Antarctic Science 12 (3): 297–313 (2000) © British Antarctic Survey Printed in the United Kingdom

Some “driving forces” structuring communities of the sublittoral Antarctic macrobenthos

JULIAN GUTT

Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstrasse, D-27568 Bremerhaven, Germany
jgutt@awi-bremerhaven.de

Abstract: Community analyses of the macrobenthos living on the Weddell Sea shelf revealed a distinct horizontal patchiness. Within some systematic groups a specific faunistic classification could clearly be defined, e.g. for asterozoans and holothurians. Whilst for fish, only a general zoogeographical pattern was discernible, there were some recognisable relationships to different microhabitats. The extreme differences in the distribution of sponges observed seems to reflect their highly variable biological characteristics. Studies using underwater imaging methods for benthic research have provided strong evidence for the ecological significance of two factors. The first, iceberg scouring, leads to a variety of simultaneous stages of recolonization, which result in an increase in beta-diversity. As a consequence, it is unlikely that regionally a stage approaching a theoretical climax will ever be attained. Secondly, the structural diversity of living substrata provides the basis for an additional variety of epibiotic species. Only weak or non-detectable correlations have been found between benthic assemblages and physical parameters, such as water depth, sediment type, bathymetric features and the abundance of deposited phytodetritus. This indicates a benthic system which is relatively uncoupled from processes in the water column. The combination of stable environmental conditions and disturbances taking place over long periods of time, which are partly a special feature of Antarctica's glacial history, shaped the diversity and faunal composition of the macrobenthos. Consequently, neither Houston's “intermediate-disturbance-hypothesis” nor Sander's “stability-time-hypothesis” can be rejected for this part of the Antarctic ecosystem.

Received 5 October 1999, accepted 3 February 2000

Key words: benthos, disturbance, epibiotic relationships, icebergs, pelago-benthic coupling, vicariance

Background

In contrast to a pronounced seasonality of processes in the water column environmental stability of the Antarctic sublittoral is often mentioned as a key factor explaining its benthic diversity (Picken 1985a, Arntz & Gallardo 1994). Has it not been the low temperature and, subsequently, the huge amount of ice present that has attracted most attention from polar researchers? During the cooling of Antarctic and deep-sea waters, which started 60 million years ago (Kennett 1977), the fauna developed a distinct stenothermy with a range not much wider than the slight seasonal variations in their natural environment (Littlepage 1965, Clarke 1990, Arntz *et al.* 1992). Thus, temperatures ranging between -1.8 and 1.5°C cannot a priori be regarded as stable from the point of view of stenothermic animals (Clarke 1987). Corresponding knowledge about the salinity and oxygen content is even poorer. Even if the benthos does live under true stable hydrographic conditions at places with a regular or sporadic occurrence of Warm Deep Water (see Foster *et al.* 1987, Fahrbach *et al.* 1994), there are more than a handful of other factors which generally have a significant relevance for benthic communities. Can we imagine any event having more serious consequences than the displacement caused by the grounding of continental ice during glacial periods (Elverhøi 1981, Gingele *et al.* 1997)? Recently, we have been able to observe similar events on a much smaller spatial scale, where icebergs have run aground leaving behind them areas of total devastation. Or what do we really know about the food and substratum requirements of thousands of macrobenthic species throughout all stages in order to understand long-term colonization processes?

Despite the many unanswered questions, considerable advances have been made in polar marine ecology over the last decades. These have been mainly due to the use of modern ice-breaking research vessels, the construction of well-equipped littoral stations (Arntz & Gallardo 1994) and the availability of satellite data. This success is confirmed by the rewarding investigations carried out across the spectrum of biological organisation, i.e. from single cells and organisms through to populations and system parameters. Nevertheless, we are still a long way away from understanding how the Antarctic benthic system functions as a whole.

The purpose of this review is to help decipher ecological principles by testing various hypotheses on easily detectable factors which are of great or little significance to the majority of the macrobenthos. The size range of the fauna investigated in each case are mentioned in the literature cited. The two general questions are:

1) How are macrobenthic assemblages in the Weddell and Lazarev Seas characterized, in an area which is representative of the high Antarctic shelf?

2) Which biological relationships and abiotic processes help explain these structures?

Both these questions have to be considered together, since it is essential to analyse the fauna in order to understand the functioning of an ecosystem. In contrast to bottom fauna in other regions of the world and Antarctic plankton, the Antarctic benthos has to cope with especially long-term processes. Thus, besides the results of recent events, it is possible to detect those which happened long before and lasted for only a short period of time. The reason for this is the slow growth (Dayton 1978, Clarke 1980, Brey & Clarke 1993) and the sessile life of many species (White 1984, Picken 1985b, Starmans *et al.* 1999), which can neither escape in the event of a disturbance nor reinvade immediately after it.

Underwater photographs and videos were the main source of data, often in combination with material from trawl catches. These methods were particularly suitable since many species of the generally abundant epifauna on the Antarctic shelf are large and, therefore, relatively rare species play an important role. Also small scale distribution patterns and interspecific relationships were relevant for the scientific approach, which are not adequately detected by traditional sampling methods.

Intermediate scale distribution patterns of assemblages

Hypothesis: The benthos shows differences in its structure which permit a geographical classification.

Most of the benthic fauna on the Antarctic shelf is often considered to have a circumpolar distribution (Bullivant 1967, Arnaud 1977, Sarà *et al.* 1992), stretching along the *c.* 35 000 km of coastline (Drewry 1983). This interpretation is mainly based on taxonomic surveys which refer only to the presence of species but not to absences or the community level. Knox (1977) summarized some zoogeographic classifications which mostly distinguished between an East and West Antarctic District or (sub-)Province, the latter including the Antarctic Peninsula and the western Weddell Sea (Knox 1960, Andriashev 1965, Hedgpeth 1971, Gruzov & Pushkin 1970). Ekman (1967) associated the entire Weddell Sea with the Peninsula region and, therefore, indicated that its fauna must differ considerably from that in the Ross Sea. In a similar way, Dell (1964) classified animals into circumpolar species and those which are restricted to the Weddell Sea, Peninsula region and Bellingshausen Sea. However, these differences seem to be unclear for some systematic groups (Hedgpeth 1969, Knox 1977, Sarà *et al.* 1992). Intensive surveys and community analyses have recently been carried out in the Weddell and Lazarev seas. They focused either on single systematic groups, identifying the fauna to species level (Ekau & Gutt 1991, Gutt 1991a, Gutt *et al.* 1994, Piepenburg *et al.* 1997a) or they covered a broader taxonomic range using a more general identification (Voß 1988, Gerdes *et al.* 1992, Galéron *et al.* 1992, Gutt & Starmans 1998, Starmans *et al.* 1999, Starmans & Gutt in press).

As far as ophiuroids and asteroids are concerned, the "east" assemblage found along the south-eastern coast of the Weddell Sea was the most distinct (Fig. 1a). The key species were also the most dominant: *Ophioplocus incipiens* (Koehler), *Ophiurolepis martensi* (Studer), *Ophiurolepis brevirima* Mortensen, *Amphiura belgicae* Koehler, *Ophiura flexibilis* (Koehler) and *Astrotoma agassizii* Lyman (all Ophiuroidea). In the southern Weddell Sea two more assemblages, "south" and "trench" were found which differed considerably in water depth. The specificity of the key species – the ophiuroid *Ophiacantha antarctica* Koehler and the asteroid *Odontaster meridionalis* (Smith) for "south", the asteroid *Hymenaster* sp. 1 and the ophiuroid *Ophiosparte gigas* Koehler for "trench" – was much lower than those for the "east" assemblage. In certain cases their biological characteristics may explain their preference for the different regions. In a similar way to many suspension feeders, *A. agassizii* feeds on plankton (Dearborn *et al.* 1986), a life mode which may be favoured by the coastal current (Fahrbach *et al.* 1992, Schröder & Fahrbach 1999). *Hymenaster* is adapted to soft, deep-sea sediments as shown by the skin found between the arms. Holothurians showed a similar geographical distribution (Fig. 1b). The clusters "suspension feeders I and II" correspond to "east" and "sediment feeders I and II" to "trench". The naming of the clusters indicates that, with a few interesting exceptions (see Gutt 1991b), holothurians of different feeding types prefer different regions of the Weddell Sea. The main difference between both of the echinoderm groups was that the transitional holothurian cluster "sediment- and suspension-feeders" had no definite key species in contrast to the asterozoan "south" cluster.

Demersal fish were classified after the results from single stations were added together to give larger geographical units (Gutt *et al.* 1994). The main cluster, "north" found in the Lazarev Sea, the adjacent area in the eastern Weddell Sea and further south inshore at Halley Bay, was primarily dominated by notothenioid and to a lesser extent, artedidraconid species (Fig. 1c, see also Hubold 1991). There was a more even numerical distribution of the Nototheniidae, Artedidraconidae, Channichtyidae and Bathydraconidae in the cluster "south", between *c.* 72°00' and 78°30'S. Schwarzbach (1988), Wöhrmann & Zimmermann (1992) and Zimmermann (1997) found a similar geographical distribution from the results of bottom trawls. Fish distribution represents a gradient between two extremes rather than separation of distinct groups which is more obvious than for the echinoderms. One reason for this might be that there is a different link between fish species and the benthos. Some species lay their eggs in sponges (Moreno 1980) and appear to display some territorial behaviour. Others depend more on the pelagic system because it provides their food. In addition, as motile species fish are less susceptible to

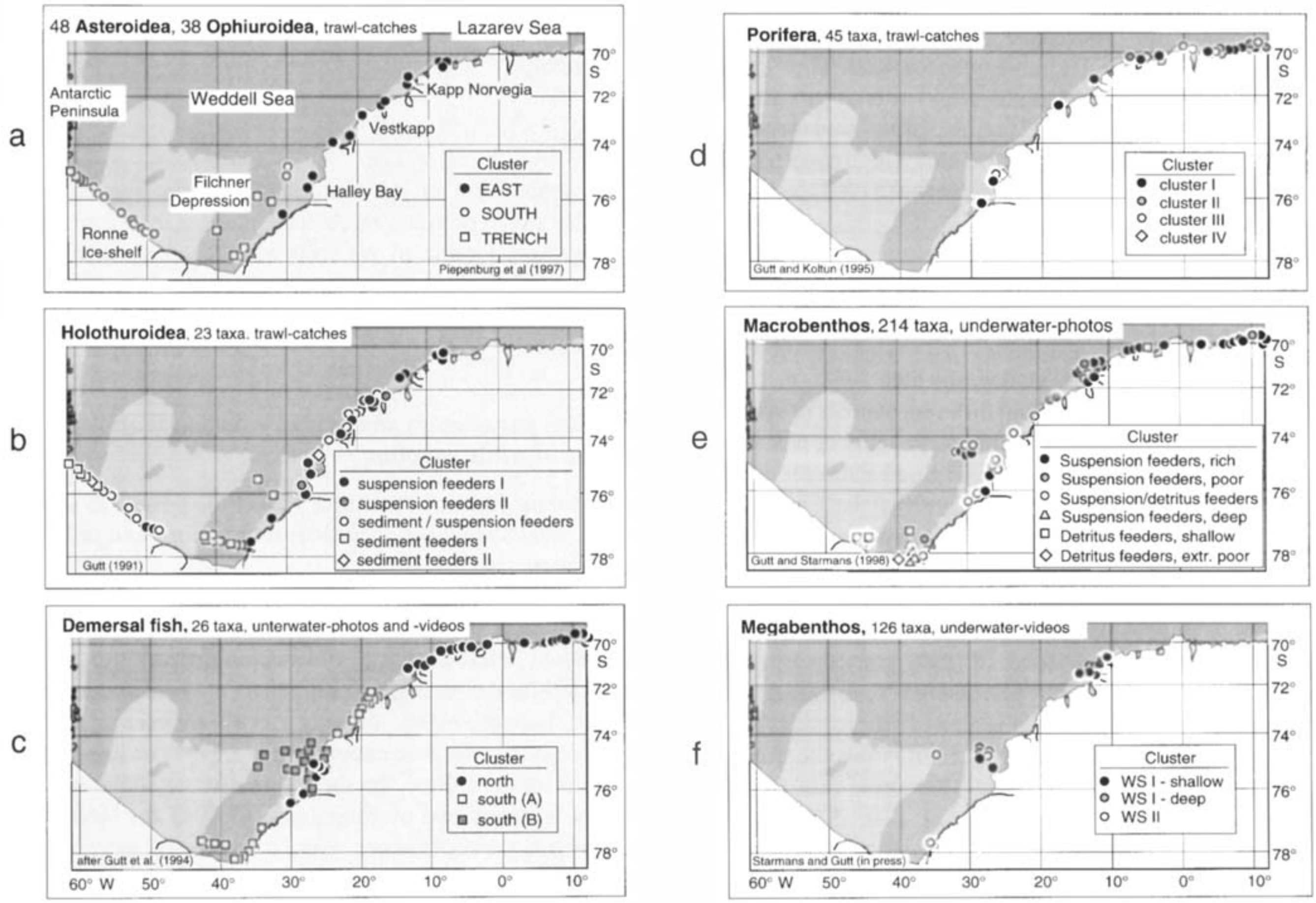

Fig. 1. Assemblages of different benthic compartments according to cluster-analyses (redrawn from publications cited in the text). **a.** Asteroids and ophiuroids, **b.** holothurians, **c.** demersal fish, **d.** porifera, **e.** macrobenthos, **f.** megabenthos.

local environmental changes and, consequently, fish patterns do not reflect such fluctuations as sessile invertebrates do.

