powell 1958
Mollusca	—	—	≈ 870	Whole Antarctic	Sieg & Wägele 1990
Isopoda	25	121	346	Whole Antarctic	Brandt 1990
Amphipoda	74	304	808	Whole Antarctic	Broyer & Jazdzewski 1993
Amphipoda (gammarids only)	28	82	174	SE Weddell Sea	Klages 1991
Decapoda	5	8	8	SE Weddell Sea	Arniz & Gorny 1991
Holothuroidea	7	22	34	SE Weddell Sea	Gutt 1988
Asteroidea	12	29	50	SE Weddell Sea	Vofß 1988
Ophiuroidea	6	15	43	SE Weddell Sea	Dahm pers. comm.

historical reasons (Hain 1990). However, *A. colbecki* may occur in disjunct populations under the shelf ice (Hain & Melles 1994). Holothurians (Gutt 1991c) and amphipods, too, have a high taxonomic diversity in the Weddell Sea (Klages 1991, Table 2). All eight species of caridean shrimps in the Weddell Sea belong to different genera (Arntz & Gorny 1991).

Very little has been published about the equitability (evenness) of the Antarctic benthos. The enormous dominance of nematodes prevents high values in the meiobenthos (Herman & Dahms 1992). Richardson & Hedgpeth (1977) recorded low equitability values at Arthur Harbor (Antarctic Peninsula). On the other hand, the dense macrofaunal assembly at McMurdo Sound revealed an extraordinary equitability: 11 species maintained populations > 2000 individuals $\cdot m^{-2}$, which differs markedly from the (often monospecific) aggregations in other dense assemblages (Dayton & Oliver 1977).

Dynamics of Antarctic benthic communities (including recolonization/succession)

Antarctic benthic communities in general are supposed to be comparatively persistent in time and do not tend to drastic seasonal oscillations, although exceptions from the latter have been reported from shallow water (Gruzov 1977). The slow rates of population growth necessitate long intervals between periods of observation and measurement to determine the persistence of benthic communities and, particularly, the resilience of the fauna after catastrophes induced, for example, by anchor ice or iceberg scouring. The best way to study these phenomena (also for interaction experiments) is the establishment of trays, panels, cages and similar designs at the seafloor as has been done in the sponge community of McMurdo Sound (Dayton & Oliver 1978).

To our knowledge, only one long-term experiment (in McMurdo Sound) and a few short-term experiments have been carried out with settling plates. Some of these have never been properly published: D. Gerdes (pers. comm.) brought out a settling plate array at 670m depth in the Weddell Sea which after one year showed no signs of colonization. Rauschert (1991) did the same in shallow water in Maxwell Bay, King George Island, where most of the plates were lost. The remainder was taken up after 3 yr and revealed a rich colonization by solitary ascidians almost 30cm in size, synascidians, bryozoans, sea urchins (*Sterechinus*), sponges, turbellarians, serpulid polychaetes, various motile crustaceans, diatoms, and a red alga (*Phycodris*). Total wet mass (alcohol preserved) amounted to $40g \cdot m^{-2}$ on a floating asbestos cement plate whereas a soft plastic plate lying on the bottom carried only a biomass of $20g \cdot m^{-2}$. Moyano (1984) reported that settling plates exposed at 10–40m depth in McMurdo Sound were colonized by 46 bryozoan species, but no data on exposure duration were presented.

The only fully successful experiment (Dayton 1989) refers to plates which were exposed in McMurdo Sound in 1974. Between 1974 and 1977 the plates collected only two serpulid polychaetes, and they were reported to be bare in 1979. However, in 1984 all the settling surfaces were heavily covered with several species of bryozoans, hydroids, soft corals, and sponges, among them *Homaxinella balfourensis*. The most interesting fact is that these sponges colonized floating substrata as much as 30m above the bottom in 1984, although they had never colonized them during the 1970s when the sponge settled heavily on the natural bottoms. Since the larval type is as yet unknown but supposed to be demersal, the larvae might have been released by those sponges that were uplifted by anchor ice which

in 1984 was particularly heavy (Dayton 1989). An ENSO influence on the events in 1984 has been hypothesized by Dayton (1989), which is corroborated by Rauschert's (1991) data of the rapid settlement of benthic fauna in Maxwell Bay that occurred also during the particularly heavy ENSO cycle 1982–84.

In the dense infaunal shallow-water community in McMurdo Sound (Dayton & Oliver 1977, see p. 258) the early recovery period of benthos during succession started with a phase characterized by motile peracarid crustaceans and fugitive polychaete species similar to what has been documented in temperate soft-bottom communities, whereas the subsequent successional stages lasted about three times longer than in temperate areas (Oliver et al. 1976). No further information seems to be available on experimental soft-bottom trays although at least one other attempt has been made (Gallardo & Retamal 1986). At Port Foster, *Echiurus* increased in 1972 as a clearly opportunistic species after volcanic eruptions (Gallardo et al. 1977) in a similar way as this genus does in the North Sea after ice winters (Rachor & Bartel 1981). In the long-term, these processes can only be followed experimentally. Experimental manipulation would also be useful in the intertidal (Castilla & Rozbaczylo 1985).

It seems as though experimental work both on hard- and soft-bottoms in the Antarctic might require some patience but might then be particularly rewarding because in this ecosystem the normally very slowly changing fauna, where even parasites have to adapt to the slow development of their hosts (Wägele 1990), seems to have a tendency to sudden proliferation. To what extent this may hold true also for deeper waters is not known; areas where the benthos is disturbed by iceberg scouring may take years (probably rather decades or centuries?) to re-establish themselves (Picken 1984). The shallow-water experiments in McMurdo Sound were discontinued in 1978 but the experimental designs remained *in situ*, leaving an opportunity for future checks at large time intervals (5–10 years; Dayton & Oliver 1978). There is an urgent need for deep water investigations of this kind in Antarctic waters.

Biotic interactions/trophic dynamics

Pelagobenthic coupling: food input from above

A general overview of particle flux and sedimentation in the Antarctic has been given by Honjo (1990) and Schalk et al. (1993). Annual vertical flux rates vary between $0.133 \text{ gC} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and $130 \text{ gC} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ although the majority of figures range between 5 and $30 \text{ gC} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Schalk et al. 1993). While some early studies suspected very high primary production in the Southern Ocean (e.g. El Sayed 1971, 1988), more recent papers have stressed the extremely seasonal nature and short duration of high productivity conditions in the water column as opposed to very poor conditions in the pelagic zone below permanent packice during the remainder of the year (for an example see Fig. 5). The most spectacular case of Antarctic waters in winter being almost devoid of particles was reported on Polarstern cruise ANT V/1–3, when a Secchi disc depth of 79 m was measured (Elbrächter et al. 1987).

Inshore waters of Signy Island (South Orkneys) are characterized by a very dense but brief summer bloom of diatoms lasting 8–10 weeks, and slight productivity associated with very

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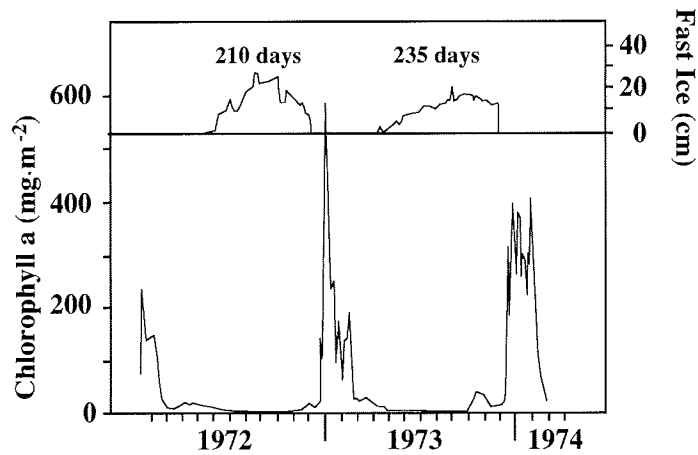


Figure 5 Annual cycle of chlorophyll *a* biomass and fast ice thickness in Borge Bay, Signy Island, South Orkney Islands. (Redrawn from Clarke 1988 after Whitaker 1982).

low biomass at other periods of the year (Clarke 1988). In the southeastern Weddell Sea a sediment trap at 250m depth, above a bottom of 630m, registered three sedimentation pulses in a 54-day period in January and February 1988, with different components predominating in the sedimenting material: faecal pellets of different sizes, krill faecal strings, full and empty diatom cells (Bathmann et al. 1991). Sedimentation rates in this area changed with the direction of the currents; vertical flux was stronger while currents perpendicular to the coast prevailed. Krill faeces contributed significantly to the first sedimentation event whereas the second pulse was due mainly to empty diatom frustules and minipellets likely to be produced after dinoflagellate feeding (Bathmann et al. 1991). The change may have been brought about by intrusion of "warm deep water" onto the continental shelf and slope, and mixing with the coastal current (Fahrbach et al. 1992). Sharp annual patterns of primary production have also been reported from McMurdo Sound (Barry 1988, Howard-Williams et al. 1990); however, faecal pellet fluxes were extremely low in this area compared with other regions of the Southern Ocean (Dayton 1990).

The number of organisms living in the sea ice may exceed those in the water column by several orders of magnitude (Spindler 1990). As in the Arctic (Carey & Boudrias 1987), detrital fallout from the sea ice may be very important to benthic communities at certain times (Dayton 1990), particularly during the period of the year when the packice retreats and melting processes occur at the receding ice edge (Bathmann et al. 1991). Observations in the Weddell Sea ice edge region just north of 60°S (Dieckmann 1987) have shown, however, that ice associated productivity may extend well into the winter since there is sufficient light at the ice edge to drive photosynthesis even in August and September. Below permanent sea ice, a substantial portion of the diatom species found in sediment traps were representative of ice algal species (Leventer & Dunbar 1987), and the ice algae may contribute as much as 30% to the total biomass production of the South Polar Sea (Spindler & Dieckmann 1991).

Patterns of decomposition of particulate organic matter arriving at the seafloor appear to be different in the Arctic and Antarctic polar ecosystems. Despite temporary high inputs from the sea ice and water column and, supposedly, slow bacterial activity carbon is not

accumulated in the sediment (Dayton 1990). Epibenthic suspension feeders are dominant over wide areas of the Southern Ocean despite the fact that there seems to be little material to be filtered during most of the year. Living "on the second floor", i.e. on other organisms, which is a common and widespread behaviour in Antarctic waters (Bullivant 1967, Dayton 1990), may not only serve as a protection against predators, but may also be a response to food shortage at certain times. Epizoic life has been found on motile fauna, e.g. foraminiferans living on scallops (Mullineaux & DeLaca 1984), or gooseneck barnacles (*Scalpellum*) living on the stone crab *Paralomis* (own obs.). Brey et al. (1993), in their study of the bivalve *Lissarca notorcadensis* living on sea urchin spines, concluded that the food input from the water column was insufficient to cover the requirements of these bivalves (as inferred from their production), and suggested lateral advection of suspended matter as an additional food source. The rôle of lateral advection and re-suspension is largely unknown although it is supposed to be important (Berkman et al. 1986, Dayton 1990).