The classification of sponges showed the most diffuse geographical pattern (Fig. 1d; Barthel & Gutt 1992, Gutt & Koltun 1995). The only generalisation was that both species richness and number of specimens were greatest at Kapp Norvegia. Stations belonging to other clusters were scattered throughout the entire investigation area, with a high degree of local patchiness. Apparently the various sponge species have an exceptionally broad range of environmental requirements and have developed an extremely wide variety of biological characteristics. One example of this is the way the enormous variation in growth rates (Dayton 1978) can affect the distribution patterns. The very slow growing hexactinellids only survive in long-term favourable areas and even events that happened long before are still recognisable, whereas the fast growing or r-strategists such as *Homaxinella* sp., can react immediately when environmental conditions change (Dayton 1989, Dawber & Powell 1997). Apparently Antarctic sponges are, in many respects, an exceptionally heterogeneous systematic group.

The three dominant demersal shrimp species do not show any distinct geographical pattern (Gutt *et al.* 1994). Local conditions, such as the abundance of other organisms which help structure the microhabitat or the availability of non-colonised soft bottom (see below), seem to be of great importance for *Chorismus antarcticus* (Pfeffer) and *Notocrangon antarcticus* (Pfeffer), respectively. Their intermediate scale horizontal distribution is superimposed by a clear depth zonation, in which *Nematocacinus lanceopes* Bate is restricted to depths < 700 m, whereas the other two species prefer shallower areas (Arntz & Gorny 1991, Gutt *et al.* 1991).

An initial attempt at analysing the macrobenthos as a whole was made by Voß (1988) and modified by Gutt & Starmans (1998), Starmans & Gutt (in press), and Starmans *et al.* (1999). The different sampling methods, trawl catches and direct observations, covered a similar size range of animals. Only the smallest fraction was not recorded on video. Three main assemblages were identified. The "Eastern Shelf Community" was found mainly in the Lazarev Sea and the adjacent area of the Weddell Sea down to 72°S, with a few additional stations further south. In the region between 72° and 76°S, the number of stations belonging to the "Southern

Shelf Community" increased. There were also similar stations found off the Filchner–Ronne ice shelf. The "Trench Community" (Gutt & Starmans 1998) was apparently not restricted to deeper waters and was also to be found west of the Filchner Depression at 250 m. In this area, a high concentration of elasipode holothurians (Gutt & Piepenburg 1991) confirmed the deep-sea affinity of the high Antarctic benthos (Bullivant 1967, Dayton *et al.* 1969, 1974, Andriashev 1977, Lipps & Hickman 1982, Gutt 1991b); in this case it concerned the polar emergence of deep sea species. The most heterogenous fauna, with the greatest number of different assemblages, was observed in the comparatively small Halley Bay area.

The combination of data from different sources provided a general view of structural characteristics, number of species, abundance, diversity and evenness. Figure 2 indicates that the "east" community is by far the richest and that the "trench" and "south" communities differ only in two parameters or sets of data, respectively.

Comparison with Bullivant's (1967) results reveals that parallel assemblages also occur in the Ross Sea. He considered that the community consisting of many sessile suspension feeders was only a "minor assemblage". However, Dell (1972) thought that this fauna is actually more widespread, which is clearly confirmed by the results from the Weddell Sea. The fauna around the Antarctic Peninsula (Lowry 1975, Gallardo *et al.* 1977, Jazdzewski *et al.* 1986, Mühlenhard-Siegel 1988, Saiz-Salinas *et al.* 1998), seem to represent a different, mainly true soft-bottom community with a high proportion of polychaetes, molluscs and bivalves. Such a zoogeographic difference is especially obvious among demersal fish (Hubold 1991, Kock 1992). The benthos in the Amundsen and Bellingshausen seas in the Pacific sector, which is dominated by mobile echinoderms, sedentary anthozoans and sessile bryozoans (Starmans *et al.* 1999) may represent an intermediate position. As the fauna in the south-eastern Weddell Sea is so heterogenous, it is impossible distinguish any longitudinal border between faunistic provinces.

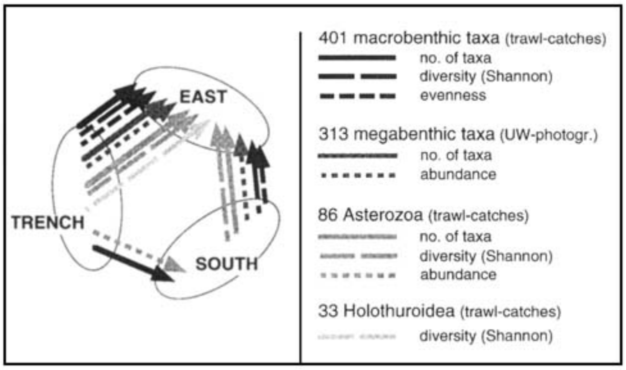

Fig. 2. Significant differences in structural characteristics between benthic assemblages in the south-eastern Weddell Sea ($P < 0.05$, Wilcoxon and *post hoc* test after Nemenyi). The arrows point to assemblages with higher values; data from publications cited in the text.

Conclusion

The composition of the macrofauna in the Weddell and Lazarev seas represents an obvious gradient from a very rich assemblage dominated by suspension feeders to a much poorer and heterogenous benthos in which a variety of different taxa and life forms, including deposit feeders, are more dominant.

Physical parameters and primary food availability, pelago–benthic coupling

Hypothesis: Benthic structures reflect the pattern of sea-ice cover, food availability, sea-floor morphology and sediment characteristics.

Sea ice dynamics, in combination with hydrographic conditions, exert a strong influence on primary production, especially at the ice edge. A high percentage of diatoms sink to the bottom, either directly or after consumption by zooplankton, which is known as an export- or loss-system (Peinert *et al.* 1989). In the alternative retention-system, which is dominated by flagellates, most of the biomass is recycled in the upper water layer. It has been discovered that there is a relationship between such biological and physical processes in the water column and the benthos e.g. by Dayton & Oliver (1977), Genin *et al.* (1986), Barry & Dayton (1988), Piepenburg & Juterzenka (1994) and Piepenburg *et al.* (1997b). Even in the deep-sea the effects of events taking place in the euphotic layer can be detected after only a short delay (Graf 1989, Rice *et al.* 1994). The sinking of a phytoplankon concentration was also observed on the high Antarctic shelf (Gleitz *et al.* 1994). In addition, when sea ice melts ice algae are released. In January/February, algal biomass in the sea ice can reach values (maxima of 30 mg chl *a* m^{-2}) as high as those in the water column one month later (Smetacek *et al.* 1992, Arrigo *et al.* 1998, Dieckmann *et al.* 1998). The fate of such organic material and, therefore, its availability to the benthos, also depends on the midwater and mainly the near bottom current. At a certain velocity the organic material never reaches the sediment surface since it is either continuously advected, or it is deposited, especially in depressions. It can also be resuspended, for example in the deep sea at a velocity > 7 cm s^{-1} (Lampitt 1985). However, the hydrodynamics do not only affect the food availability but also various sediment characteristics which are of general significance for benthic life (Lowry 1975, Gray 1981, Picken 1985a, Dunbar *et al.* 1985, 1989). Comparing oceanographic processes at a large general scale I consider two components of an ecosystem to be coupled if one depends on the other in a similar way to Cushing's (1990) demonstration of the "match–mismatch" between fish larvae and their food in the North

Atlantic. If one part of a system, e.g. benthos, does not react predictably on events in the other part, e.g. phytoplankton, or if the majority of processes in first part is temporally or spatially independent from the second I consider these to be relatively uncoupled. A total uncoupling between primary production and the high Antarctic benthos as known from hydrothermal vent communities can be excluded for the south-eastern Weddell Sea.

A simple calculation may demonstrate the relevance of identifying relationships between complex processes in the euphotic zone (see e.g. Bodungen *et al.* 1988) and the sea-floor. Based on results of Fahrbach *et al.* (1992, 1994) let us assume that the coastal horizontal current above a 300 m deep shelf area has an average net velocity of 0.05m s^{-1}. Then small particles, such as coccolithophorids and dinoflagellates with a vertical sinking speed of 0.5m d^{-1} (Smayda & Bienfang 1983), intermediate sized diatoms sinking between 100 and 150m d^{-1} (Billett *et al.* 1983), and large foraminiferans, aggregates and faecal pellets sinking at up to 360 m d^{-1} (Alldredge & Gottschalk 1988) will reach the sea-floor at a distance of 2600 km, 10 km or only 1.3 km, respectively, from the place where sinking started. A valuable source of information for investigating possible links between processes in the upper water column and the benthos are satellite images showing the sea-ice cover over 19 successive years (Heygster *et al.* 1996). These images have been used to calculate the