Feeding habits of benthic fauna

The study of the trophic rôle of benthic animals has been quite intense for some taxa (such as crustaceans) in the South Polar Sea whereas we do not know anything about the feeding habits of others. While there is no doubt about the dominant rôle of epibenthic suspension feeders in structuring benthic communities in the Antarctic as compared to Arctic benthos (Knox & Lowry 1977, Hempel 1985), the part that is, for example, played by various size fractions of small plants (nano- and picophytoplankton) in the food of these organisms, has received little attention.

The study of food and feeding habits of Antarctic benthos have received considerable attention, since they may explain part of the apparent discrepancy between seasonally limited food resources and the existence of a rich benthic life. Aquarium observations (especially the use of cool containers working approximately at ambient temperature) have greatly contributed to the understanding of trophic interactions.

A widespread predilection for necrophagy, both obligatory and facultative, among amphipods, holothurians, gastropods, ophiuroids, echinoids and nemerteans has been observed by various authors (Arnaud 1970, 1977, 1992, Presler 1986). Necrophagy is not such a common trait in the Arctic benthic fauna which has evolved more recently (Picken 1984). In Admiralty Bay (King George Island) nearly 300 000 specimens of animals belonging to almost 100 taxa were caught, 23 taxa of which were proven, and 10 further taxa were suspected, to be scavengers. Of the clearly necrophagous animals most species were seastars (11 spp.), amphipods (5) and gastropods (3) (Presler 1986).

Amphipods are the best recently investigated benthic group in the Antarctic in terms of feeding habits, both from aquarium observations and stomach content analyses. Herbivorous species, mainly gammarideans, are common only in areas where there are macroalgae, especially in the Subantarctic (Knox & Lowry 1977). With a few exceptions such as *Ampelisca richardsoni* which is a detritivore, most amphipods in the Weddell Sea are either scavengers, predators or omnivores; all of these groups including the detritus feeders can utilize food resources the year round (Klages 1991). The families Lysianassidae, about 150 species in the Antarctic most of which are scavengers, Eusiridae (ca. 110 spp.) feeding mainly on motile macrozoobenthos and Iphimediidae (ca. 75 spp.) feeding predominantly on epibenthic suspension feeders, contribute > 55% of all gammarids known hitherto from

the Antarctic (Klages 1991). Some of the predators are highly specialized which is also reflected by the morphology of their mouth parts: *Bathypanoploca schellenbergi* (Stilipedidae) feeds on holothurians, *Maxilliphimedia longipes* (Iphimediidae) and *Parandania boeckii* (Stegocephalidae) feed on coelenterates. *Echiniphimedia hodgsoni* feeds on sponges (Coleman 1989a, c, 1990b), whereas *Gnathiphimedia mandibularis* feeds exclusively on bryozoans (Coleman 1989b, Klages & Gutt 1990b). The latter species competes with the echinoid *Sterechinus neumayeri* and some gastropod species (Klages 1991). *Paraceradocus gibber* (Gammaridae), which was suspected to be detritivorous by Coleman (1989a), seems to be rather a carnivore in the eastern Weddell Sea; like *Epimeria robusta* and *Gnathiphimedia mandibularis* it spends long periods inactive in the aquarium. *G. mandibularis* can survive 6 months without its natural (bryozoan) food (Klages & Gutt 1990a). *Epimeria rubriques* discovered only in the 1980s despite its large size and conspicuous pink colour, is an ambush predator (Broyer & Klages 1991) whereas *Eusirus perdentatus* and *E. properdentatus* (Eusiridae) are predators which "sit-and-wait" motionless at the bottom until a prey comes by. Then they immediately develop high activity levels for a short period of time. This seems to be an optimal (i.e. economical) foraging strategy under the special conditions of the Antarctic (Klages & Gutt 1990a). Different feeding habits within one family have been shown for two *Orchomene* species (Lysianassidae) in McMurdo Sound: *O. plebs*, living in deeper water, is a scavenger whereas *O. pinguides* preys on invertebrates, particularly on planktonic copepods which approach the bottom in winter (Slattery & Oliver 1986).

Among the isopods, the more developed Arcturidae live as filter feeders on phytoplankton and detritus. They are passive filterers without having the ability to produce a current, but their filtering apparatus is highly sophisticated (Wägele 1987b; Wägele & Brandt 1992). Most isopods, however, belong to higher trophic levels and seem to be similarly independent as most amphipods of the seasonality of primary production (Wägele & Brandt 1992). *Serolis polita* (Serolidae), for example, is a predator with an unspecialized diet in which amphipods and polychaetes predominate (Luxmoore 1985), the fish parasite *Gnathia calva* (Gnathiidae) sucks blood (Juilfs & Wägele 1987). Further information on the food of Antarctic isopods is presented in Wägele & Brandt (1992).

Most Antarctic shrimps (Decapoda, Caridea) seem to be omnivorous (Gorny 1992) as are most of their relatives in temperate waters. The Subantarctic shrimp *Nauticarid marionis* off Prince Edward Islands, which forms a suprabenthic layer extending 5–10m above the bottom, and the larvae of which perform diel vertical migrations, holds a key rôle in making pelagic and benthic production available to large predators. The megalope larvae use phytoplankton directly as a food source while the adults do so indirectly by grazing on benthic suspension feeders (bryozoans, foraminiferans, corals). *N. marionis* is a major component of the benthic community, being second in biomass only to bryozoans, and is a major prey for penguins and other seabirds (Perissinotto & McQuaid 1990). Krill (*Euphausia superba*), normally an inhabitant of open waters or living in or close to the packice, have occasionally been observed to form similar layers just above the seafloor, and sediment has been found in their stomachs (J. Gutt & V. Siegel pers. comm.). Due to the large size and migration capability of the krill swarms such aggregations may not only contribute locally to the uptake of suspended matter close to the bottom, but also to the exchange between the benthic and pelagic zones.

The stone crab *Lithodes murrayi* (Lithodidae) near Crozet Islands has a very diverse diet, consisting mainly of hydroids, polychaetes, bryozoans and bivalves. This crab is largely opportunistic (including necrophagy) and its trophic function is similar to that of brachyuran crabs and pagurids in temperate, and of amphipods and isopods in (high) Antarctic waters

(Arnaud & Miquel 1985). Large, carnivorous lithodid crabs are almost totally restricted to the Subantarctic. The brittleness of molluscan shells may be not only the result of an increased cost of calcification, but also a response to the lack of large decapod predators (Clarke 1990a). Antarctic scallops, for example, are exposed to very low mortality from predators in the Ross Sea (Stockton 1984, Berkman 1990).

Many gastropod species in the eastern Weddell Sea are omnivorous (e.g. Buccinidae) or carnivorous (e.g. Turridae and septibranchiate bivalves, Hain 1990). *Harpovoluta charcoti* (Volutidae), which always lives with the commensal actinian *Isosicyonis alba*, is a predator and scavenger (Arnaud 1978). In this group, too, herbivores such as the limpet *Nacella concinna* are restricted to areas where algae grow (Castilla & Rozbaczylo 1985). Among Antarctic nudibranchs, the Austrodoridae and Aegiretidae are exclusively sponge eaters. *Aegires albus* feeds on calcareous, *Austrodoris kerguelensis* on siliceous sponges, *Tritoniella belli* feeds on synascidians, and *Tritonia* spp. feed on *Cephalodiscus* (Tentaculata). Bathydoridae (3 spp.) are omnivorous whereas *Notaeolidia subgigas* had eaten exclusively hydrozoans (H. Wägele 1988).

Different ecological niches of various holothurian groups have been described by Gutt (1988, 1991a). Some species have an almost exclusively epizoic way of life. The dendrochirotid holothurians, living mainly on the shelf of the southeastern Weddell Sea, are sessile suspension feeders whereas the aspirochirotid and elasipodid sea cucumbers living on the deeper soft bottoms of this area are deposit feeders (Gutt 1991a).

Other echinoderms that have received considerable attention in a trophic context are brittle stars (Ophiuroidea) and starfish (Asteroidea). Most ophiuroids in the Antarctic are benthos or zooplankton predators (Dearborn 1977, Fratt & Dearborn 1984, Dearborn et al. 1986). For example, *Astrotoma agassizii*, living off South Georgia and the Antarctic Peninsula, feeds on copepods, mysids, chaetognaths and euphausiids (Dearborn et al. 1986). The copepod food, all calanoids which are generally considered pelagic, is particularly interesting as it demonstrates how carbon fixed in surface waters can be transferred to the benthos. *Ophionotus victoriae* (Ophiuridae) ingests benthic microflora (Kellogg et al. 1983) but also derives its diet from a variety of other phyla including krill *Euphausia crystallophias* (Dearborn 1977). A variety of feeding methods is used but not suspension feeding (Fratt & Dearborn 1984). The starfish *Labidiaster annulatus* in the Scotia Arc region is a predator and scavenger which consumes macroinvertebrates and even small fishes. *Odontaster validus*, the most abundant species, also has opportunistic feeding habits, whereas other asteroids (*Acodontaster hodgsoni*, *Perknaster fuscus antarcticus*) which feed on sponges, are very restricted in their diets (Dearborn 1977).

Most "worm" groups have received little attention in the trophic context. *Priapulus tuberculatospinosus* from King George Island have sponge spicules, polychaete remainders (Nereidae) and, occasionally, gastropod shells in their intestines (Rauschert 1986). In the Weddell Sea, eight polynoid polychaetes investigated in more detail were found to be predatory, feeding mainly on ophiuroids, crustaceans and polychaetes (M. Stiller, pers. comm.).

It can be concluded that a large proportion of Antarctic benthic organisms has developed a high degree of independence from fluctuating food conditions.

Benthos as food for other organisms

Contrary to Arctic waters, the South Polar Sea lacks many bottom-feeding fish groups almost completely (flatfishes, gadoids, sharks, rays). Mammals that could be called benthos

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feeders such as walruses and gray whales, and predominantly benthophagous seabirds, are also largely absent in the Antarctic (Dayton 1990). At the South Shetland Islands the limpet *Nacella concinna* is preyed upon by the gull *Larus dominicanus* (Castilla & Rozbaczylo 1985). At the Prince Edward Islands the shrimp *Nauticaris marionis* contributes 26% by mass to annual consumption of gentoo penguins and 19% to that of imperial cormorants. In 1983–84, this shrimp contributed 49% and 60%, respectively to all crustacean items identified in the stomachs of macaroni and rockhopper penguins. It is also found in the stomachs of fish and sea-stars (Perissinotto & McQuaid 1990 and refs therein). Benthic octopods may provide significant portions of the diets of Weddell seals and elephant seals (Clarke & Macleod 1982a,b, *vide* Kühl 1988). The mysid *Antarctomysis maxima* was found in crabeater seal droppings, and amphipods as well as decapod crustaceans in leopard seal droppings, near Davis Station (Green & Williams 1986). Weddell seals have also been observed to take benthic shrimps off McMurdo (Dearborn 1965) and off Davis (Green & Burton 1987) but clearly prefer pelagic food in deeper water as off the continental ice edge in the Weddell Sea where the only benthic food consisted of octopodid cephalopods (Plötz 1986, Plötz et al. 1991). Emperor penguins in this area did not feed on benthos at all (Klages 1989).

Benthic food is taken by various fish families in Antarctic waters. Most Nototheniidae feed on epifauna such as amphipods and errant polychaetes (Casaux et al. 1990, Eastman 1985, Schwarzbach 1988), but even species which are considered to be typical benthos feeders such as *Nothothenia neglecta* may predominantly feed on krill, *E. superba*, when it is abundant close to the seafloor (Barrera-Oro & Casaux 1990, Casaux et al. 1990) (Fig. 6). Artedidraconidae feed on motile epifauna such as polychaetes, amphipods and isopods (Wyanski & Targett 1981, Duarte & Moreno 1981, Daniels 1982, Schwarzbach 1988). Among the Bathydraconidae, *Prionodracon* has the largest share of benthic food (Schwarzbach 1988).

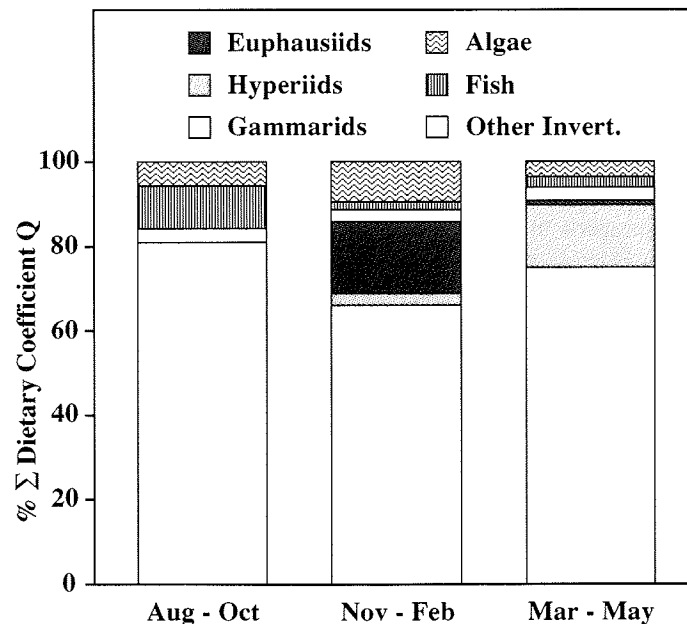


Figure 6 Seasonal variation in food consumption of *Notothenia neglecta* in Potter Cove, King George Island. Share of several taxa in terms of the dietary coefficient Q (= %number · %biomass of each prey type). (Redrawn from Casaux et al. 1990).

Harpagifer georgianus antarcticus feeds exclusively on amphipods at King George Island (Otto & MacIntosh 1992). The normally sparse endofauna in the high Antarctic is rarely eaten by fish; the same is true for holothurians no matter whether they are endo- or epibenthic (Gutt 1991c). Benthos feeding fishes generally have a wider food spectrum in Antarctic waters than plankton feeders (Schwarzbach 1988).

Among the five main trophic groups of fish distinguished by Kock (1992) in the southeastern Weddell Sea, three had major shares of benthic (including epibenthic) food in their diets. Plunderfish were found to be primarily benthos feeders, skates fed on benthos and fish, nototheniids revealed no preference for certain food categories, and dragonfish fed on epibenthos and plankton. *Prionodraco evansii* had a 10% share of infauna and epifauna. In the near-bottom layer the prey species most commonly taken were shrimps (*Notocrangon antarcticus* and *Chorismus antarcticus*). *Trematomus lepidorhinus* took epibenthos and a considerable portion of infauna, *Racovitzia glacialis* fed almost entirely on epibenthos, with equal shares of shrimps and mysids. Bottom feeders in the southeastern Weddell Sea took predominantly amphipods, isopods and polychaetes, however in different composition. Only *Trematomus scotti* contained priapulids and brittle stars. Resource partitioning was found to be the rule; mechanisms mitigating competition for food are feeding in different areas, vertical segregation of feeding localities and food (benthos/epibenthos/plankton) and taking different portions or sizes from the same prey. Comparing the results from the southeastern Weddell Sea with those from former studies in the Scotia Arc it can be seen that fish species which are not represented in both areas have morphologically similar equivalents feeding on similar food items (Kock 1992). However, benthic or epibenthic feeding fish species are more numerous in the high Antarctic. Further data on trophic relations of coastal fish, also with reference to the benthos, have recently been published by Gröhsler (1992 *vide* Kock 1992).

Other interactions and interaction experiments

The lack or scarceness of certain groups in the Antarctic, mentioned in the trophic context, is also important from a disturbance point of view. Among the invertebrates there is not only a lack of reptant decapods in most parts of the South Polar Sea but also – in comparison to the Arctic – a relative scarceness of surface-burrowing species such as echinuroids, sipunculids, priapulids, polychaetes and echinoderms (Dayton 1990); the fish have already been mentioned. Although there is some degree of biotic disturbance, and although this may be quite important locally (Zamorano et al. 1986, Gallardo 1987a, see pp. 263f), most Antarctic bottoms “lack the persistent overwhelming disturbances characterizing the Arctic” (Dayton 1990).

The only serious *in situ* interaction studies on Antarctic benthos have been done in McMurdo Sound (Dayton et al. 1974, Dayton 1979, 1989, Oliver & Slattery 1985). Fifty cages, each with an adjacent control, were exposed in 1967 to define relative growth rates of different sponge species and the feeding rates of their predators. In some experiments, predators were excluded from, or included in, sponge complexes.

Dayton et al. (1974) stress predation as the cardinal factor in preventing space monopolization by a single species in shallow waters of McMurdo Sound; this is similar to what occurs in intertidal rocky communities. For all sponge species (which are dominant in this area), competition for space does not seem to be an important factor influencing the patterns of distribution and abundance.

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Due to its rapid growth, the sponge *Mycale acerata* is a potential dominant in competition for substratum space on shallow (30–60m) bottoms of McMurdo Sound. However, it is prevented from dominating the space resource by the predation of the 2 asteroids *Perknaster fuscus antarcticus* and *Acodontaster conspicuus*. *A. conspicuus* and the dorid nudibranch *Austrodoris mcmurdensis* are most important predators on 3 spp. of rosselid sponges. Despite this (relatively heavy) consumption, and the fact that these sponges have no refuge in growth from predation by *A. conspicuus*, the rosselid sponges have developed large standing stocks. This seems to be result of predation on larval and young *Acodontaster* and *Austrodoris* by *Odontaster validus*. There is also predation on adult *A. conspicuus* by *O. validus* and the actinian, *Urticinopsis antarcticus* which annually kills about 3.5% of the population (Dayton et al. 1974).

Despite the predation load from different species, a supply of 1386yr of *Rossella racovitzae*, 311yr of volcano sponge, and 163yr of *Tetila leptoderma* were estimated to be available to sponge consumers in McMurdo Sound (Dayton et al. 1974). Energy contents of sponges in McMurdo Sound were found to be low. Lipids and carbohydrates (combined) contributed to less than 25% of the overall energy, whereas insoluble protein accounted for the greatest contribution. More than half of the 16 investigated sponge species were toxic, the most toxic species being *Mycale acerata* and *Lencetta leptorhopsis*. The asteroid *Perknaster fuscus antarcticus* specializes on the fast-growing, highly toxic *Mycale acerata*, but most Antarctic sponge-eating predators appear to be generalists which feed on the more abundant, non- to mildly toxic sponge species (McClintock 1987).

Under certain circumstances, however, competition for space may be important. Dayton et al. (1974) refer to arborescent growth as a morphological adaptation of certain sponges which allows them to grow on relatively narrow bases, thus ameliorating competition with the more prostrate forms. The small bivalve *Lissarca notorcadensis* normally settles on the spines of the cidaroid echinoid *Notocidaris* sp. or on branches of hydrozoan and bryozoan colonies. On the cidaroids they are strongly concentrated on the upper spines; juvenile *Lissarca* rather drift away than settle on the lower spines of their parents' sea urchin. The negative relation between the biomass of these bivalves already present and recruitment success gives strong evidence that there is intraspecific competition for space. Furthermore, there may be interspecific competition as well since colonial anthozoans and bryozoans also prefer the upper spines for settlement. Bivalves and other colonists are mutually exclusive in the same area of a cidaroid spine (Brey et al. 1993).

The dense benthic assembly near McMurdo Station studied by Oliver & Slattery (1985) is also maintained principally by predation. The tanaid *Nototanaid dimorphus* and the phoxocephalid amphipod *Heterophoxus videns* prey on larvae, juveniles, and small individuals of polychaetes. This assembly has a well-developed vertical canopy structure where some species, such as the actinian *Edwardsia meridionalis*, are capable of consuming larvae while they themselves sustain a modest predation from fishes. Small individuals of soft-bodied infauna are rare in this dense infaunal assemblage. Since most of the soft-bodied species have a size refuge from crustaceans, the assemblage is dominated by large and relatively long-lived forms. Its persistence is related to the absence of grovelling or disruptive bottom-feeding fishes and mammals referred to above (Oliver & Slattery 1985, Dayton 1990).

From a caging experiment, Zamorano et al. (1986) stated that large bivalves (*Laternula elliptica*) unburied and accumulated at the surface in the Palmer Archipelago were consumed

by six different invertebrate species. These bivalves which normally live deeply buried (> 50 cm) lack avoidance and escape responses like those of scallops or of the Subantarctic limpet *Nacella edgari*, which successfully flees the seastar *Anasterias perrieri* (Castilla & Rozbaczylo 1985).

Physiology and autecology

Polar organisms pay for their ability to live at very low temperatures ("fine tuning", Clarke 1990a) with a limited thermal tolerance. This stenothermy seems to be more restrictive for Antarctic invertebrates than for their Arctic counterparts; for example, the lethal temperature for the giant isopod *Glyptonotus antarcticus*, as for many other invertebrates in the Antarctic, is +6°C whereas its Arctic counterpart *Saduria entomon* survives up to 20°C (George 1977, Arnaud 1985). Limpets (*Nacella concinna*) from the intertidal of Signy Island have a slightly larger temperature range up to +9°C (Peck 1989).