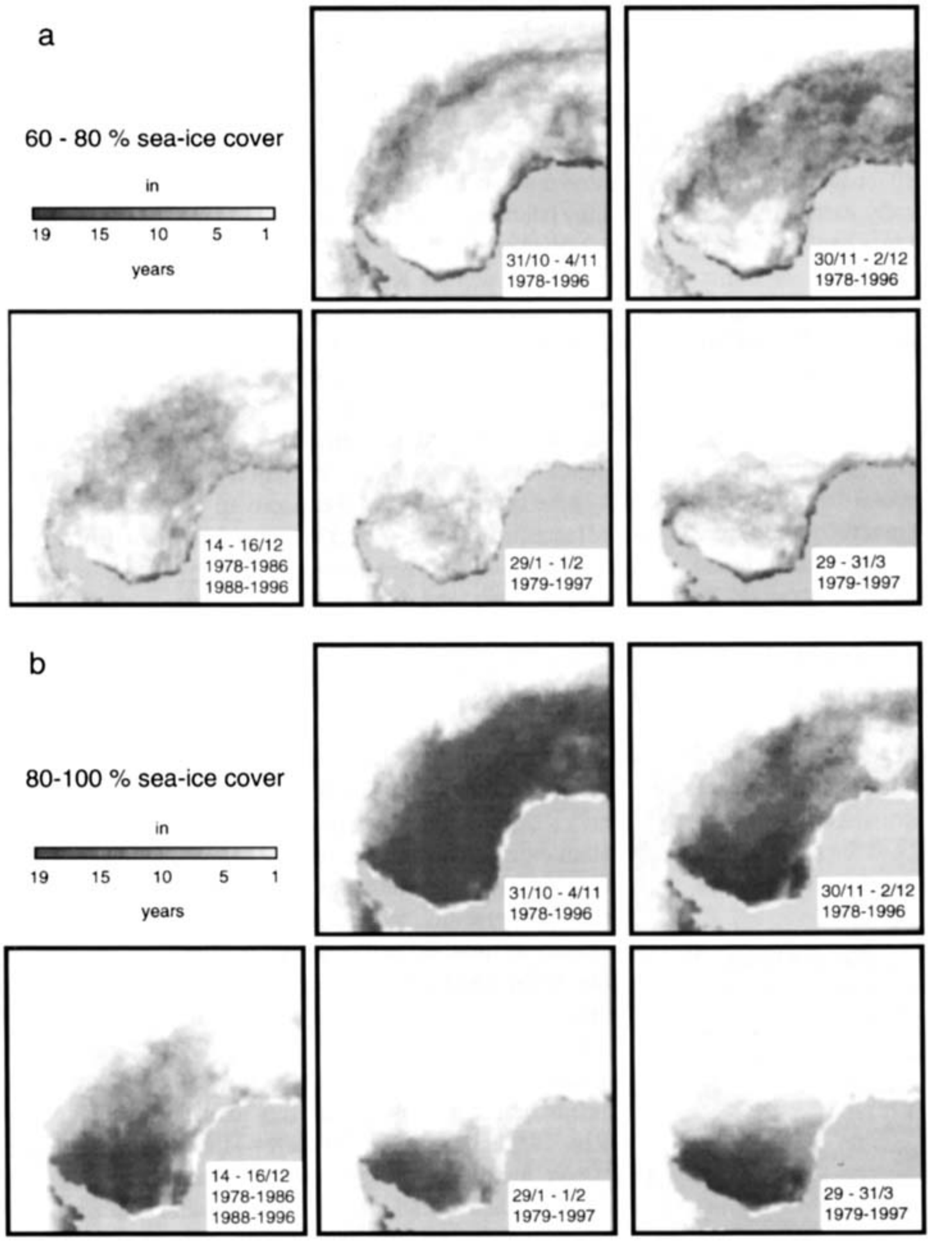

Fig. 3. Probability of sea-ice occurrence from satellite images taken between 1978 and 1997 (Heygster *et al.* 1996). **a.** ice margin defined as 60–80% ice cover, **b.** showing open water (white to gray) as reciprocal product of the 80–100% sea-ice cover (grey to black).

probability of the sea-ice edge (sea-ice cover 60–80%, Fig. 3a) and open water (< 80% sea-ice cover, Fig. 3b). The maps show that the predictability of the ice-edge is extremely low. Consequently, there is no relationship detectable between these ice data and benthic patterns. From the end of October until the end of March open water, as defined above, was regularly found as a coastal polynya in those parts of the south-eastern Weddell Sea where the suspension feeder assemblage was predominant. The only exception was the area south of Halley Bay where, interestingly, there was marked heterogeneity in both the long-term ice cover and benthic communities.

As long as direct data on the spatial pattern of food availability for the benthos are not available recording phytodetritus of planktonic origin visible on sea-bed photographs currently provides a good indirect method (Gutt *et al.* 1998). In areas where the shelf was wider than 80 km, the sediment showed a significantly higher amount of phytodetritus than on the narrower shelf. This can be explained by the low current velocity over the broad shelf where organic particles sink relatively quickly to the sea-floor. Deposit feeders profit most from such a situation, whilst the generally more dominant filter feeders seem to be better adapted to a higher velocity which mainly transports particles horizontally. A similar relationship was observed by Ravaioli *et al.* 1999 on the deeper shelf of the Ross Sea. No significant relationships were found between the occurrence of phytodetritus and other physical parameters such as a SW–NE gradient, the time of the observations between January and March, water depth or the distance between the station and the ice shelf edge. In a similar approach, the above mentioned environmental data and values for the amount of sea-floor covered by macrobenthos were used for a factor analysis. Shelf width was not included because it was correlated with the SW–NE gradient ($r = 0.77$). The phytodetritus cover loaded as the only parameter high on factor 2 which means that it does not show any relationship with the other parameters, nor with the total benthic abundance (Table I).

Studies on reproduction, feeding and early life history of filter feeders also provide a good opportunity to investigate the degree of pelago–benthic coupling. There was no significant difference in the size of brooded juveniles of the holothurian *Psolus dubiosus* Ludwig & Heding sampled on 21 October and 14 February (Gutt 1991c). However, the data sets were from two different years and two different localities. All the same, within one season the average size of juveniles belonging to different females varied considerably. Also the size–frequency distribution of mature oocytes showed heterogenous spatial and irregular temporal patterns, rather than a marked seasonality. This indicates a long, if not continuous reproductive phase. In contrast, similar data from a non-brooding holothurian, *Ekmocucumis steineni* (Ludwig), indicated a shorter period of reproduction from October to January (Gutt *et al.* 1992). The amount of organic material found in the stomachs of these two species was generally higher in the autumn than in the spring and thus showed a degree of seasonality. However, *E. steineni* were found in the autumn at one of the most southerly stations, with values (stomach filling and gonad indices) similar to individuals found in the spring. This species seems to have a varied reaction to environmental change, whereas the results for *P. dubiosus* indicate no direct link with seasonal processes taking place in the euophotic zone. Barnes & Clarke (1995a) found out that 12 of the 13 suspension feeders investigated at Signy Island interrupted their feeding for only a short phase of 2–3 months within one year. On the other hand, the asteroid *Odontaster validus* Koehler was found to show, in shallow waters off Signy Island, a clear spawning peak in winter with a striking interannual variability which was also observed for the occurrence of its larvae (Stanwell-Smith & Clarke 1998). Different spawning strategies of three echinoderms indicate, according to Stanwell-Smith & Peck (1998), that larval food supply and predation during planctonic phase are not important for these species. Also the capacity of *O. validus* to feed on seal faeces in the high Antarctic (Pearse 1965) can be interpreted as a buffer mechanism between primary production in the euphotic zone and life at the sea-floor. Another buffer mechanism also having the effect of delaying the availablility of food is proposed by Cattaneo-Vietti *et al.* (2000a). Sponges may store diatoms for a longer period in their tissue. The three dominant demersal shrimp species in the Antarctic show a distinct seasonal oocyte maturation and spawning pattern (Gorny *et al.* 1992, Gorny & George 1997, Mascetti *et al.* 1997). Apparently, different components of the benthic system exhibit varying degrees of pelago–benthic coupling (White 1984), even when they are closely related species. For further interpretation see later section 'Long-term development of the high Antarctic environment' (p. 306).

Due to an incomplete data set it is only possible to compare examples of benthic patterns and sediments found on the shelf of the south-eastern Weddell Sea. The asterozoan and holothurian fauna along the RonneIce Shelf at depths < 500 m belong almost exclusively to one assemblage (Gutt 1991a, Piepenburg *et al.* 1997a). The surface sediments, however, are dominated by different sized fractions of either muddy to sandy mud or well sorted sand (Haase 1986). Totally different benthic assemblages, however, are found at Kapp Norvegia and off Halley Bay where the proportion of

Table I. Loading factors from factor analysis for comparison between environmental data, phytodetritus deposited on the sea-floor and sea-floor cover by macrobenthos (changed after Gutt *et al.* 1998).

	factor 1	factor 2	factor 3
contribution to the total variance (%)	49	26	25
phytodetritus cover	-0.004	0.954	-0.049
depth	-0.801	-0.002	0.165
date	0.073	-0.035	0.966
SW/NE gradient	0.679	0.397	0.219
distance between station and ice shelf edge	-0.625	-0.123	-0.217
cover of macrobenthos on sea-floor	0.773	-0.177	0.057

gravel is relatively high (Grobe 1986, Weber 1992). Gingele *et al.* (1997) found well sorted sand at the ice shelf edge and sandy to muddy silt in inner-shelf depressions in the eastern Lazarev Sea. On the other hand, benthologically this part of the shelf is the most homogenous. The finding that unusual assemblages, which differ from typical soft bottom communities are not found everywhere on coarser sediments, may be explained by the key role the near-bottom current plays in this part of the ecosystem. Its velocity affects both the sediment and the organisms. Also its direction, especially at the ice shelf edge, can be crucial for the benthos because the food supply can depend significantly on it, as clearly demonstrated by Barry & Dayton (1988) in the McMurdo Sound.

Attempts were made by Gutt & Koltun (1995), Gutt & Starmans (1998), and Starmans & Gutt (in press) to elucidate such ecological relationships using the BIOENV-method (Clarke & Ainsworth 1993). A comparison between biological (megafauna, macrofauna, sponges) and environmental data (same as used for factor analysis and coarse sediment characteristics) from the same stations did not show any clear relationship on the shelf. However, it must be recognized that the same method could lead to a more clear differentiation if other environmental parameters, such as C/N relationship of potential food or POM in the nepheloid layer could be included in an analysis with a sufficiently high spatial resolution.

There is evidence that, in addition to a general dependence of benthic processes on those in the water column, the reverse might also be true. When demersal fish feed on benthic items and are in turn eaten by seals, there is a transfer of energy from the deep to the surface waters. Of special interest in this context may be the krill swarms and "dispersed aggregations" *sensu* Miller & Hampton (1989), which occur at a depth of up to 415 m (Gutt & Siegel 1994, Gutt unpublished observations). If favourable food conditions close to the sea-floor are the main reason for an extended vertical migration, this species not only has a key role in a downward directed "biological carbon pump" (Volk & Hoffert 1985) because of its fast sinking faecal pellets (Bodungen 1986, Wefer *et al.* 1988, Bathmann *et al.* 1991) but also in the opposite direction, by providing a main food source for many higher predators.

Within the south-eastern Weddell Sea there is a general geographical agreement between the large-scale patterns of macrobenthic, pelagic fish and zooplankon communities (Hubold & Ekau 1987, Boysen-Ennen & Piatkowski 1988, Piatkowski 1989, Smith & Schnack-Schiel 1990, Boysen-Ennen *et al.* 1991) especially in the area between Halley Bay and the Filchner–Ronne Ice Shelf. However, the nature of this relationship or even its possible cause is not yet understood at all.

Conclusion

At present there is no clear evidence that physical factors shape benthic patterns directly at an intermediate spatial scale (10–100 km). Even though part of the benthic system is triggered by events in the euphotic zone, it seems to be at least temporally relatively independent from seasonal processes. If demersal fish and hyperbenthic krill feed close to the sea-floor and then migrate vertically, there is also an upward energy flux to take into account.

Iceberg scouring

Hypothesis. The grounding and scouring of icebergs contribute considerably to the benthic structure on the Antarctic shelf.

Up until now, the benthos of deeper Antarctic shelf areas has been considered to live under stable and homogenous environmental conditions. In addition, a considerable part of the benthic system seems to be partly independent of the marked seasonality in the upper water column. In contrast, the littoral fauna between 0 and 60 m is greatly affected by various physical disturbances, resulting in a clear vertical zonation (Dayton *et al.* 1970, Zamorano 1983, Dayton 1990, Gambi *et al.* 1994, Sahade *et al.* 1998, Cattaneo-Vietti *et al.* 2000b, for review see also Gutt in press). Traditional surveys carried out on the deeper macrobenthos in the south-eastern Weddell Sea and Lazarev Sea showed an obvious horizontal patchiness in species composition and diversity over a scale of roughly 10 to 100 km (see e.g. Piepenburg & Gutt 1991, Barthel & Gutt 1992, Brey *et al.* 1998). Imaging methods with a high spatial resolution along transects of several hundred metres length have provided further insight into such patterns. They showed for the first time that iceberg scouring destroys benthic life on the continental Antarctic shelf and how devastated areas are recolonized by mobile invaders and sessile pioneer species. Following similar findings from both shallower Antarctic waters (Peck & Bullough 1993) and the Arctic (Conlan *et al.* 1998), this phenomenon has recently attracted a lot of attention. One reason for this might be the opportunity for studying the causes underlying the high number of invertebrate species in the Antarctic and the role these physical disturbances play in this context. There is also a chance to gain a better understanding of the resilience of this diverse system, e.g. what the consequences might be when more icebergs calve due to global warming or the effects of local anthropogenic disturbance such as oil spills, waste, or sewage.