While short-term and seasonal changes of seawater temperature are small compared with other marine ecosystems (see p. 247), the temperature changes from the early Tertiary until today were about 8°C, with some intermediate periods of more rapid change (Clarke 1990a). This is quite a difference but equivalent to only 0.003°C in a thousand years, an almost negligible change in relation to what many benthic organisms cope with in much shorter times nowadays. This should not have posed a major challenge to the marine fauna on an evolutionary time scale (Clarke 1990a).

Moreover, most of the benthic fauna in the world ocean lives at relatively low temperatures. The mean temperature of all seawater is only 3.8°C; thus, cold water is not an unusual environment for marine organisms (Clarke 1988). However, polar organisms must be able to grow, reproduce, feed and evade predators – among them many warm-blooded animals – at temperatures close to or even below 0°C. From the start of physiological studies in the Antarctic attempts have been made to explain how this may have been achieved.

The first idea finally turned out to be erroneous. The concept of "cold adaptation" as a metabolic adaptation of coldwater poikilotherms (for references see Clarke 1980, 1983, 1991), which had raised many discussions from the 1950s to the early 1970s, was increasingly doubted from the mid-1970s when the first well-controlled experiments with polar benthic invertebrates were published (White 1975, Maxwell 1977, Ralph & Maxwell 1977a, b, Everson 1977, Ivleva 1980). More recent experiments have confirmed these doubts (Houlihan & Allan 1982, Davenport 1988, Peck 1989). All these experiments indicated that former findings in favour of metabolic "cold adaptation" were apparently based on experimental artefacts. When compared to their temperate relatives, for example, polar crustacean species reveal a low level of metabolic activity at ambient temperature, which should be expected empirically from the temperature dependent behaviour of physico-chemical reaction rates (Maxwell & Ralph 1985).

Low metabolic activity has usually been measured as oxygen consumption rates, and data referring to benthic species have been published e.g. for isopods (Luxmoore 1984), amphipods (Klekowski et al. 1973, Klages 1991, Aarset & Torres 1989), caridean shrimps (Maxwell & Ralph 1985), prosobranch gastropods (Houlihan & Allan 1982, Clarke 1990b), bivalves (Davenport 1988) and brachiopods (Peck et al. 1986, 1987). They all coincide in that no elevation of oxygen consumption attributable to evolutionary history or zoogeographical position of polar animals is detectable. Recently, Clarke has argued, furthermore, that

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respiration is a particularly misleading indicator of temperature compensation (both in evolutionary terms and in acclimation experiments) because it represents the summation of many processes each of which may react differently to temperature; the use of respiration rates to assess temperature compensation should therefore be abandoned (Clarke 1990b).

Complete energy budgets for Antarctic benthic animals, covering all aspects of population dynamics, activity budgets, excretion and secretion, faecal egestion and, where applicable, calcification costs have not yet been constructed. Where part of these data are available as, for example, *Nacella concinna* (Clarke 1990b) or for the isopod *Serolis polita* (Luxmoore 1985), they are restricted to the summer months or do not cover all energy sinks. However, there is no reason to compensate for low temperatures except for calcification, a metabolic cost that indeed increases at lower temperatures, but these costs have never been estimated. Polar shelled molluscs tend to be small and brittle, which may be a consequence of this (Nicol 1967, Clarke 1990a); however, another reason may be the lack of decapod predators which at lower latitudes exert an evolutionary pressure for larger and more solid shells (Hain 1990). Dwarfing in Antarctic (and deep-sea) organisms often occurs in species that secrete calcium carbonate (Lipps & Hickman 1982). As to other metabolic costs, there is even a distinct energetic advantage of living in cold water (Clarke 1983, 1987a, b): the cost of basal (i.e. maintenance, resting or "standard") metabolism is about six times greater at 30°C than at 0°C.

Since basal metabolism represents energy that is ecologically wasted, in the sense that it cannot be used for growth, activity or reproduction, for a given intake of energy from food, relatively less is "wasted" at low temperatures. This means that, all other things being equal, ecological growth efficiencies will be higher in polar waters (Clarke 1987b).

With the costs of other aspects of metabolism (other than basal) such as locomotor activity, growth or reproduction being roughly comparable for invertebrates living in polar, temperate and tropical marine environments (Clarke 1990a), and basal metabolism being "cheaper" in cold water, immediately the question arises: Why, then, do polar invertebrates (and fish) not grow more rapidly, reproduce earlier and more frequently, move faster and more often than their temperate or tropical counterparts?

There seem to be two answers: incomplete adaptation at the molecular level, and seasonal food limitation (see p. 251). The first alternative is difficult to confirm or reject because of the almost complete lack of biochemical studies on Antarctic benthic invertebrates. Clarke (1991) presents the example of microtubules (however, again of fish) which function at polar temperatures and which must have been subject to some kind of modification during evolution, and refers to polar foraminiferan cold-stable microtubules reported by Bowser & DeLaca (1985). Recently, Dittrich (1990, 1992a, b) has shown that caridean shrimps and isopods from the Weddell Sea require a significantly (about one-half) lower activation energy of proteolytic enzymes at polar temperatures than related species from lower latitudes. In the few cases where the growth of an Antarctic organism is much faster than that of related species (e.g. the sponge *Mycale acerata*; Dayton et al. 1974, or certain ascidians: Rauschert 1991), we can infer that growth has evolved compensation for temperature, but in the normal case where annual growth rates in polar organisms are low we cannot simply conclude that this is due necessarily to direct limitation by temperature (Clarke 1991), since in several species strong seasonal oscillations in growth have been observed, which cannot be due to temperature oscillations (see p. 282). While sluggishness of most Antarctic

invertebrates kept in aquaria is obvious (Arnaud 1977, calls it “Antarctic lethargy” and compares it to hibernation), even extremely inactive species such as isopod parasites (*Aega antarctica*: Wägele 1990, *Gnathia calva*: J. W. Wägele 1988) can be quite active when searching for their hosts. Amphipod scavengers, especially Lysianassidae, often rest motionless for long periods but become hyperactive (and quite fast!) when there is a food stimulus. There are also distinct specific differences: *Orchomene plebs* approach a food source much more rapidly than *Waldeckia obesa* and are always found in much higher numbers in baited traps (Klages 1991). We can hypothesize that while there must have been some kind of temperature compensation on a molecular level for the Antarctic fauna during its evolution, as can be seen from the relative richness of the fauna present, this compensation may have been only partial for many animals. Moreover, without further biochemical investigations, we can say very little about the mechanisms by which this adaptation to low temperatures has been achieved (Clarke 1987a).

The second alternative indicates that in many cases temperature – at least where its seasonal oscillations are small – is not the primary factor at all. Instead it is food limitation. Parry (1983) presents some evidence for a general trend towards lower metabolic rates via reduced growth rates in poikilotherm animals if food is scarce. The seasonally restricted availability of food resulting from short summer periods of phytoplankton production (Picken 1984, Clarke 1988, Bathmann et al. 1991, Arntz et al. 1992) may force Antarctic organisms to save metabolic costs by growing slower, reproducing later and exhibiting a lower locomotor activity. However, temperature plays quite an important part as a secondary factor, since the low ambient temperatures cause a shift towards low basic metabolic rates and may enable Antarctic animals better to survive predictable but seasonally fluctuating levels of food (Clarke 1980, Brey & Clarke 1993).

The importance of food availability can best be seen in species where growth is strongly seasonal. On an annual basis growth is very slow in Antarctic benthos even in species which have been described as “relatively fast growing”, such as the scallop *Adamussium colbecki* which grows an order of magnitude more slowly than temperate scallop species (Berkman 1990). However, when growth is actually in progress, it may proceed relatively fast as has been shown for the shrimp *Chorismus antarcticus*, the gammarid *Paramoera walkeri* (Sagar 1980), the bivalve *Lissarca miliaris* (Clarke 1988) and other species. (Note that the (biochemical) *capacity* for faster growth exists, at least in these cases!)

Reproduction of Antarctic animals, too, is closely tied to the seasonal cycle of food availability in some cases whereas it is totally uncoupled in others (see p. 282). In the first case energy is deposited in the ovary only during summer, in the second ovary development is slow but steady over a long period of time. The latter is especially the case in animals that live at higher levels of the food web and are thus sufficiently uncoupled from the seasonal supply of food (White 1977, Clarke 1988). Benthic organisms do not appear to need seasonal lipid stores, possibly because their metabolic rates are so low that they do not require such reserves (Clarke 1977, 1982, 1988). The different strategies, and various behavioural adaptations, are treated in some more detail in the next section.

Life history patterns and strategies

Ever since Antarctic marine biologists started to look at life histories, a number of features have been assigned to Antarctic poikilotherms many of which were either deduced from

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animals which had been studied in the Arctic, or were hypothesized against the background of the specific environmental conditions in polar seas as an extremely cold, highly seasonal environment where primary production is confined to a brief period during summer (White 1984). These features comprise

- prolonged gametogenesis
 - delayed maturation
 - seasonal reproduction
 - low fecundity
 - large yolky eggs
 - non-pelagic development
 - brooding, brood protection, viviparity
 - slow embryonic development
 - advanced newly-hatched juvenile stages
 - slow growth rate
 - seasonal growth
 - large adult size
 - prolonged longevity
 - low mortality
 - low metabolic rate, low activity.
- “Thorson’s rule”
(Thorson 1950, Pearse et al. 1991)

The subject has been dealt with extensively in the older literature, and numerous examples have been given (see, e.g. the reviews of White 1984 and Picken 1984, and papers by Arnaud 1978, Picken 1979a, b, 1980a, b).

More recent literature, especially from the high Antarctic, confirms that the above patterns, which are largely consistent with *K*-strategies, are characteristic of many benthic species in Antarctica while revealing, at the same time, that differentiation is necessary.

Duration of embryonic development; egg sizes

There are large variations in the degree of retardation of embryonic development and maturation from species to species. Very slow rates of embryonic development have been found in Antarctic isopods; *Serolis* sp. (Wägele 1987b) and *Glyptonotus antarcticus* (White 1970) need up to 20 months (as against 1–3 months in temperate species), the parasitic isopod *Aega antarctica* > 32 months (Wägele 1990). In nature *Aega* may have a generation time of at least 13yr: a minimum of 10yr before the females spawn for the first time, another 2.7yr for embryonic development (Wägele 1987b, 1990). The blood-sucking isopod fish parasite *Gnathia calva* also has a very long development cycle (J. W. Wägele 1988).

The duration of embryonic development of gammaridean amphipod species increases exponentially with decreasing habitat temperature. The embryonic development of the giant predatory amphipod *Eusirus perdentatus* lasts a minimum of 14 months (Klages 1993, Arntz et al. 1992). Extremely long intermoult stages (4 months) have been observed in *Epimeria robusta* (Broyer & Klages 1991). Females of the shrimp *Chorismus antarcticus* at South Georgia become sexually mature in their third post-metamorphic summer. Vitellogenesis takes about 6 months, and the large eggs are spawned in January. Then they are brooded by the female for 9–10 months (Clarke 1985). Benthic caridean shrimps from the Weddell

Sea become mature only after 4–6yr when the females spawning for the first time have grown to a considerable size (*Chorismus antarcticus*: 14mm, *Notocrangon antarcticus*: 17mm, *Nematocarcinus lanceopes*: 27mm carapace length). Embryonic development lasts about 1.5yr (first in the ovary; later, after spawning, the eggs are attached to the pleopods). Spawning may be repeated several times in the life cycle, but every second year only (Gorny 1989, Arntz et al. 1992, Gorny et al. 1993).