Initial studies calculated the rate of disturbance in the Weddell, Amundsen and Bellingshausen seas. The results, based on 4.4% affected area, indicated that statistically the sea-floor is disturbed on average once every 230 years (Gutt *et al.* 1996). In this calculation it was assumed that the scour mark had a maximum age of 10 years. However, a later investigation of one pioneer species, the bryozoan *Cellaria incula* Hayward and Ryland, showed that the maximum age was 14 years (Brey *et al.* 1999), indicating that the benthos recovers even more slowly than first thought. This would then give a rate of disturbance of once every 320 yr. Based on the age of a *Yoldia eightsi* Couthouy bivalve population off Signy Island, Peck & Bullough (1993) estimated a corresponding value of 50–75 yr for shallower waters around the South Orkney Islands. This variation between high Antarctic shelf areas makes it worthwhile thinking about the long-term and wide-ranging consequences. Why go to the trouble of sampling sponges (*Rossella nuda* Topsent/ *Scolymastra joubini* Topsent) growing on the Weddell Sea shelf at 150–500 m, which only reach a height of 1.3 m, when specimens of 2 m can be found at about 50 m depth at Mirny, Molodeznaya and in the Ross Sea (Andriashev 1965, Dayton *et al.* 1974)? If sub-optimal conditions are the cause of their relatively small size in the Weddell Sea, two questions arise: why are they so successful in the Weddell Sea in terms of abundance, and why are there no really large sponges at two exceptionally shallow sites (80–60 m deep), a bank north of Kapp Norvegia and the southern part of the Atka Bay? The answers could be that the entire Weddell Sea shelf is exposed to iceberg scouring and the two other shallow areas are sheltered from this effect because small pieces of ice rarely reach this depth and true icebergs would have a greater draught. This would mean that the Weddell Sea benthos could never reach a climax defined by the presence of really large hexactinellid sponges.

In another study the influence of iceberg scouring on the structure and biodiversity of a benthic community in the south-eastern Weddell Sea has been evaluated (Gutt *et al.* 1998). The results of a MDS-plot showed that the species composition in undisturbed areas was dominated by sessile suspension feeders and was much more homogenous than in formerly scoured areas. The pooled data indicates an increased between-habitat diversity (Fig. 4) which supports Huston's "intermediate disturbance hypothesis" (Connell 1978, Huston 1979) at an ecological time scale. However, so far it has been impossible to discover any general trend in temporal succession during recolonization. In addition to the above mentioned bryozoan, some of the other pioneer species found in the Weddell Sea were mobile ophiuroids and the sponges *Stylocordyla borealis* (Loven), *Latrunculia apicalis* Ridley & Dendy (only at one station), *Homaxinella* sp., the polychaete *Pista* sp., the colonial ascidian *Synoicium adareanum* (Herdman), and the gorgonian *Primnoisis antarctica* (Studer). All these species were present in much higher numbers inside the scour marks than outside (Gutt *et al.* 1996, Gutt unpublished data). The first stage of recolonization is dependent on unknown biological or physical conditions and can be characterised by the appearance of a very few species, which vary with the location. These may have a very successful rate of recruitment which leads to an extremely low between-habitat diversity. If such opportunistic initial species fail to colonise successfully, the relatively low number and abundance of other more specialised species increases slightly. This leads to diversity values comparable to those of undisturbed assemblages, even in the relatively early stages of recolonization. The "mosaic-cycle concept" (Reise 1991) does not apply here because of the low predictability of the faunal succession. Therefore, the data from the Weddell Sea can be better explained by the "patch-dynamics concept" developed by White & Picket (1985).

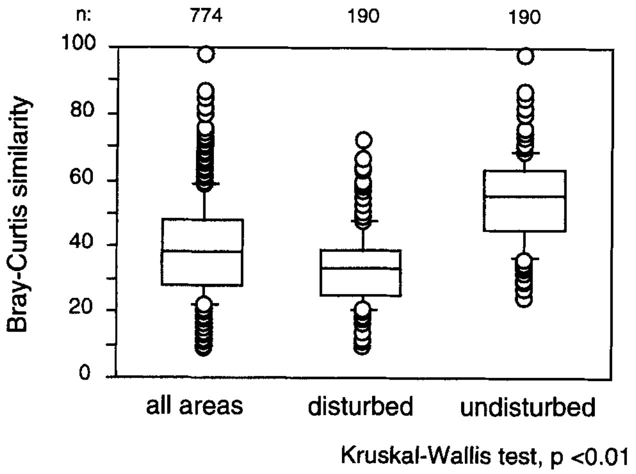

Fig. 4. Between-habitat (beta-) diversity due to iceberg scouring. Due to the greater heterogeneity (lower Bray-Curtis similarities) in the disturbed areas (and in areas including both disturbed and undisturbed substrata) the diversity of macrofaunal assemblages is higher compared to unaffected areas. For the methodology see Magurran (1988). A total of 140 taxa from 79 areas at four stations were analysed covering the full systematic range of the mega-epibenthos visible on video-transects.

Nowadays it is generally accepted that, due to iceberg scouring, the benthic environment is not as homogenous and stable as was earlier assumed. However, since detailed studies have so far failed to provide totally satisfactory results, this might be an appropriate time to list some outstanding questions of general interest.

1. Is the disturbance regime *sensu* White & Pickett (1985) defined by its spatial distribution, frequency, predictability and the size of area affected?
2. Can communities with different faunal compositions and biodiversity be attributed to different regimes of iceberg scouring?
3. How can the ageing of scour marks be improved?
4. Will it actually prove impossible to make generalizations about recolonization after scouring?
5. Can the impact of iceberg scouring on the high Antarctic benthos be compared to similar events in other large ecosystems in more detail than at present (Gutt & Starmans in press)?

Conclusion

Iceberg scouring is an important factor that significantly shapes the structure of the macrobenthos in the otherwise relatively stable and homogenous Antarctic sublittoral. More detailed investigations of this phenomenon are needed to prove ecological hypotheses. In certain cases, corresponding studies could help improve our knowledge of the resilience of other endangered benthic systems which have been influenced by man for decades or even centuries.

Epibiotic relationships

Hypothesis. Epibiotic relationships contribute considerably to the so-called "three-dimensional" or "multistoried" assemblages and, thereby, have the effect of increasing the diversity.

It was mainly the introduction of underwater photography to Antarctic research (Bullivant 1959, 1961) which allowed epibiotic relationships to be seen for the first time, e.g. crinoids and ophiuroids living on sponges. Most of these relationships are part of so-called "multistoried" assemblages (Andriashev 1968, Knox & Lowry 1977, Dearborn *et al.* 1986). They were even compared to reef communities off southern California (Hedgpeth 1971), and Dayton (1984) concluded that physical stability is the main reason for the development of such significant intraspecific behavioural, as well as complex trophic relationships (Dayton *et al.* 1970, 1994). Moyano & Wendt (1981) were the first to study the epibiotic life by looking at the holothurian, *Psolus charcoti* Vaney in Paradise Bay. They found several bryozoans, of which *Fenestrulina malusi* (Audouin) and *Celleporella antarctica* Moyano & Gordon were the most abundant, the enteroproct *Barentsia discreta* (Busk), hydrozoans, pycnogonids and foraminiferans covering the holothurian by up to 87%. Most of the encrusting epibionts were thought to protect the sea cucumber, which, in contrast to related species, has no solid calcareous test. At Signy Island, Barnes & Clarke (1995b) investigated similar relationships in which the brachiopod *Liothyrella uva* Broderip, and the limpet *Nacella concinna* (Strebel), were the main substratum organisms. The epibionts were classified into generalists (which live on all types of substrata), host-specific species (which were found on only a few hosts), low specificity epibiotic species (which occur on various animals but occasionally on rocks) and background species (which are rarely found on other animals). It seemed that the main reason for some species developing epibiotic behaviour in shallow waters, was that a host provides higher substratum stability compared with the smaller nearby rocks which are moved mainly by waves. Other epibiotic interactions were found to be usually hierarchical, where sponges grow over bryozoans, bryozoans grow over the annelid *Spirorbis* and occasionally small brachiopods.

Quantitative studies carried out on the high Antarctic shelf focused on epibiotic relationships which mainly contribute to the three-dimensional structure. The fish, *Trematomus lepidorhinus* Pappenheim, *T. loennbergi* Regan and *T. eulepidotus* Regan showed a relatively close relationship with the sessile invertebrates structuring the benthic habitat. For such species Hubold's (1991) "sit-and-wait" strategy was modified to a "sit-observe-and-hide" strategy (Ekau & Gutt 1991, Gutt & Ekau 1996, see also Dayton *et al.* 1974). Here the fish use cup-shaped hexactinellid sponges and lower growth forms, such as colonial ascidians. Moreno (1980) found that *T. bernacchii* Boulenger even lays its eggs in the osculum of sponges, which may also be true of the other *Trematomus* species. In contrast *Prionodraco evansii* Regan, *Dolliodraco longedorsalis* Roule and *T. scotti* (Boulenger) were most abundant in areas without stones, gravel or an abundant mega-epifauna, the so-called "non-structured habitat". Epibiotic holothurians in the Weddell Sea were found to show either a facultative or an obligative preference for branched colonies of bryozoans and hydrozoans or tall sponges (Gutt 1991a, 1991b). One very specific behaviour was that of *Echinopsolus acanthocola* Gutt, which lives almost exclusively on the spines of pencil sea-urchins (Cidaridae). In addition, previously unpublished results (Fig. 5) from two representative stations show the clear relevance of the substratum organisms *Thouarella/Dasystenella* (Gorgonaria) and hexactinellid sponges for the epibiont *Astrotoma agassizii* (Ophiuroidea).

A comprehensive quantitative study, using underwater photography, revealed 374 different epibiotic relationships

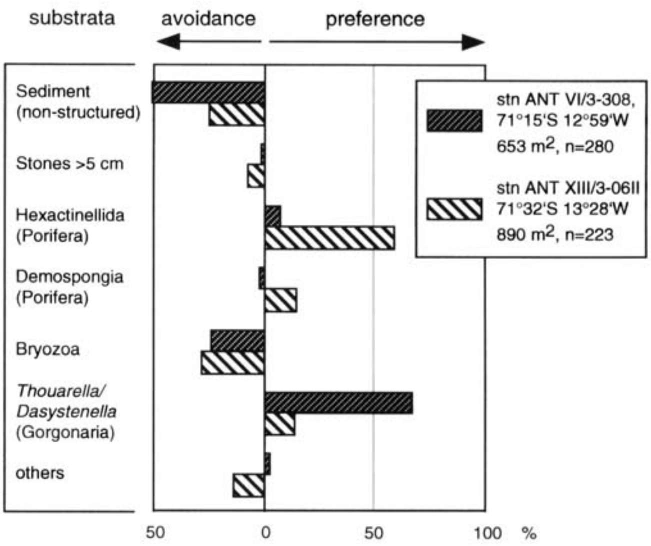

Fig. 5. A comparison between the availability of mineral and biogenic substrata at two sites in the south-eastern Weddell Sea and the use of these substrata by the ophiuroid *Astrotoma agassizii* show a significant preference by this epibiont for the gorgonians *Thouarella/Dasystenella* and hexactinellid sponges of the genera *Scolymastra* and *Rossella* ($P < 0.05$, 2 x 2 and k x 2 contingency table test, as described by Gutt & Schickan 1998). The length of the bars represent the difference between the sea-floor cover by the different types of substrata and the relative abundance of *A. agassizii* observed by underwater-video on these substrata.

between 47 epibiotic and 96 substratum taxa (Gutt & Schickan 1998). Six abundant obligatory relationships had highly specialized epibionts such as the gastropod *Margaritesa* sp., living on the hexactinellid sponge *Rossella nuda*, or the bivalve *Lissarca notorcadensis* Melvill & Standen, on the spines of pencil sea-urchins (Brey *et al.* 1993). The epibionts involved in a further eight relationships significantly preferred a specific composition of living and elevated mineral substrata. Most of these relationships were regarded as commensalism (after Odum 1971) because the suspension feeding epibiont profits from the elevated position. Here it has better access to food because of a generally higher current velocity (see Cacchione *et al.* 1978) than directly above the sediment. The substratum organism also acts as an obstacle in the current and may cause its own current due to filtering activities. The locally high abundance of sessile animals and, therefore, the opportunity for finding an elevated position, together with the epibiotic life mode of other species has been interpreted as one of the major reasons for the high species richness in the benthic fauna. Justifiably the sponges attract special attention in this context. Based on data published later by Kunzmann (1996), Barthel (1992) demonstrated how two hexactinellid sponges, *Rossella antarctica* Carter and *R. racovitzae* Topsent, serve as substrata for other invertebrates. The highest proportion of animals found in the suboscular cavity were gastropods, polychaetes, isopods, amphipods and nudibranchs. In an attempt to evaluate the role sponges play in the biodiversity of the high Antarctic megafauna, Gutt & Starmans (1998) found a positive correlation between the abundance of large (but not intermediate or small sized) sponges and the number of all other megabenthic taxa. These results indicate that, over evolutionary time scales, the Antarctic macrobenthos is biologically accommodated rather than physically controlled (after Sanders 1968, see also Lipps & Hickman 1982).