Much longer developmental time, as compared to related species living in temperate regions, have also been reported for Antarctic molluscs, the extreme case being prosobranch gastropods with a developmental time of about 2yr till hatching (Hain 1990). Juvenile nudibranchs at a size of ca. 2mm also hatch after about 2yr (H. Wägele 1988 & refs. therein). Solenogastres and polyplacophorans have a 3–7 times longer development than their temperate counterparts (Hain 1990, Arntz et al. 1992). Development in the brooding bivalve *Lissarca notorcadensis* takes about 2yr, one year of egg development in the ovary and a second year of embryonic development in the parental mantle cavity (Fig. 7) (Brey & Hain 1992).

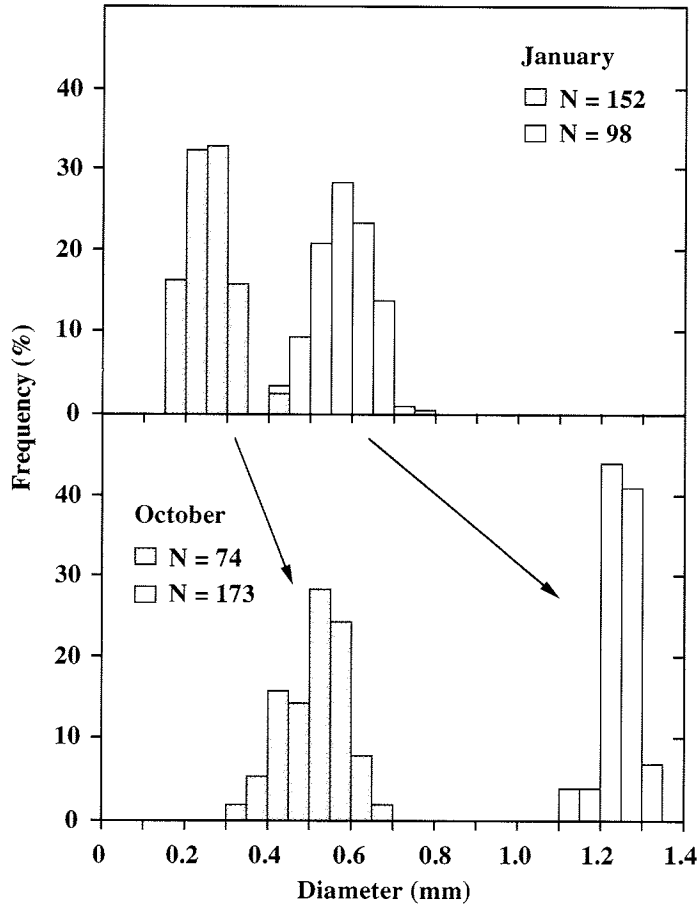


Figure 7 The brooding Antarctic bivalve *Lissarca notorcadensis*. Size-frequency distributions of eggs in the ovary (stippled bars) and of embryos simultaneously brooded in the mantle cavity (white bars) in January and in October (pooled material from several females). Egg and embryo counts are normalized separately to 100%. (Redrawn from Brey & Hain 1992).

Long-lasting metamorphosis in echinoderms has been reported by Bosch et al. (1987) from McMurdo Sound and by Gutt (1991b) for holothurians. The rate of development of the "shallow water" sea urchin *Sterechinus neumayeri* is extremely slow; hatching of ciliated blastulae needs about twice the time after fertilization that closely related temperate species require near their normal ambient temperature. Larvae reared at -1.8 to -0.9°C are capable of feeding 20 days after fertilization and are competent to metamorphose after 115 days (Bosch et al. 1987).

In most cases long developmental times have been found to be connected with large egg sizes and, consequently, low fecundity. Examples include the polychaete *Scoloplos marginatus* (Hardy 1977), mysids, with a low number of offspring (Siegel & Mühlenhardt-Siegel 1988); the amphipods *A. richardsoni*, *P. gibber*, and *E. perdentatus* the egg diameters of which (1.1–2.7 mm) are about 2.5 times greater than those of gammarids in temperate or tropical areas (Klages 1991); octopod cephalopods (Kühl 1988) and other molluscs, with extremes in solenogastres and polyplacophorans where the egg diameters (625–775 μm and 920–960 μm , respectively), are the largest ever found within these groups (Hain & Arnaud 1992). The nudibranch *Bathydoris clavigera* produces only eight eggs of 2.1 mm diameter (H. Wägele 1988). The mature eggs of the holothurians *Ekmocucumis steineni* and *Psolus dubiosus* measure up to 1.0 mm and 1.3 mm diameter, respectively (Gutt et al. 1992). The viviparous Subantarctic brittle star *Ophionotus hexactis* has brood sizes up to 54 juveniles (Dayton & Oliver 1978). While latitudinal clines within higher taxonomic categories have been well known for some time (for amphipods, see e.g. Bone 1972 and Bregazzi 1972), recently also differences in the same crustacean species occurring in the low and high Antarctic have been detected. Caridean shrimps (*Chorismus antarcticus*, *Notocrangon antarcticus*) and the isopod *Ceratoserolis trilobitoides* bear fewer and larger eggs in the southeastern Weddell Sea compared with South Georgia and the Antarctic Peninsula region, respectively (Gorny et al. 1992, Clarke & Gore 1992; Wägele 1987a). Fig. 8 shows egg number and egg mass of *C. antarcticus* for an example. In the bivalve *Lissarca notorcadensis* the number of embryos brooded per female is slightly but significantly higher in the northern Weddell Sea than on the southeastern shelf (Fig. 9) (Brey & Hain 1992).

Brooding and (the lack of) pelagic larvae

The predominance of brooding species in the Antarctic benthos and the "relative absence" of pelagic larvae, with all their advantages under polar conditions and their disadvantages for dispersal and recolonization, have been discussed extensively in the literature (e.g. Picken 1979a, b, 1980b, 1984, White 1984). This discussion dates back to "Thorson's rule" (Thorson 1950). Thorson hypothesized – mainly from evidence collected in the Arctic – that there is a strong general trend towards non-pelagic development and brood production in polar waters due to the insecurity of prolonged larval life in these waters where primary production is restricted to a short period each year.

The general validity of "Thorson's rule" has been challenged recently by Pearse et al. (1986, 1991) and Berkman et al. (1991) because of the increasing number of benthic species found recently with pelagic larvae. Some of these even have planktotrophic larvae (Table 3).

There is a certain danger of overemphasizing these findings, interesting as they may be. As Pearse et al. (1991) state themselves, even excluding those groups such as the peracarids

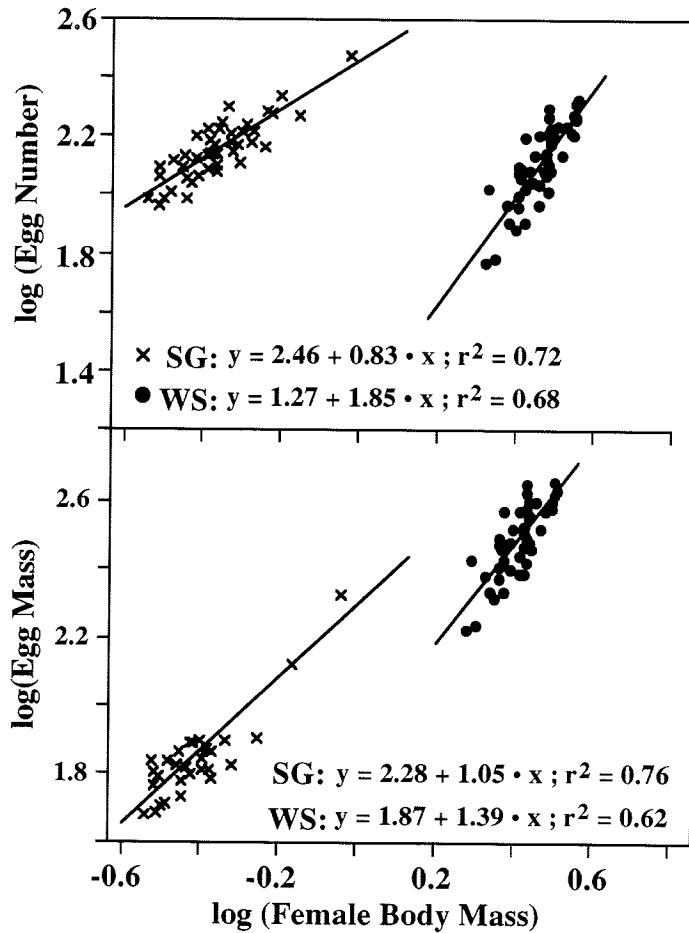


Figure 8 Relation of egg number and egg mass (mg wet mass) to female body mass (g wet mass) in the shrimp *Chorismus antarcticus* at different latitudes (sg: South Georgia, ws: eastern Weddell Sea). (Redrawn from Gorny et al. 1992).

which are brooders in other oceans as well, and which are particularly dominant in the Antarctic, some groups do indeed display unusually high incidences of brooding. Nearly all (43) species of echinoids, mostly cidaroids and spatangoids, are brooders. The “birth giving” brooder *Urechinus mortenseni* even has special brood pouches (David & Mooi 1990). *Sterechinus neumayeri* and the three asteroids listed in Table 3 with their planktotrophic larvae seem to be exceptions. A few asteroids have pelagic lecithotrophic larvae. No pelagic echinoderm larvae have been detected so far in the Weddell Sea in the vicinity of the Antarctic continent.