Conclusion

Both quantitative and qualitative results show strong evidence that various living structures, especially hexactinellid sponges, bryozoans and gorgonians play an important role in providing a suitable elevated micro-habitat for a considerable number of Antarctic invertebrates, many of which are echinoderms. The availability of such substrata, as well as the development of an epibiotic mode of life, can partly explain the locally high number of species in Antarctic waters.

Long-term development of the high Antarctic environment

Question. Is the recolonization of the high Antarctic shelf since the end of the last glaciation period almost finished or do the large-scale differences in benthic communities around the continent still reflect an ongoing dispersion of species?

Variations in species composition and structural characteristics ranging over orders of magnitude can be observed over distances of between ten and several hundred kilometres. Such patchy distribution can generally be explained by recent environmental conditions, or by events which took place long ago whose effects are still detectable. One factor which had an enormous impact on the Antarctic benthos was the extinction of benthic life by grounded inland-ice during the last glacial period, which covered large areas of the continental shelves up to 500 m depth (Elverhøi 1981, Clarke & Crame 1992, Hughes 1998). Geological findings from the Mac.Robertson Shelf, Davis Sea indicate that *c.* 10% of the sediments were not eroded (Harris & O'Brien 1996). Such ice surges can possibly be traced back to the late Oligocene, 25–30 million years ago (Barrett *et al.* 1989, Hambrey *et al.* 1991). During periods of glaciation the benthic invertebrates, which now dominate present day shelf assemblages, lived on the upper continental slope. Data on palaeosedimentation, however, indicate that the food availability here was significantly reduced (Bonn *et al.* 1998). There is also no evidence that the fauna covering the shelf at that time was as abundant and rich as it is now at *c.* 300 m depth. Alternative areas where most benthic species could have lived during the glaciation periods are sub-Antarctic islands or the coast of southern South America. Wherever the major habitats were at the time of the ice ages, the species probably lived in communities similar to those today. This is most likely since the development of interspecific relationships (see above) and the evolution of the species involved took longer than the period since at least the last ice age.

We may never be able to discover all the relevant effects resulting from the glacial–interglacial changes, or reach a complete understanding of all the recent environmental conditions and biological demands of the benthos. Nevertheless, the part played by glacials as a "driving force" behind the Antarctic benthos should be considered in the light of new results.

The following arguments can be used to show that the recolonization of the continental Antarctic shelf, which started at the end of the last glacial period *c.* 10 000 years ago, is still continuing.

> Large-scale features of the Antarctic such as hydrography, sediment composition and long-term primary production, are relatively homogenous and stable compared to other large ecosystems (Hedgpeth 1969, 1977, Gallardo *et al.* 1977, White 1984, Picken 1985a, 1985b, Arntz & Gallardo 1994). However, no clear correlation has been found with any environmental data in an area of the Weddell Sea where the spatial distribution of macrofauna can be very heterogenous (Gutt & Koltun 1995, Gutt & Starmans 1998, Starmans *et al.* 1999). Thus, if the large-scale patchiness of the benthos does not reflect recent environmental conditions there must be some other explanation. The most likely explanation is that it is due to the conditions during the last period of glaciation.
>
> The lack of any close link between food availability and

benthic distribution patterns (Gutt *et al.* 1998), as well as the observed feeding of sessile suspension feeders under poor food conditions (Pearse *et al.* 1991, Barnes & Clarke 1995a) can be interpreted as an adaptation to the conditions which prevailed during glacial periods. This would mean that, at present, the benthos is actually experiencing a food surplus. Another indication that a considerable part of the Antarctic benthos does not directly depend on phytoplankton production is a concentration of filter feeders, including hexactinellid sponges, under the Ross Ice Shelf (Dayton 1990, Dayton *et al.* 1994) at a distance of up to 50 km from the ice-edge.

Not only is a considerable part of the benthos temporally somehow uncoupled in terms of metabolism from recent biological processes taking place in the upper water column, but they also spawn during the winter when phytoplankton production is extremely low (Gutt 1991c, Pearse *et al.* 1991, Gutt *et al.* 1992, Barnes & Clarke 1995a).

If the high Antarctic fauna emigrated during periods of glaciation to sub-Antarctic areas, they would only be able to reinvade with difficulty when the shelves were again available as habitat at the beginning of the interglacial. Pelagic larvae would have to cover long distances and negotiate the circumpolar current system, which acts as an effective barrier. Problems would also arise when benthic larvae or adults have become ecologically and physiologically adapted to the deep-sea.

Many species, especially some sessile suspension feeders, are found together within an area of 10 km^2 and it is unlikely that they have distinct ecological niches. This can be explained by the "climate diversity pump" (Clarke & Crame 1997), a special form of the vicariance model (Clarke & Crame 1992). In this case populations have either been locally split by the grounded ice during glacials or they lived around scattered sub-Antarctic islands and continued to evolve. When they mixed again during the recolonization of the continental shelf they could no longer interbreed. This leads to species with similar ecological demands occurring in the same place, if competitive displacement of the less well-adapted species is incomplete.

The alternative hypothesis, that the recolonization of the entire shelf has already been completed, can be supported by the following arguments.

So far, investigations have only looked at the effects of a very limited number of environmental parameters on a handful of species. Apparently, it is the slightly higher temperature which accounts for the occurrence of the stone crab, *Lithodes murrayi* Henderson at Peter I Island in the Bellingshausen Sea but not on the continental shelf (Klages *et al.* 1995). Many other species with a marked stenoecy may also live at the limit of their distribution in some high Antarctic areas which generates a benthic patchiness. Gallardo *et al.* (1977) have suggested that such minor variations in habitat characteristics can cause large variations in the fauna.

For a smaller and relatively shallow (< 100 m) area in the McMurdo Sound Barry & Dayton (1988) proved that recent environmental changes (e.g. diatom flux, the chlorophyll *a* content in the sediment and in the water column) significantly affect various benthic parameters (production of microalgae, microbial ATP-assimilation, abundance of arthropods, bacteria and "vermes").

Although the different species assemblages in the Weddell Sea represent a continuum rather than distinct communities, obvious differences were found in a limited area off Halley Bay. It is unlikely that this heterogeneity is influenced by distribution limits which have been effective for at least the past 5000 years.

A simple calculation for the dispersion of species can support both hypotheses. Assuming a generation time of 10 years, a continental coast line of 25 000 km and eight equidistant refugia for the benthos on the shelf during a glacial period, each successive generation would have to move 3.1 km in one direction from the place of its parents generation in order to disperse around the entire continent in 10 000 yr. At a given net velocity of the bottom-near current of 5 cm d^{-1} in this case, pelagic larvae would have to stay in the water column for less than one day. Thus, despite the slow growth (Dayton 1978, Brey & Clarke 1993, Brey *et al.* 1998, Brey *et al.* 1999) and resulting long generation times, species with pelagic early-life stages have had the chance of a relatively fast and effective dispersion. For brooding or budding species, however, the number of refugia would have to be much higher to have achieved circumpolar distribution by now. White (1984) estimated the route of dispersion and colonisation rates to be greater than the direct effects of environmental parameters the degree of isolation of the fauna. Sebens (1985) assumed that the re-establishment of macroalgal communities in north-west Atlantic waters since the last glacial period is not yet finished, although organisms in the northern hemisphere can migrate along north–south running coastlines during the changeover from glacials to interglacials.

An indirect effect of the last glacial period is seen in "trophic group amensalism" (Rhoads & Young 1970, Gallardo 1987). If a pristine area is firstly re-occupied by a rich infauna and mobile deposit feeders, these can modify their small-scale habitat. They can cause bioturbation and can change the sediment stability, adversely affecting the recruitment of sessile suspension feeders in such areas (Dayton & Oliver 1980). Hints for an unusually abundant infauna were given by mounds off Halley Bay (Gutt unpublished results) and high concentrations of deposit feeding (deep-sea) holothurians (Gutt & Piepenburg 1991) were found in the southernmost

Weddell Sea where the sessile epifauna was scarce. In contrast, deposit feeders might be outcompeted where life forms with a filigreed skeleton or a spiny surface, such as bryozoans and sponges, are the first successful organisms. This is because these species do not leave enough free space for mobile animals and create poor feeding conditions for the infauna.

Conclusion

Current knowledge of the benthos and glacial history does not allow us to answer the question of whether the recolonization of the Antarctic shelf is almost finished or still continuing. There are results which provide good arguments for both scenarios, including the indirect effects of regional differences in the initial colonization. Even if slow growing species which we know structure the micro-habitat had not yet dispersed around the continent, the consequences for benthic communities could still be visible.

General conclusions

Questions. Which of the above mentioned parameters or phenomena are of greater or lesser importance in shaping the high Antarctic macrobenthic structures? Which hypotheses about the relationship between structure and functioning are most applicable to this system?

None of the studies carried out in the south-eastern Weddell Sea provide any clear evidence that the "classical" environmental parameters significantly shape the structure of the macrobenthos. In spite of all the scientific, logistic and technological effort that has been invested, it must be admitted that the present state of knowledge is still at a basic level. It seems most likely that a relationship could be proved between relatively strong near-bottom currents and assemblages dominated by suspension feeders, if more long-term data were available. This has been demonstrated in the North Atlantic by Piepenburg & Juterzenka (1994), Piepenburg *et al.* (1997b) and for the Jasper Seamount in the North Pacific by Genin *et al.* (1986). More experimental studies and quantitative investigations on essential ecological requirements, such as food and reproductive cycles, could reveal if the above described uncoupling of a very few species from processes in the euphotic zone is general, and how independent of primary production the bulk of the species really are. Obvious differences in faunal composition can also indicate that the recolonization of shelf areas after the last glacial period is not yet finished. Consequently, another long period of species dispersion and increasing efficiency of concurrence will lead to a less heterogenous distribution. In order to understand why there has so far been no link found between the sediment composition and other environmental parameters and the benthos it is particularly important to understand the early life history.

One environmental factor that has recently been identified as having a major impact, at least locally, is the scouring by true icebergs (Gutt *et al.* 1996). The recolonization of devastated areas seems to be very slow for the macrofauna but not for the meiofauna (Peck *et al.* 1999); it generates a intermediate scale pattern of different stages in which the species composition of the initial fauna and subsequent succession is hardly, if at all predictable (Gutt *et al.* 1998). In this case the Antarctic macrobenthos partly follows the criteria of the "equal chance hypothesis" (see Connell 1978) which demands that species have the same potential to recolonize pristine areas and that the recruitment of pioneering species is independent of the population of the parents. Thus, the development of the Antarctic macrobenthos seems to follow the "patch dynamics concept" (White & Pickett 1985) rather than the "mosaic cycle concept" (Reise 1991). The first results of the ecological consequences of iceberg scouring also provide a good opportunity for evaluating which of the hypotheses explaining the diversity of ecosystems (see Connell 1978, Thiery 1982) could be applied to the high Antarctic macrobenthos, i.e. Huston's (1979) "intermediate disturbance hypothesis" or the contrasting Sander's (1969, 1979) "stability–time hypothesis".

From the 4–5% area which has been calculated as being disturbed over the past 14 years, we must conclude that the Antarctic benthos does not live under generally stable conditions. However, variations in hydrographical conditions, such as current, wave action, temperature and salinity are extremely low compared to other benthic systems, especially in shallower waters. The poor predictability of the heavily pulsed food supply does not seem to affect a considerable part of the Antarctic benthos and thus it does not seem to play an important role in this context. Proof that the between-habitat diversity in areas scoured by icebergs is higher than that in undisturbed assemblages provides evidence that, on this spatial scale, physical disturbance contributes to a high diversity. Since these results refer to an average of different scour marks in different areas of the south-eastern Weddell Sea, the frequency of the scouring can be considered to be intermediate. Despite the lack of information about the disturbance regime, the "intermediate disturbance hypothesis" can be applied for the high Antarctic macrobenthos. The low productivity of the system leads to a low competitive displacement so that the diversity and species richness does not reach very high values.

With the background of a stable and homogenous environment the "stability-time hypothesis" was developed (Sanders 1969, 1979) for the deep-sea. It assumes that species do not have to adapt to a changing physical environment and, as a consequence, competition leads to a high specialisation of co-occurring species with non-overlapping niches (Grassle & Sanders 1973). As mentioned above, most of the relevant environmental parameters are stable and uniform and this might also have contributed to distinct niche diversification and a high number of species on Antarctic shelves (Gray 1997). In contrast, Dayton & Hessler (1972) consider predominant non-selective predation and, as a consequence, reduced competition as important for the evolution and maintenance of benthic deep-sea communities. How the community structure on the Antarctic shelf is controlled by such relationships between sponges, asteroids and ophiuroids was impressively demonstrated by Dayton (1972). Although Grassle & Sanders (1973) did not agree with the interpretation of Dayton & Hessler (1972), they emphasised that the stability–time hypothesis does not allow for disturbance to play a role in governing diversity if distinct time scales are considered.

Based on the various results summarized here I think that the species richness and diversity of the Antarctic benthos can not be explained at present by either stable conditions or disturbance alone. In saying this it has to be kept in mind that the disturbance regime is not yet understood as a complex phenomenon adequately characterized by its descriptors (White & Pickett 1985), that diversity and its development always refer to specific temporal as well as spatial scales and finally that diversity and species richness (number of species) are different variables. On an ecological time scale, in which competition is an important factor it is comparatively easy to confirm Huston's hypothesis. In addition, it might be of high relevance if the environmental conditions between distinct disturbance events are stable or highly variable. Also at an evolutionary time scale of millions of years many species may not exclusively originate, when environmental conditions are continuously stable. The spatial separation of populations and consequently an independent evolution with resulting new species can only be imagined in case of large-scaled and long-term disturbances. Apparently in the Antarctic a specific combination of environmental stability and disturbance at different spatial and temporal scales generated a high, but not very high species richness and diversity as well as a distinct patchiness of faunal assemblages.

Acknowledgements

Thanks to P.M. Arnauld, J.M. Gili and one anonymous referee for their comments on the manuscript. Supported by German Research Association. This is AWI publication no. 1725.

References

Alldredge, A.L. & Gottschalk, C. 1988. *In situ* settling behaviour of marine snow. *Limnology and Oceanography*, **33**, 339–351.

Andriashev, A.P. 1965. A general review of the Antarctic fish fauna. *In* Oye, P.V. & Miegham, J.V., *eds. Biogeography and ecology of Antarctica*. The Hague: Junk, 491–550.

Andriashev, A.P. 1968. The problem of the life community associated with the Antarctic fast ice. *In* SCAR, SCOR, IAPO & IUBS, *eds. Symposium on Antarctic Oceanography, Santiago, Chile, 13–16 September 1966*. Cambridge: Scott Polar Research Institute, 147–155.

Andriashev, A.P. 1977. Some additions to schemes of the vertical zonation of marine bottom fauna. *In* Llano, G.A., *ed. Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 351–360.

Arnaud, P.M. 1977. Adaptations within the Antarctic marine benthic ecosystem. *In* Llano, G.A., *ed. Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 135–157.

Arntz, W.E. & Gallardo, V.A. 1994. Antarctic benthos: present position and future prospects. *In* Hempel, G., *ed. Antarctic science*. Berlin: Springer Verlag, 243–277.

Arntz, W.E. & Gorny, M. 1991. Shrimp (Decapoda, Natantia) occurrence and distribution in the eastern Weddell Sea, Antarctica. *Polar Biology*, **11**, 169–177.

Arntz, W.E., Brey, T., Gerdes, D., Gorny, M., Gutt, J., Hain, S. & Klages, M. 1992. Patterns of life history and population dynamics of benthic invertebrates under high Antarctic conditions of the Weddell Sea. *In* Colombo, G., Ferrari, I., Ceccherelli, V.U. & Rossi, R., *eds. Marine eutrophication and population dynamics (Proceedings of the 25th European Marine Biology Symposium)*. Fredensborg, Denmark: Olsen & Olsen, 221–230.

Arrigo, K., Worthen, D.L., Dixon, P. & Lizotte, M.P. 1998. Primary productivity of near surface communities within Antarctic pack ice. *Antarctic Research Series*, **73**, 23–43.

Barnes, D.K.A. & Clarke, A. 1995a. Seasonality of feeding activity in Antarctic suspension feeders. *Polar Biology*, **15**, 335–340.

Barnes, D.K.A. & Clarke, A. 1995b. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the United Kingdom*, **75**, 689–703.

Barrett, P.J., Hambrey, M.J., Harwood, D.M., Pyne, A.R. & Webb P.-N. 1989. Synthesis. *In* Barrett, P.J., *ed. Antarctic Cenozoic history from the CIROS-1 drillhole, McMurdo Sound. Bulletin of the New Zealand Department of Scientific and Industrial Research*, No. 245, 241–251.

Barry, J.P. & Dayton, P.K. 1988. Current patterns in McMurdo Sound, Antarctica, and their relationship to local biotic communities. *Polar Biology*, **8**, 367–376.

Barthel, D. 1992. Antarctic hexactinellids: a taxonomically difficult, but ecologically important benthic component. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **85.2**, 271–276.

Barthel, D. & Gutt, J. 1992. Sponge associations in the eastern Weddell Sea. *Antarctic Science*, **4**, 137–150.

Bathmann, U., Fischer, G., Müller, P.J. & Gerdes, D. 1991. Short-term variation in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. *Polar Biology*, **11**, 185–195.

Billett, D.S.M., Lampitt, R.S., Rice, A.L. & Mantoura, R.F.C. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature*, **302**, 520–522.

Bodungen, B. von. 1986. Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica – implications from sediment trap collections. *Polar Biology*, **6**, 153–160.

Bodungen, B. von, Nöthig, E.-M. & Sui, Q. 1988. New production of phytoplankton and sedimentation during summer 1985 in the south-eastern Weddell Sea. *Comparative Biochemistry and Physiology*, **B90**, 475–487.

Bonn, W.J., Gingele, F.X., Grobe, H., Mackensen, A., & Fütterer, D.K. 1998. Palaeoproductivity at the Antarctic continental margin: opal and barium records for the last 400 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **139**, 195–211.

Boysen-Ennen, E. & Piatkowski, U. 1988. Meso- and macro-zooplankton communities in the Weddell Sea, Antarctic. *Polar Biology*, **9**, 17–35.

Boysen-Ennen, E., Hagen, W., Hubold, G. & Piatkowski, U. 1991. Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. *Marine Biology*, **111**, 227–235.

Brey, T. & Clarke, A. 1993. Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? *Antarctic Science*, **5**, 253–266.

BREY, T., GUTT, J., MACKENSEN, A. & STARMANS, A. 1998. Growth and productivity of the high Antarctic bryozoan *Melicerita obliqua*. *Marine Biology*, **132**, 327–333.

BREY, T., STARMANS, A., MAGIERA, U. & HAIN, S. 1993. *Lissarca notorcadensis* (Bivalvia: Philobryidae) living on *Notocidaris* sp. (Echinoidea: Cidaridae): population dynamics in limited space. *Polar Biology*, **13**, 89–95.

BREY, T., GERDES, D., GUTT, J., MACKENSEN, A. & STARMANS, A. 1999. Growth and age of the Antarctic bryozoan *Cellaria incula* on the Weddell Sea shelf. *Antarctic Science*, **11**, 408–414

BULLIVANT, J.S. 1959. Photographs of the bottom fauna in the Ross Sea. *Bulletin of the New Zealand Department of Scientific and Industrial Research*, **2**, 485–497.

BULLIVANT, J.S. 1961. Photographs of Antarctic bottom fauna. *Polar Record*, **68**, 505–508.

BULLIVANT, J.S. 1967. Ecology of the Ross Sea benthos. *Bulletin of the New Zealand Department of Scientific and Industrial Research*, **176**, 49–78.

CACCHIONE, D.A., ROWE, G.T. & MALAHOFF, A. 1978. Submersible investigation of outer Hudson submarine Canyon. *In* STANLEY, D.J. & KELLING, G., *eds. Sedimentation in submarine canyons, fans and trenches*. Stroudsburg, PA: Dowden, Hutchinson & Ross, 42–50.

CATTANEO-VIETTI, R., CHIANTORE, M., GAMBI, M.C., ALBERTELLI, G., CORMACI, M. & DI GERONIMO, I. 2000a. Spatial and vertical distribution of benthic littoral communities in Terra Nova Bay. *In* FARANDA, F.M., GUGLIELMO, L. & IONORA, A., *eds. Ross Sea ecology*. Berlin: Springer Verlag, 503–514.

CATTANEO-VIETTI, R., BAVESTRELLO, G., CERRANO, C., GAINO, E., MAZZELLA, L., PANSINI, M. & SARÀ, M. 2000b. The role of sponges in the Terra Nova Bay ecosystem. *In* FARANDA, F.M., GUGLIELMO, L. & IONORA, A., *eds. Ross Sea ecology*. Berlin: Springer Verlag, 539–549.

CLARKE, A. 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. *Biological Journal of the Linnean Society*, **14**, 77–92.

CLARKE, A. 1987. The adaptation of aquatic animals to low temperatures. *In* GROUT, B.W.W. & MORRIS, G.J., *eds. The effects of low temperatures on biological systems*. London: Edward Arnold, 315–348.

CLARKE, A. 1990. Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna. *In* KERRY, K.R. & HEMPEL, G., *eds. Antarctic ecosystems: ecological change and conservation*. Berlin: Springer Verlag, 9–22.

CLARKE, A. & CRAME, J.A. 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Philosophical Transactions of the Royal Society of London*, **B338**, 299–309.

CLARKE, A. & CRAME, J.A. 1997. Diversity, latitude and time: patterns in shallow seas. *In* ORMOND, R.F.G., GAGE, J.D. & ANGEL, M.V., *eds. Marine biodiversity: patterns and processes*. Cambridge: Cambridge University Press, 122–147.

CLARKE, K.R. & AINSWORTH, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205–219.

CONLAN, K.E., LENIHAN, H.S., KVITEK, R.G. & OLIVER, J.S. 1998. Ice scour disturbance to benthic communities in the Canadian High Arctic. *Marine Ecology Progress Series*, **166**, 1–16.

CONNELL, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1309.

CUSHING, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in marine biology*, **26**, 249–293.

DAWBER, M. & POWELL, R.D. 1997. Epifaunal distribution at Antarctic marine-ending glaciers: influences of ice dynamics and sedimentation. *In* RICCI, C.A., *ed. The Antarctic region: geological evolution and processes*. Siena: Terra Antarctica Publication, 875–884.

DAYTON, P.K. 1972. Toward an understanding of community resilence and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *In* PARKER, B.C., *ed. Proceedings of the Colloquium on Conservation Problems in Antarctica held on 10-12 September, 1971, Blacksberg, Virginia*. Lawrence, KS: Allen Press, 81–96.

DAYTON, P.K. 1978. Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. *Colloques internationaux du Centre national de la recherche scientifique*, **291**, 271–282.

DAYTON, P.K. 1984. Processes structuring some marine communities: are they general? *In* STRONG, D.S. & SIMBERLOFF JR, D., ABELE, L.G. & THISTLE, A.B., *eds. Ecological communities: conceptual issues and the evidence*. Princeton, NJ: Princeton University Press, 181–197.

DAYTON, P.K. 1989. Interdecadal recruitment and destruction of an Antarctic sponge population and its effect on local populations of Asteroids. *Science*, **245**, 1484–1486.