Brooding is assumed to be a common feature for Antarctic bivalves although it has been documented for relatively few species. Interestingly it is just the common three larger bivalve species in McMurdo Sound (*Adamussium colbecki*, *Laternula elliptica*, *Limatula hodgsoni*) that have pelagic developmental stages. The other, > 60, species of Antarctic bivalves are assumed to have non-planktonic development (Pearse et al. 1986). Among the

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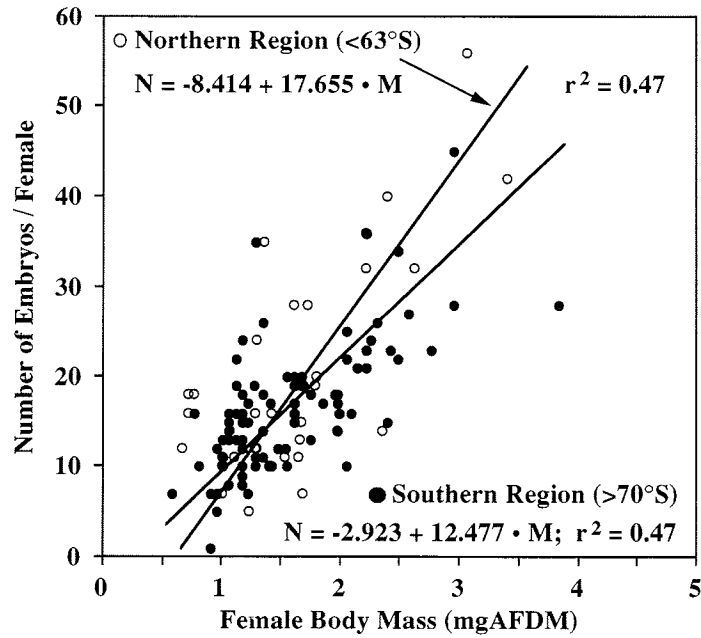


Figure 9 Relation between number of embryos brooded per female and female body mass in the bivalve *Lissarca notorcadensis* in the northern and southern Weddell Sea. (Redrawn from Brey & Hain 1992).

Table 3 Recently detected pelagic larvae (from Pearse et al. 1991, if not otherwise cited).

Embryos	Pelagic Larvae	Taxon	Species	
Pelagic	Planktotrophic	Bivalves	<i>Limatula hodgsoni</i> <i>Adamussium colbecki</i> (Berkman et al. 1991)	
		Polychaetes	<i>Flabelligera</i> sp.	
		Asteroids	<i>Odontaster validus</i> <i>O. meridionalis</i>	
			<i>Porania antarctica</i>	
		Echinoids	<i>Sterechinus neumayeri</i>	
		Nemerteans	<i>Parborlasia corrugatus</i>	
		Pelagic	Lecithotrophic	Actinians
Bivalves	<i>Laternula elliptica</i> (Berkman et al. 1991)			
Asteroids	<i>Acodontaster hodgsoni</i> <i>Perknaster fuscus</i>			
	Not exactly known			Not exactly known
Not exactly known	Not exactly known	Sponges	<i>Mycale acerata</i> <i>Tedamia tantulata</i> <i>Iophon radiatus</i> (Pel. larvae ≤ 3 days? Barthel et al. 1991) Halicionidae <i>Rossella racovitzae</i> (?)	
			Gastropods	<i>Capulus subcompressus</i> – Echinospira (Hain 1990) <i>Marseniopsis</i> sp. – <i>Limacosphaera</i> (Hain 1990)
				Cirripedes

southeastern Weddell Sea bivalves (≈ 50 spp. of 16 families) 12 have been shown to be brooders so far. In some cases very large juveniles may fill up most of their mothers' mantle cavities (Arntz et al. 1992, Hain & Arnaud 1992). Even large neogastropods and opisthobranchs have a non-pelagic development (H. Wägele 1988, Pearse et al. 1991), and intracapsular metamorphosis is the rule with Antarctic gastropods (Hain & Arnaud 1992). Pelagic lecithotrophic development as in *Nacella concinna* (Picken 1980a) is an exception. "Thorson's rule" seems to hold at least for gastropods (Pearse et al. 1991). However, even there surprises cannot be excluded. In the Weddell Sea pelagic, even planktotrophic, larvae are found in two families: the Echinospira of *Capulus subcompressus* (Capulidae) and the Limacosphaera of *Marseniopsis* (Lamellariidae) (Bandel et al. in press). The latter is able to switch from plankton to embryonic deposits when food becomes scarce (Hain & Arnaud 1992).

The two benthic shrimps *Chorismus antarcticus* and *Notocrangon antarcticus* also have pelagic larval stages (Boysen-Ennen 1987, Piatkowski 1987) whereas such stages have never been found of the third common benthic shrimp species in the Weddell Sea, *Nematocarcinus lanceopes* (Arntz & Gorny 1991). Recently the juveniles of the two former species have been reared from the eggs in the Helgoland aquarium (Gorny et al. 1993). A spectacular recent detection were balanomorph barnacle larvae in the plankton at McMurdo Sound (Foster 1989).

We urgently need more data from deep water. From Pearse et al.'s (1991) data it looks as though it is mostly large species living in shallow water that account for the most notable exceptions to "Thorson's rule". Although non-pelagic development may not be as overwhelmingly prevalent among Antarctic invertebrates as believed until a short time ago, the number of pelagic, and particularly of planktotrophic, larvae that have been found is still very small compared with the immense total number of species in the Antarctic benthos. New sampling designs may improve the record to some extent, but the total number of species with pelagic larvae is likely to remain low. In fact, the selective conditions in the Antarctic pelagic rather encourage the evolution of benthic or short-term, non-feeding drifting stages (Pearse et al. 1991).

Growth, longevity and final size

Slow growth, (often) large final size and prolonged longevity have often been mentioned as another facet of living under polar conditions, although there may be some exceptions (George 1977, White 1984). It remains to be finally determined whether slow growth (and development) rates reflect some inherent inability to adapt to low temperature, or are a response to factors not directly related, though correlated, to temperature such as limited seasonal food availability (Clarke 1990a). At the one hand there is an empirical inverse relationship between annual growth rate and maximum size in ectotherms, at the other hand somatic growth is intimately related to reproduction, especially in an area where food is likely to be limited. Mortality, longevity and the body size that can be attained are not only subject to physiological constraints, but also linked to predation pressure (see pp. 268ff). The physiological aspects have been dealt with earlier (pp. 272ff).

Estimates of annual growth rates are available from a restricted number of population dynamic approaches in the field (limited, most likely, because of the remoteness and limited accessibility of the area of study), an even smaller number of field experiments, and from a few successful aquarium experiments. Growth studies on Antarctic benthos in aquaria have

so far been rather a failure for molluscs and amphipods (Klages 1991), but they have provided some useful data for isopods (Luxmoore 1985, Wägele 1990) and caridean shrimps (Maxwell & Ralph 1985, Gorny et al. 1993).

Most Antarctic benthic species seem to correspond to the traditional view of low annual growth rates, large final size and prolonged longevity. The Antarctic crustaceans *Chorismus antarcticus*, *Serolis cornuta* and *S. polita* grow distinctly slower than comparable boreal species (Luxmoore 1984). Caridean shrimps also reveal another latitudinal cline: the largest *Chorismus antarcticus* encountered at South Georgia measured 14.6 mm carapace length (CL; Maxwell 1977), the largest *Notocrangon antarcticus* 68 mm total length (TL; Makarov 1970) whereas the maximum lengths recorded in the southeastern Weddell Sea were 21.5 mm CL and 117 mm TL, respectively (Arntz & Gorny 1991, Gorny et al. 1993). *Nematocarcinus lanceopes* is supposed to live up to 10 yr in the southeastern Weddell Sea (Arntz et al. 1992). Antarctic nudibranchs seem to grow extremely slowly and may reach a final size of 10–20 cm; their age then, however, is not known (H. Wägele 1988). Females of the amphipod *Eusirus perdentatus* may reach a total length of about 10 cm and an age of 8–9 yr (Klages 1993). Assuming that growth rings on Aristotle's lantern are annual, Brey (1991) concluded that the echinoid *Sterechinus antarcticus* needs 50 yr to grow to a diameter of 40 mm and may reach a maximum age of 75 yr.

However, there are some exceptions: The sponges *Mycale acerata* and *Homaxinella balfourensis* in McMurdo Sound (Dayton et al. 1974, Dayton 1989) and the ascidians *Ascidia challengerii*, *Cnemidocarpa verrucosa* and *Molgula pedunculata* at King George Island (Rauschert 1991) revealed remarkably fast growth in comparison with other species in the same environment. Everson (1977) showed that three species of Antarctic bivalves (*Kidderia bicolor*, *Lissarca miliaris*, *Yoldia eightsi*) grew slower than the temperate *Venus striatula*, but another three species (*Adamussium colbecki*, *Gaimardia trapesina*, *Laternula elliptica*) grew faster.

To decide whether or not growth of Antarctic benthic species is slower than of non-Antarctic species all available quantitative growth data, i.e. growth functions, of Antarctic species were compared with those of boreal and subtropical species. Since non-linear functions such as growth curves are not easy to compare directly, a measure of overall growth performance, the index $\phi = \log_{10}(K) + 0.667 \cdot \log_{10}(M_{\infty})$ of Munro & Pauly (1983) was used. K and M_{∞} are parameters of the generalized von Bertalanffy growth function (see Moreau et al. 1986 for further details). Growth data of 28 Antarctic populations (taken from Brey & Clarke 1993 and Gorny et al. 1993) were compared with data of 141 non-Antarctic populations taken from the available literature. The index ϕ is significantly smaller in Antarctic populations ($P < 0.002$, Mann-Whitney test), indicating that on average in Antarctic species growth performance is lower than in species living in temperate and subtropical regions. However, Fig. 10 indicates a large variability in growth performance of benthic populations and a considerable overlap of Antarctic and non-Antarctic values.

Seasonality vs. non-seasonality of reproduction and growth

A final question in the context of "strategies" is the coupling or decoupling of the reproductive and growth cycles to/from the extremely seasonal conditions of the Antarctic, reflected especially by short pulses of food input in summer. Pelagic planktotrophy in this context is not an easy way of life. Pelagic lecithotrophy may be a better adaptation to the

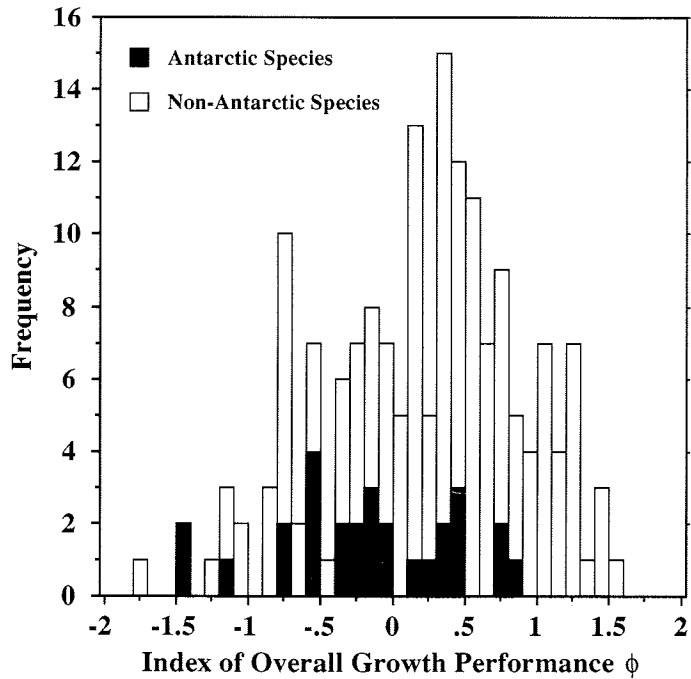


Figure 10 Frequency distribution of the index of overall growth performance $\phi (= \log(K) + 0.667 \cdot \log(M_{\infty}))$ in Antarctic ($N = 28$) and non-Antarctic ($N = 141$) benthic populations. The index is significantly smaller in Antarctic populations ($P < 0.002$, Mann-Whitney test).

combination of poor food availability most of the year and slow rates of development, and represent just another form of decoupling as does laying demersal yolky eggs. Several species have been found which exhibit strong seasonal oscillations in growth. Their observed summer peak growth rates may well be in the range of comparable boreal species (see e.g. Bregazzi 1972, Seager 1978, Picken 1979b, Richardson 1979, Sagar 1980, see also p. 273).