DAYTON, P.K. 1990. Polar benthos. *In* SMITH, W.O., *ed. Polar oceanography, Part B: Chemistry, biology, and geology*. San Diego, CA: Academic Press, 631–685.

DAYTON, P.K. & HESSLER, R.R. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Research*, **19**, 199–208.

DAYTON, P.K. & OLIVER, J.S. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science*, **197**, 55–58.

DAYTON, P.K. & OLIVER, J.S. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. *In* TENORE, K.R. & COULL, B.C., *eds. Marine benthic dynamics*. Columbia, SC: University of South Carolina Press, 93–120.

DAYTON, P.K., MORDIDA, B.J. & BACON, F. 1994. Polar marine communities. *American Zoologist*, **34**, 90–99.

DAYTON, P.K., ROBILLARD, G.A. & DEVRIES, A.L. 1969. Anchor ice formation in McMurdo Sound, Antarctica, and its biological effects. *Science*, **163**, 272–274.

DAYTON, P.K., ROBILLARD, G.A. & PAINE, R.T. 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. *In* HOLDGATE, M.W., *ed. Antarctic ecology*. Vol.1. London: Academic Press, 244–258.

DAYTON, P.K., ROBILLIARD, G.A., PAINE, R.T. & DAYTON, L.B. 1974. Biological accomodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs*, **44**, 105–128.

DEARBORN, J.H., FERRARI, F.D. & EDWARDS, K.C. 1986. Can pelagic aggregations cause benthic satiation? Feeding biology of the Antarctic brittle star *Astrotoma agassizii* (Echinodermata: Ophiuroidea). *Antarctic Research Series*, **44**, 1–28.

DELL, R.K. 1964. Zoogeography of Antarctic benthic Mollusca. *In* CARRICK, R., HOLDGATE, M. & PRÉVOST, J., *eds. Biologie Antarctique. Premier Symposium Organisé par le SCAR*. Paris: Hermann, 259–262.

DELL, R.K. 1972. Antarctic benthos. *Advances in marine biology*, **10**, 172–216.

DIECKMANN, G.S., EICKEN, H., HAAS, C., GARRISON, D.L., GLEITZ, M., LANGE, M., NÖTHIG, E.-M., SPINDLER, M., SULLIVAN, C.W., THOMAS, D.N. & WEISSENBERGER, J. 1998. A compilation of data on sea ice algal standing crop from the Bellingshausen, Amundsen and Weddell seas from 1983 to 1994. *Antarctic Research Series*, **73**, 85–92.

DREWRY, D.J. 1983. *Antarctic: glaciological and geological folio. Sheet 1*. Cambridge: Scott Polar Research Institute.

DUNBAR, R.B., ANDERSON, J.B. & DOMACK, E.W. 1985. Oceanographic influence on sedimentation along the Antarctic continental shelf. *Antarctic Research Series*, **43**, 291–312.

DUNBAR, R.B., LEVENTER, A.R. & STOCKTON, W.L. 1989. Biogenic sedimentation in McMurdo Sound, Antarctica. *Marine Geology*, **85**, 155–179.

EKAU, W. & GUTT, J. 1991. Notothenioid fishes from the Weddell Sea

Ekau, W. & Gutt, J. 1991. Notothenioid fishes from the Weddell Sea and their habitat, observed by underwater photography and television. *Proceedings of the National Institute of Polar Research Symposium on Polar Biology*, **4**, 36–49.

Ekman, S. 1967. *Zoogeography of the sea*. London: Sidgwick & Jackson, 417 pp.

Elverhøi, A. 1981. Evidence for a late Wisconsin glaciation of the Weddell Sea. *Nature*, **293**, 641–642.

Fahrbach, E., Rohardt, G. & Krause, G. 1992. The Antarctic coastal current in the southeastern Weddell Sea. *Polar Biology*, **12**, 171–182.

Fahrbach, E., Peterson, R.G., Rohard, G., Schlosser, P. & Bayers, R. 1994. Suppression of bottom formation in the southeastern Weddell Sea. *Deep-Sea Research I*, **41**, 389–411.

Foster, T.D., Foldvik, A. & Middleton, J.H. 1987. Mixing and bottom water formation in the shelf break region of the southern Weddell Sea. *Deep-Sea Research*, **34**, 1771–1794.

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

Gallardo, V.A. 1987. The sublittoral macrofaunal benthos of the Antarctic shelf. *Environment International*, **13**, 71–81.

Gallardo, V.A., Castillo, J.G., Retamal, M.A., Yáñez, A., Moyano, H.I. & Hermosilla, J.G. 1977. Quantitative studies on the soft-bottom macrobenthic animal communities of shallow Antarctic bays. *In* Llano, G.A., *ed. Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 361–387.

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

Genin, A., Dayton, P.K., Lonsdale, P.F. & Spiess, F.N. 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature*, **322**, 59–61.

Gerdes, D., Klages, M., Arntz, W.E., Herman, R.L., Galéron, J. & Hain, S. 1992. Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. *Polar Biology*, **12**, 291–301.

Gingele, F.X., Kuhn, G., Maus, M., Melles, M. & Schöne, T. 1997. Holocene ice retreat from the Lazarev Sea shelf, East Antarctica. *Continental Shelf Research*, **17**, 137–163.

Gleitz, M., Bathmann, U.V. & Lochte, K. 1994. Build-up and decline of summer phytoplankton biomass in the eastern Weddell Sea. *Polar Biology*, **14**, 413–422.

Gorny, M. & George, M.R. 1997. Oocyte development and gonad production of *Nematocarcinus lanceopes* (Decapoda: Caridea) in the eastern Weddell Sea, Antarctica. *Polar Biology*, **17**, 191–198.

Gorny, M., Arntz, W.E., Clarke, A. & Gore, D.J. 1992. Reproductive biology of caridean decapods from the Weddell Sea. *Polar Biology*, **12**, 111–120.

Graf, G. 1989. Benthic–pelagic coupling in a deep-sea benthic community. *Nature*, **341**, 437–439.

Grassle, J.F. & Sanders, H.L. 1973. Life histories and the role of disturbance. *Deep-Sea Research*, **20**, 643–659.

Gray, J.S. 1981. *The ecology of marine sediments: an introduction to the structure and function of benthic communities*. Cambridge: Cambridge University Press, 185 pp.

Gray, S.J. 1997. Gradients in marine biodiversity. *In* Ormond, R.F.G., Gage, J.D. & Angel, M.V., *eds. Marine biodiversity: patterns and processes*. Cambridge: Cambridge University Press, 18–34.

Grobe, H. 1986. Spätpleistozäne Sedimentationsprozesse am antarktischen Kontinentalhang vor Kapp Norvegia, östliche Weddell See. *Berichte zur Polarforschung*, **27**, 1–127.

Gruzov, E.N. & Pushkin, A.F. 1970. Bottom communities of the upper sublittoral of Enderby Land and the South Shetland Islands. *In* Holdgate, M.W., *ed. Antarctic ecology*, Vol. 1. London: Academic Press, 235–238.

Gutt, J. 1991a. On the distribution and ecology of holothurians in the Weddell Sea (Antarctica). *Polar Biology*, **11**, 145–155.

Gutt, J. 1991b. Are Weddell Sea holothurians typical representatives of the Antarctic benthos? – A comparative study with new results. *Meeresforschung*, **33**, 312–329.

Gutt, J. 1991c. Investigations on brood protection in *Psolus dubiosus* (Echinodermata: Holothuroidea) from Antarctica in spring and autumn. *Marine Biology*, **111**, 281–286.

Gutt, J. in press. On the direct impact of ice on benthic communities, a review. *Polar Biology*.

Gutt, J. & Starmans, A. in press. Quantification of iceberg impact and benthic recolonization patterns in the Weddell Sea (Antarctica). *Polar Biology*.

Gutt, J. & Ekau, W. 1996. Habitat partitioning of dominant high Antarctic demersal fish in the Weddell Sea and Lazarev Sea. *Journal of Experimental Marine Biology and Ecology*, **206**, 25–37.

Gutt, J. & Koltun, V.M. 1995. Sponges of the Lazarev and Weddell Sea, Antarctica: explanations for their patchy occurrence. *Antarctic Science*, **7**, 227–234.

Gutt, J. & Piepenburg, D. 1991. Dense aggregations of three deep-sea holothurians in the southern Weddell Sea, Antarctica. *Marine Ecology Progress Series*, **68**, 277–285.

Gutt, J. & Schickan, T. 1998. Epibiotic relationships in the Antarctic benthos. *Antarctic Science*, **10**, 398–405.

Gutt, J. & Siegel, V. 1994. Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). *Deep-Sea Research*, **41**, 169–178.

Gutt, J. & Starmans, A. 1998. Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biology*, **20**, 229–247.

Gutt, J., Ekau, W. & Gorny, M. 1994. New results on the fish and shrimp fauna of the Weddell Sea and Lazarev Sea (Antarctic). *Proceedings of the National Institute of Polar research Symposium on Polar Biology*, **7**, 91–102.

Gutt, J., Gerdes, D. & Klages, M. 1992. Seasonality and spatial variability in the reproduction of two Antarctic holothurians (Echinodermata). *Polar Biology*, **11**, 533–544.

Gutt, J., Gorny, M. & Arntz, W. 1991. Spatial distribution of Antarctic shrimps (Crustacea: Decapoda) by underwater photography. *Antarctic Science*, **3**, 363–369.

Gutt, J., Starmans, A. & Dieckmann, G. 1996. Impact of iceberg scouring on polar benthic habitats. *Marine Ecology Progress Series*, **137**, 311–316.

Gutt, J., Starmans, A. & Dieckmann, G. 1998. Phytodetritus deposited on the Antarctic shelf and upper slope: its relevance for the benthic system. *Journal of Marine Systems*, **17**, 435–444.

Gutt, J., Storch, V. & Arntz, W.E. 1998. Benthosforschung im Südpolarmeer: Störung schafft Vielfalt. *Biologie in unserer Zeit*, **28**, 362–370.

Haase, G.M. 1986. Glaciomarine sediments along the Filchner/Rønne ice shelf, southern Weddell Sea – first results of the 1983/84 ANTARKTIS-II/4 expedition. *Marine Geology*, **72**, 241–258.

Hambrey, M.J., Ehrmann, W.U. & Larsen, B. 1991. Cenozoic glacial record of the Prydz Bay continental shelf, East Antarctica. *Proceedings of the Ocean Drilling Program Scientific Results*, **119**, 77–132.

Harris, P.T. & O'Brien, P.E. 1996. Geomorphology and sedimentology of the continental shelf adjacent to Mac.Robertson Land, East Antarctica: a scalped shelf. *Geo-Marine Letters*, **16**, 287–296.

Hedgpeth, J. 1969. Introduction to Antarctic zoogeography. *Antarctic Map Folio Series*, **11**, 1-9.

Hedgpeth, J.W. 1971. Perspectives in benthic ecology in Antarctica. *In* Quam, L.O., *ed. Research in the Antarctic.* Washington, DC: American Association for the Advancement of Science, 667–684.

Hedgpeth, J.W. 1977. The Antarctic marine ecosystem. *In* Llano, G.A., *ed. Adaptations within Antarctic ecosystems.* Washington, DC: Smithsonian Institution, 3–10.

Heygster, G., Pedersen, L.T., Turner, J., Thomas, C., Hunewinkel, T., Schottmüller, H. & Viehoff, T. 1996. PELICON: Project for estimation of long-term variability of ice concentration. *EC Contract Report EV5V-CT93-0268* (DG XII).

Hubold, G. 1991. Ecology of notothenioid fish in the Weddell Sea. *In* di Prisco, G., Maresca, B. & Tota, B., *eds. Biology of Antarctic fish.* Berlin: Springer Verlag, 3–22.

Hubold, G. & Ekau, W. 1987. Midwater fish fauna of the Weddell Sea, Antarctica. *In* Kullander, S.O. & Fernholm, B., *eds. Fifth congress of European ichthyologists, proceedings, Stockholm, 1985*, Stockholm: Swedish Museum of Natural History, 391–396.

Hughes, T.J. 1998. *Ice sheets.* New York: Oxford University Press, 343 pp.

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.

Jazdzewski, K., Jurasz, W., Knittel, W., Presler, E., Presler, P. & Sicinski, J. 1986. Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. *Polar Biology*, **6**, 5–16.

Kennett, J.P. 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. *Journal of Geophysical Research*, **82**, 3843–3860.

Klages, M., Gutt, J., Starmans, A. & Bruns, T. 1995. Stone crabs close to the Antarctic Continent: *Lithodes murrayi* Henderson, 1888 (Crustacea; Decapoda; Anomura) off Peter I Island (68°51'S, 90°51'W). *Polar Biology*, **15**, 73–75.

Knox, G.A. 1960. Littoral ecology and biogeography of the southern oceans. *Proceeding of the Royal Society of London*, **B152**, 577–625.

Knox, G.A. 1977. The Antarctic polychaete fauna: its characteristics, distribution patterns, and evolution. *In* Llano, G.A., *ed. Adaptations within Antarctic ecosystems.* Washington, DC: Smithsonian Institution, 1111–1131.

Knox, G.A. & Lowry, J.K. 1977. A comparsion between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and the Polychaeta. *In* Dunbar, M.J., *ed. Polar oceans.* Montreal: Arctic Institute of North America, 423–462.

Kock, K.-H. 1992. *Antarctic fish and fisheries.* Cambridge: Cambridge University Press, 359 pp.

Kunzmann, K. 1996. Die mit ausgewählten Schwämmen (Hexactinellida und Demospongiae) aus dem Weddellmeer, Antarktis, vergesellschaftete Fauna. *Berichte zur Polarforschung*, **210**, 1–93.

Lampitt, R.S. 985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Research*, **32**, 885–897.

Lipps, J.H., Ronan Jr, T.E. & DeLaca, T.E. 1979. Life below the Ross Ice Shelf, Antarctica. *Science*, **203**, 447–449.

Lipps, J.H. & Hickman, C.S. 1982. Origin, age and evolution of Antarctic and deep-sea faunas. *In* Ernst, W.G. & Morin, J.G., *eds. The environment of the deep sea.* Englewood Cliffs, NJ: Prentice-Hall, 324–356.

Littlepage, J.L. 1965. Oceanographic investigations in McMurdo Sound, Antarctica. *Antarctic Research Series*, **5**, 1–31.

Lowry, J.K. 1975. Soft bottom macrobenthic community of Arthur Harbor, Antarctica. *Antarctic Research Series*, **23**, 1–19.

Magurran, A.E. 1988. *Ecological diversity and its measurements.* London: Croom Helm, 179 pp.

Mascetti, P., Fernandez de la Reguera, R., Albornoz, L., Oyarzún, S., Gorny, M. & Wehrtmann, I. 1997. Gonophore development and sex change in the Antarctic shrimp *Chorismus antarcticus* (Caridea: Hippolytidae). *Polar Biology*, **17**, 384–388.

Miller, D.G.M. & Hampton, I. 1989. *Biology and ecology of Antarctic krill (Euphausia superba* Dana*): a review. BIOMASS* Vol. 9. Cambridge: SCAR, SCOR & Scott Polar Research Institute, 166 pp.

Moreno, C.A. 1980. Observations on food and reproduction in *Trematomus bernacchii* (Pisces: Nototheniidae) from the Palmer Archipelago, Antarctica. *Copeia*, **1980**, 171–173.

Moyano, H.I. & Wendt, A. 1981. Bryozoa epizoos de *Psolus charcoti* Vaney, 1907 (Holothuroidea, Psolidae). *Serie Cientifica Instituto Antartico Chileno*, 7, 5–11.

Mühlenhardt-Siegel, U. 1988. Some results on quantitative investigations of macrozoobenthos in the Scotia Arc (Antarctica). *Polar Biology*, **8**, 241–248.

Odum, E.P. 1971. *Fundamentals of ecology. 3rd edition.* Philadelphia, PA: Saunders, 574 pp.

Pearse, J.S. 1965. Reproductive periodicities in several contrasting populations of *Odontaster validus* Koehler, a common Antarctic asteroid. *Antarctic Research Series*, **5**, 39–85.

Pearse, J.S., McClintock, J.B. & Bosch, I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. *American Zoologist*, **31**, 65–80.

Peck, L.S. & Bullough, L.W. 1993. Growth and population structure in the infaunal bivalve *Yoldia eightsi* in relation to iceberg activity at Signy Island, Antarctica. *Marine Biology*, **117**, 235–241.

Peck, L.S., Brockington, S., Vanhove, S. & Beghyn, M. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Marine Ecology Progress Series*, **186**, 1–8.

Peinert, R., Bodungen, B. von & Smetacek, V.S. 1989. Food web structure and loss rates. *In* Berger, W.H., Smetacek, V.S. & Wefer, G., *eds. Productivity of the ocean: present and past.* Chichester: Wiley, 35–48.

Picken, G.B. 1985a. Marine habitats – benthos. *In* Bonner, W.N. & Walton, D.W.H., *eds. Key environments: Antarctica.* Oxford: Pergamon Press, 154–172.

Picken, G.B. 1985b. Benthic research in Antarctica: past, present and future. *In* Gray, J.S. & Christiansen, M.E., *eds. Marine biology of polar regions and effects of stress on marine organisms.* Chichester: Wiley, 167–184.

Piatkowski, U. 1989. Macrozooplankton communities from Weddell Sea surface waters, Antarctica. *Pesquisa Antártica Brasileira*, **1**, 1–10.

Piepenburg, D. & Juterzenta, K. von. 1994. Abundance, biomass and spatial distribution pattern of brittle stars (Echinodermata: Ophiuroidea) on the Kolbeinsey Ridge north of Iceland. *Polar Biology*, **14**, 185–194.

Piepenburg, D., Voß, J. & Gutt, J. 1997a. Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off northeast Greenland (Arctic): a comparison of diversity and abundance. *Polar Biology*, **17**, 305–322.

Piepenburg, D., Ambrose Jr, W.G., Brandt, A., Renaud, P.E., Ahrens, M.J. & Jensen, P. 1997b. Benthic community patterns reflect water column processes in the northeast water polynya (Greenland). *Journal of Marine Systems*, **10**, 467–482.

Ravaioli, M., Frignani, M., Gambi, M.C., Labbrozzi, L. & Langone, L. 1999. Particle fluxes and sediment characteristics at three selected sites in the Ross Sea (Antarctica). *In* Spezie, G. & Manzella, G.M.R., *eds. Oceanography of the Ross Sea, Antarctica.* Milan: Springer Verlag, 209–221.

Reise, K. 1991. Mosaic cycles in the marine benthos. *In* Remmert, H., *ed. The mosaic-cycle concept of ecosystems.* Berlin: Springer Verlag, 61–82.

RHOADS, D.C. & YOUNG, D.K. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research*, **28**, 150–178.

RICE, A.L., THURSTON, M.H. & BETT, B.J. 1994. The IOSDL DEEPSEAS programme: introduction and photographic evidence for the presence and absence of a seasonal input of phytodetritus at contrasting abyssal sites in the northeastern Atlantic. *Deep-Sea Research*, **41**, 1305–1320.

SAHADE, R., TATIÁN, M., KOWALKE, J., KÜHNE, S. & ESNAL, G.B. 1998. Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica. *Polar Biology*, **19**, 85–91.

SAIZ-SALINAS, J.I., RAMOS, A., MUNILLA, T. & RAUSCHERT, M. 1998. Changes in the biomass and dominant feeding mode of benthic assemblages with depth off Livingston Island (Antarctica). *Polar Biology*, **19**, 424–428.

SANDERS, H.L. 1968. Marine benthic diversity: a comparative study. *American Naturalist*, **102**, 243–282.

SANDERS, H.L. 1969. Benthic marine diversity and the stability–time hypothesis. *Brookhaven Symposia in Biology*, **22**, 71–81.

SANDERS, H.L. 1979. Evolutionary ecology and life-history patterns in deep sea. *Sarsia*, **64**, 1–7.

SARÀ, M., BALDUZZI, A., BARBIERI, M., BAVESTRELLO, G. & BURLANDO, B. 1992. Biogeographic traits and checklist of Antarctic demosponges. *Polar Biology*, **12**, 559–585.

SCHRÖDER, M. & FAHRBACH, E. 1999. On the structure and the transport of the eastern Weddell Gyre. *Deep-Sea Research II*, **46**, 501–527.

SCHWARZBACH, W. 1988. Die Fischfauna des östlichen und südlichen Weddellmeeres: geographische Verbreitung, Nahrung und trophische Stellung der Fischarten. *Berichte zur Polarforschung*, **54**, 1–94.

SEBENS, K.P. 1985. The ecology of the rocky subtidal zone. *American Scientist*, **73**, 548–557.

SMAYDA, T. & BIENFANG, P.K. 1983. Suspension properties of various phyletic groups of phytoplankton and tintinnids in an oligotrophic, subtropical system. *Marine Ecology*, **4**, 289–300.

SMETACEK, V., SCHAREK, R., GORDON, L.I., EICKEN, H., FAHRBACH, E., ROHARD, G. & MOORE, S. 1992. Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea, Antarctica. *Deep-Sea Research*, **38**, 153–168.

SMITH, S.L. & SCHNACK-SCHIEL, S. 1990. Polar Zooplankton. *In* SMITH, W.O., *ed. Polar oceanography Part B: chemistry, biology, and geology.* San Diego: Academic Press, 527–598.

STANWELL-SMITH, D. & CLARKE, A. 1998. Seasonality of reproduction in the cushion star *Odontaster validus* at Signy Island, Antarctica. *Marine Biology*, **131**, 479–487.

STANWELL-SMITH, D. & PECK, L. 1998. Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. *Biological Bulletin* **194**, 44–52.

STARMANS, A. & GUTT, J. in press. Mega-epibenthic diversity: a polar comparison. *Contemporary Issues in Marine Biodiversity, 17–18th September 1998.* London: Linnean Society of London & The Natural History Museum.

STARMANS, A., GUTT, J. & ARNTZ, W.E. 1999. Mega-epibenthic communities in Antarctic and Arctic shelf areas. *Marine Biology*, **135**, 269–280.

THIERY, R.G. 1982. Environmental instability and community diversity. *Biological Reviews*, **57**, 691–710.

VOLK, T. & HOFFERT, M.I. 1985. Ocean carbon pumps, analysis of relative strengths and efficiencies in ocean-driven atmospheric CO_2 changes. *Geophysical Monograph*, **32**, 99–110

VOß, J. 1988. Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres (Antarktis). *Berichte zur Polarforschung*, **45**, 1–145.

WEBER, M. 1992. Spätquartäre Sedimentation am Kontinentalrand des südöstlichen Weddellmeeres, Antarktis. *Berichte zur Polarforschung*, **109**, 1–165.

WEFER, G., FISCHER, G., FÜTTERER, D. & GERSONDE, R. 1988. Seasonal particle flux in the Bransfield Strait, Antarctica. *Deep-Sea Research*, **35**, 891–898.

WHITE, M.G. 1984. Marine benthos. *In* LAWS, R.M., *ed. Antarctic ecology.* Vol. 2. London: Academic Press, 421–461.

WHITE, P.S. & PICKETT, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. *In* PICKETT, S.T.A. & WHITE, P.S., *eds. The ecology of natural disturbance and patch dynamics.* Orlando, FL: Academic Press, 3–13.

WÖHRMANN, A.P.A. & ZIMMERMANN, C. 1992. Comparative investigations on fishes of the Weddell Sea and the Lazarev Sea. *In* BATHMANN, U., SCHULZ-BALDES, M., FAHRBACH, E., SMETACEK, V. & HUBBERTEN, H.-W., *eds. The expeditions ANTARKTIS IX/1-4 of the research vessel "Polarstern" in 1990/91. Berichte zur Polarforschung*, **100**, 208–222.

ZAMORANO, J.H. 1983. Zonación y Biomassa de la macrofauna benthónica en Bahia South, Archipiélago de Palmer, Antártica. *Serie cientifica. Instituto Antartico Chileno*, **30**, 27–38.

ZIMMERMANN, C. 1997. On the demersal fish fauna of the Lazarev Sea (Antarctica): composition and community structure. *In* BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., *eds. Antarctic communities: species, structure and survival.* Cambridge: Cambridge University Press, 26–32.