Literature shows that many different strategies have been realized in the Antarctic, from strict coupling to total decoupling of reproduction and growth (Bregazzi 1972, Rakusa-Suszczewski 1972, Clarke & Lakhani 1979, Peck et al. 1986, 1987, Peck 1989, Picken 1979a, b, 1980a, b, 1984, White 1984). Among the bivalves, for example, *Adamussium colbecki* has rare unprotected planktotrophic larvae which feed in the water column and are spawned during austral spring. In contrast, *Laternula elliptica* has common protected lecithotrophic larvae which are nourished by egg yolk reserves and released during austral winter. These early development modes and release periods are influenced by the dependence or non-dependence of the larvae on seasonally produced food sources (Berkman et al. 1991). A further step then, that has been developed by the majority of bivalves (see above), is total avoidance of the dangerous pelagic zone by brood protection.

Early developmental stages (blastulae etc.) and larvae of the echinoid *Sterechinus neumayeri* were collected from the plankton near McMurdo station in early November and December. This species releases feeding larvae into the plankton during the abbreviated summer peak of phytoplankton abundance. Recruitment of juveniles most likely occurs in synchrony with

the subsequent period of high level of benthic chlorophyll *a* concentrations (Bosch et al. 1987). In shallow water off Davis Station, no clear seasonality was noted for epifaunal macrobenthic species, but small infaunal amphipods and tanaidaceans exhibited distinct seasonal cycles of abundance which could be correlated with the seasonal cycle of primary producers. Females of these infaunal species protected their brood throughout the winter and released their juveniles at times that coincided with the period of high primary productivity (Tucker 1988).

Conditions for the southeastern Weddell Sea, where the whole range of strategies exists, have been summarized in Arntz et al. (1992). They include species such as the shrimps *C. antarcticus* and *N. antarcticus* and the holothurian *E. steineni* which make use of the improved food conditions for their larvae (or small juveniles) in Antarctic summer; even the deep-water shrimp *Nematocarcinus lanceopes* releases its larvae (if they exist) or juveniles in shallower water in summer. Disconnection from the seasonal production cycle has been achieved by the holothurian *Psolus dubiosus* and a number of bivalves (e.g. *Philobrya sublaevis*, *Lissarca notorcadensis*) which produce fewer, larger eggs and protect their brood. Of the two suspension feeding holothurians, *E. steineni* has a distinct annual spawning cycle, with large yolky oocytes 0.3–1.0 mm in diameter present in spring and nearly none present in autumn whereas no seasonal differences were found in *P. dubiosus*, a brood-protecting species with a lower fecundity and even larger eggs up to 1.5 mm in diameter (Gutt et al. 1992). An almost complete disconnection from the high Antarctic seasonal cycle is the case for most amphipods as they are scavengers, predators, or detritus feeders which brood their young and release their juveniles as fully developed organisms throughout the year, thus avoiding larval stages which need fresh phytoplankton. There does not seem to be a general rule: even planktotrophic larvae, which have to be seasonal in occurrence, are not always linked very closely to the midsummer pulse of primary production, yet they do not show evidence of starvation. Possibly they depend on unusual sources of food such as bacteria (Pearse et al. 1991). One way this can be managed is shown impressively by the *Limacosphaera* larvae (see above). Decoupling seems to occur more often in the high Antarctic, in deeper water and with trophic generalists and scavengers which appear to be more common here than in shallow areas at lower latitudes, where primary food limitation is presumably less severe.

Productivity

Productivity has not been measured directly for macrobenthic communities in the Antarctic and only rarely for individual species. Table 4 (extended from Brey & Clarke 1993) summarizes the actual knowledge on production and productivity of Antarctic macrozoobenthic populations. Production values range between < 0.001 (*Sterechinus antarcticus*) and > 6 g Carbon \cdot m⁻² \cdot yr⁻¹ (*Adamussium colbecki*), whereas annual P/\bar{B} ratios range between 0.1 (*Sterechinus antarcticus*, *Yoldia eightsi*) and > 1.0 (*Laevilacunaria antarctica*, *Bovallia gigantea*).

Brey & Clarke (1993) compared P/\bar{B} ratios of Antarctic and non-Antarctic populations statistically. In general, P/\bar{B} values of Antarctic benthic invertebrates were significantly lower than those of their temperate counterparts (Fig. 11A). However, these differences are removed by taking the effects of water temperature and water depth on the P/\bar{B} ratio into account (Fig. 11B), i.e. with respect to productivity Antarctic species do not exhibit any unique features.

Table 4 Production and productivity in Antarctic macrobenthic populations. Figures recalculated by Brey & Clarke (1993) based on data given by the original authors. Units of body mass: g organic Carbon.

Species	Area/Author	Biomass [g·m ⁻²]	Somatic production		Gonad production		Total production	
			P _S [g·m ⁻² ·yr ⁻¹]	P _S /B [yr ⁻¹]	P _G [g·m ⁻² ·yr ⁻¹]	P _G /B [yr ⁻¹]	P _{Total} [g·m ⁻² ·yr ⁻¹]	P _T /B [yr ⁻¹]
<i>Adamussium colbecki</i>	McMurdo Sound							
	Stockton 1984	29.625	5.037	0.170	—	—	—	—
	Berkman 1990	33.000	6.545	0.198	—	—	—	—
<i>Lissarca miliaris</i>	Signy Isl.							
	Richardson 1977, 1979	—	—	0.664	—	0.114	—	0.778
<i>Lissarca notorcadensis</i>	Weddell Sea							
	Northern Shelf	—	—	0.316	—	0.128	—	0.444
	Southern Shelf	—	—	0.305	—	0.115	—	0.420
	Brey & Hain 1992							
<i>Yoldia eightsi</i>	Signy Isl.							
	Rabarts 1970a, b	34.506	4.023	0.117	—	—	—	—
	Nolan 1988	—	—	0.162	—	—	—	—
<i>Laevilacunaria antarctica</i>	Signy Isl. 1975–76	0.039	0.034	1.706	—	—	—	—
	Signy Isl. 1976–77	0.150	0.236	1.577	—	—	—	—
	Picken 1979b							
<i>Nacella concinna</i>	Signy Isl.							
	Picken 1980a	5.785	1.427	0.247	0.461	0.080	1.888	0.326
	Nolan 1987	—	—	0.203	—	0.093	—	0.296
<i>Philine gibba</i>	South Georgia							
	Seager 1978	5.157	2.109	0.409	2.377	0.461	4.486	0.870

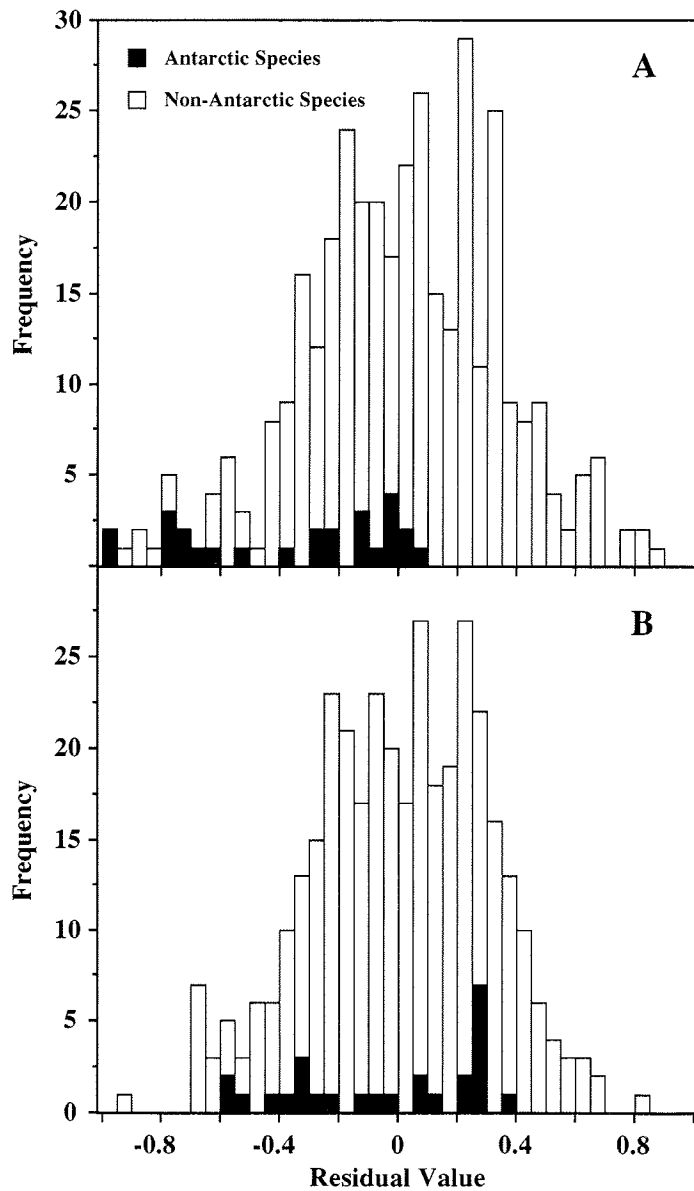


Figure 11 Comparison of annual population P/\bar{B} ratios of Antarctic ($N = 26$) and non-Antarctic ($N = 337$) benthic populations. (Redrawn from Brey & Clarke 1993).

A. Distribution of residuals of multiple regression of $\log(P/\bar{B})$ versus $\log(\text{Mean ind. body mass})$ and dummy variables for main taxa. Significant difference ($P < 0.001$) between Antarctic and non-Antarctic data.

B. Distribution of residuals of multiple regression of $\log(\text{Residuals})$ from A versus $1/\text{Temperature}$ and $\log(\text{Depth} + 1)$. No significant difference ($P > 0.5$) between Antarctic and non-Antarctic data.

Although P/\bar{B} ratios are generally low, benthic community production in shallow waters as well as the shelf and slope regions is not necessarily lower than in boreal areas of comparable depth, since community biomass can be distinctly higher (see pp. 260 & 273). There are two indirect estimates of Antarctic benthic community production: For a shallow bay at Signy Island, Everson (1970) estimated about $11 \text{ gC} \cdot \text{m}^{-2}$ of benthic secondary production to be required to maintain the actual stock of the system key predator, the demersal fish *Notothenia neglecta*. From annual sedimentation and average benthic ecological efficiency Schalk et al. (1993) estimate annual macrobenthic production on the southeastern Weddell Sea shelf to be in the range of $0.3\text{--}7.5 \text{ gC} \cdot \text{m}^{-2}$.

Conservational aspects

Early protection measures in the Antarctic such as the Convention for the Regulation of Whaling were species-directed rather than environment-directed (Bonner 1989). A few crustacean species are used commercially in the Subantarctic (Kock in press, Moreno pers. comm.), but no Antarctic benthic invertebrate species has been exploited despite the fact that high Antarctic scallops (*Adamussium colbecki*) and shrimps (see pp. 258f) may be both abundant and large in size in some areas. However, their stocks would presumably not stand any serious exploitation because of their low productivity except at extremely low levels of fishing mortality (Berkman 1990, Arntz & Gorny 1991). Furthermore, harvesting the scallops with conventional dredges would not only destroy the fragile shells, but also disrupt the apparently stable population and perturb the oligotrophic habitat (Berkman 1990).

The latter is particularly important because it stresses that species should not only be protected for their own sake but also as members of an ecosystem. Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), signed in 1980, was an improvement compared with the Whaling Convention (and other, similar agreements) in that it stresses the responsibility to maintain the balance of ecological relationships between harvested, dependent and related populations. This allows the Commission to take a wider view than conventional fisheries protection measures (Bonner 1989).

Some benthic species are significant as food for demersal fish or other organisms (pp. 268ff), but a much greater importance must be assigned to the fragile 3-dimensional structure of epibenthic communities providing protection and many niches for fish and motile benthos. The structure of these communities has become known better in recent years due to the increased use of underwater video and camera transects (see, e.g. Barthel & Gutt 1992). Habitat destruction and other adverse impacts of bottom trawling have been reviewed by Kock (1990) and Constable (1991). The latter author also stressed the importance of protected areas as recovery sites for affected species in trawled areas.

Pollution of most kinds is still much lower in the Southern Ocean than in other seas (Cripps & Priddle 1991) although certain substances, e.g. organochlorines may occur in similar concentrations. Since Antarctic invertebrates live much longer than temperate species and are an important food for fish, an accumulation of these substances in higher trophic levels of the Southern Ocean has to be assumed (Ernst & Klages 1991). Furthermore, the growing number of scientific stations in some areas such as King George Island, as well as increasing ship traffic connected with these stations and also with tourism, certainly present a menace to some areas. Sewage from various Antarctic stations has led to eutrophication and greater turbidity of sublittoral waters of Maxwell Bay (King George Island), with

negative impacts on the flora and fauna in this area (Rauschert 1991). As detrimental effects last longer than at lower latitudes due to the low resilience and slow recovery of benthic assemblages in the Antarctic (see p. 263), disturbance of any kind is more problematic.

From all these arguments it is obvious that there exists a strong requirement for benthic conservation sites in the Antarctic (Chittleborough 1987, Gallardo 1987b, 1991). A breakthrough for the protection of Antarctic was reached by the Antarctic Treaty Parties during the 1991 Madrid XI Special Consultative Meeting in the shape of a "Protocol on Environmental Protection within the Antarctic Treaty" (PEPAT) and Annexes I–IV (Antarctic Treaty 1991). In essence PEPAT designates Antarctica as a natural reserve, devoted to peace and science, prohibiting any activity relating to mineral resources other than scientific research, and, in general, committing all parties to a comprehensive protection of the Antarctic environment and dependent and associated ecosystems. Up to now, the Antarctic Treaty approved, for the purposes of limited benthic conservation, two purely marine "Sites of Special Scientific Interest" (sssi): Chile Bay (Discovery Bay), Greenwich Island and Port Foster, Deception Island, both in the South Shetland Islands, and another, which is mostly marine but includes a small coastal area (South Bay, Doumer Island, Palmer Archipelago). The first two "Marine Sites of Special Scientific Interest" (msssi), with the intention of "protecting inshore marine sites of scientific interest where harmful interference" might occur, were created at the 1991 Bonn XVI ATCM. They include Western Bransfield Strait (between latitudes 63°20'S and 63°35'S and longitudes 61°45'W and 62°30'W, totalling 4360 km²) and East Dallman Bay (between latitudes 64°00'S and 64°20'S and from longitude 62°50'W east to the intertidal zone of the western shore of Brabant Island, Palmer Archipelago, with a surface area of about 560 km²). These two sites are exceptional within the Antarctic Treaty System conservation efforts in that they relate to potential negative impacts of fishing activities, and in the extension encompassed within their boundaries (Gallardo 1991).

It is not clear why Chile Bay and Port Foster were not considered msssis at the same time since both of them are fully marine areas. In the future, protection may be provided to any previously designated conservation area which includes intertidal and sublittoral zones within its boundaries, and also to marine belts surrounding protected islands (for examples see Gallardo 1991). Furthermore it is desirable to define sublittoral conservation sites close to the Antarctic Continent with a particularly rich fauna such as, e.g. off Kapp Norvegia in the southeastern Weddell Sea. For this purpose recently acquired knowledge from scientifically oriented trawling and dredging, bottom photography and video should be used.

Methodological aspects

Benthic marine biologists are comparatively conservative in their methods. With relatively little modification, Petersen's grab (Petersen & Boysen Jensen 1911) or Reineck's box corer (Reineck 1963) have been used for decades. Even nowadays, a large amount of samples is taken by this type of equipment or with trawls and dredges of different kinds. Especially the latter, which provide at most semiquantitative data, cannot be used for quantitative assessments of the fauna; they are, however, still quite useful for a general large-scale overview and for collecting large amounts of material to be used, e.g. by taxonomists and physiologists. In the 3-dimensional Antarctic epibenthos they may cause a great deal of destruction; therefore their use should be banned in protected areas.

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One of the major problems in the high Antarctic is that sampling, which has to be done at considerable water depth, is often hampered by dropstones from melting icebergs. This leads to a high percentage of failures in grab and corer casts which may prove expensive in terms of ship time. However, in recent years, several multiple corers have been developed which take a greater number of samples simultaneously. These corers include the multiple corer for meiofauna sampling (Barnett et al. 1984) and the "multibox corer" for sampling macrobenthos (Gerdes 1990) which is supplied with a video camera. The multibox corer, which is capable of indicating differences in small-scale distribution of the benthic fauna in the square meter range, has performed well even in very coarse sediment of the eastern Weddell Sea shelf and slope (Gerdes et al. 1992, Galéron et al. 1992).

Underwater still (including stereographic) cameras and remotely operated vehicles (ROVs) with video cameras have increased greatly in importance. They are particularly useful in the Antarctic where the greater part of the benthic fauna lives either at or above the seafloor. UW cameras have been used for studies of the density and distribution of larger organisms (Hamada et al. 1986), and have been shown to be of great use for comparison with trawl catch data (Barthel et al. 1991, Brey & Gutt 1991, Gutt et al. 1991, Gorny et al. 1993). The use of video cameras and ROVs for quantitative assessments still requires considerable improvement, both in terms of calculations of scanned area and in terms of additional mechanical designs to take samples. Larger underwater vehicles of the ALVIN or NAUTILUS type have, to our knowledge, never been used in the Antarctic.

The icegoing research vessel POLARSTERN has enabled German Antarctic research to explore and investigate the permanent packice zone of the Weddell Sea. It represents a new research ship type which combines icebreaking abilities with facilities for all kinds of gear to be used in the water column and at the seafloor, ample laboratory space, and cool containers where live organisms can be kept at ambient temperature. This combined approach of studying preserved material from plankton nets, trawls, dredges and cores, and live organisms in the cool containers, and later in the cool lab at the institute, has provided many good scientific results in recent years. Recently other vessels of similar capabilities have become operational such as the AURORA AUSTRALIS (Australia) and the JAMES CLARKE ROSS (Great Britain).

Future benthic research in Antarctica

Both ship and shore based work can contribute to the future development of Antarctic benthic research. Vessels of the POLARSTERN type and perhaps also, manned or automatic underwater vehicles may explore the last unknown areas on the Antarctic map such as the permanent and seasonal packice zones around the continent, or certain areas beneath the ice shelves. These shipboard studies should focus on certain areas rather than continue the large-scale approach that had to be taken by many interdisciplinary cruises due to the restricted time available for individual fields of research. The study of processes such as pelago-benthic and benthic-pelagic coupling, including the rôle of the sea ice, will increase in importance and may open new interesting areas of research in the context of global warming. Increasing ozone depletion and resulting higher UV-B levels may have minor effects on the deeper zoobenthos, which mostly lacks pelagic larvae, but are likely to be important for shallow-water benthos (Karentz 1991). Major changes also have to be expected at the shelf ice edges. Small-scale resolution of bottom topography, which will be

helpful to explain colonization and distribution patterns of benthic fauna, can be obtained using hydrosweep/parasound techniques and may be particularly rewarding in areas of heavy iceberg scour. Hopefully, additional equipment will be developed to sample short-lived larval stages or drift stages close to the seafloor. It may be desirable to define sublittoral research areas close to the Antarctic continent which are monitored over several decades. For this purpose recently acquired knowledge from scientifically oriented trawling and dredging, bottom photography and video should be used.

At the same time there may be a revival and increased use of shore based stations, principally because they can serve for certain types of studies which are difficult or even impossible to carry out from research vessels. These approaches include continuous sampling year-round; direct observations by divers; interaction experiments (predator exclusion and inclusion, colonization and succession) *in situ*; and aquarium studies with a natural food supply from running seawater. Enclosed shallow-water areas of the "Benthosgarten" type (Arntz & Rumohr, 1982; Gallardo & Retamal 1986), similar to the studies at McMurdo, may provide further insight into the population dynamics and production of individual species, their interactions and community dynamics. Experimental work on these items requires some patience in the Antarctic but may turn out to be particularly rewarding in the long term. As in deep water, the monitoring of specific areas may be useful. Some crowded areas such as the South Shetland Islands or the Palmer region where human interference by pollution from the shore, oil spills, etc. has become severe, should also serve for studies of the human impact on the benthic ecosystem.

Both in deep and shallow water, certain neglected fields of research should be intensified. Physiological and biochemical studies on polar poikilotherms almost exclusively refer to fish whereas very little has been published on invertebrates despite several decades of discussion on "cold adaptation". The population dynamics and production biology of all but a handful of benthic species are virtually unknown, and interaction research has almost exclusively been done at McMurdo Sound. Both meio- and microfauna have received little attention at any depth, and macrofaunal studies in the deep sea have been extremely scarce. Finally, benthic taxonomy must not be further reduced since "all evolutionary, biogeographical, and ecological research absolutely depends on competent systematic research" (Dayton, 1990).

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