A unique assemblage of epibenthic sessile suspension feeders with archaic features in the high-Antarctic

Josep-Maria Gili[a,*], Wolf E. Arntz[b], Albert Palanques[a], Covadonga Orejas[b], Andrew Clarke[c], Paul K. Dayton[d], Enrique Isla[a], Nuria Teixidó[a], Sergio Rossi[a], Pablo J. López-González[e]

[a]*Institut de Ciències del Mar (CMIMA-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain*
[b]*Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstrasse, 27568 Bremerhaven, Germany*
[c]*British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[d]*Scripps Institution of Oceanography, La Jolla, CA 92093-0227, USA*
[e]*Departamento de Fisiología y Zoología, Universidad de Sevilla, Av Reina Mercedes 6, 41012 Sevilla, Spain*

Abstract

We suggest that the epibenthic communities of passive suspension feeders that dominate some high-Antarctic seafloors present unique archaic features that are the result of long isolation, together with the effects of environmental features including reduced terrestrial runoff and favourable feeding conditions. These features probably originated during the Late Cretaceous, when the high-Antarctic environment started to become different from the surrounding oceans. Modern Antarctic communities are thus composed of a mixture of Palaeozoic elements, taxa that migrated from the deep ocean during interglacial periods, and a component of fauna that evolved from common Gondwana Cretaceous ancestors. We explore this hypothesis by revisiting the palaeoecological history of Antarctic marine benthic communities and exploring the abiotic and biotic factors involved in their evolution, including changes in oceanic circulation and production, plankton communities, the development of glaciation, restricted sedimentation, isolation, life histories, and the lack of large predators. The conditions favouring the retention of apparently archaic features in the Antarctic marine fauna remain to be fully elucidated, but high-Antarctic communities are clearly unique and deserve special conservation.

1. Introduction

Antarctic benthic communities have a predominantly circumpolar distribution, probably related to the powerful Antarctic Circumpolar Current (Clarke and Johnston, 2003). There is, however, also significant spatial heterogeneity generated by variations in ice cover, sediment dynamics, and local hydrodynamic and trophic factors (Clarke and Crame, 1989). Current data suggest that the continental shelves of the Weddell and Ross seas exhibit the greatest diversity and the highest biomass levels in the Antarctic (Dayton et al.,

*Corresponding author. Fax: +34 93 221 7340.
E-mail address: gili@icm.csic.es (J.-M. Gili).

1974; Arntz et al., 1994; Gutt and Starmans, 1998). Indeed these habitats, extending from the edge of the continental ice sheet beyond the shelf edge, often to depths greater than 600 m, are among the richest in terms of sessile fauna in the world ocean (Dayton, 1990). These high-Antarctic benthic ecosystems are unusual in a number of ways, notably in the depth of the shelf, the dominance of sessile suspension feeders, and the development of complex three-dimensional biogenic structures on soft bottoms. Although the Antarctic shelf fauna contains a recent component, which probably arrived along shallow-water routes, it also contains relict taxa whose evolutionary history can be traced back in some cases to the Palaeozoic (Feldmann and Crame, 1998). Here we argue that the composition of the modern communities in the Weddell Sea, and other high-Antarctic areas, is the result of a low-sedimentation environment, which was also characteristic of Cretaceous epicontinental seas (Leckie et al., 2002).

The evolutionary pattern followed by these communities has differed from the pattern in other oceans because of the very different ecological influences to which they have been exposed. In many respects these conditions are akin to the conditions existing in the oceans at the beginning of the Palaeocene (Dingle and Lavelle, 2001). Our hypothesis thus is that this similarity of certain environmental conditions might have resulted in the development of communities with life forms convergent on Cenozoic rather than Palaeozoic faunas. In this review we examine the apparently archaic features in the structure and morphotypes of the benthic communities of high-Antarctic shelf in the Weddell Sea (Gutt and Starmans, 1998), Ross Sea (Dayton et al., 1974; Dearborn, 1977), and other areas (Dell, 1972), and attempt to explain these features.

1.1. Composition of benthic communities in the high Antarctic

Although the shallow-water communities of the Antarctic continental shelf have a distinctly archaic, deep-sea character, the taxa themselves are not necessarily ancient or primitive, and many are highly derived (Aronson et al., 1997). The main components of the sessile suspension-feeding communities in the high-Antarctic are: Porifera (Demospongia, Hexactinellida, Calcaria), Gorgonaria, Pennatularia (mostly deeper), Alcyonaria, Stolonifera, Hydrozoa (incl. Milleporidae), Actiniaria,

Bryozoa, Brachiopoda, and both solitary and colonial Ascidiacea. The mobile epifauna includes: Echinodermata (regular Echinoidea, Asteroidea, Ophiuroidea, Holothurioidea); Peracarida (Amphipoda, Isopoda, Tanaidacea, Mysidacea, Cumacea), Ostracoda, Caridea, Teleostei, Selachii (Rajidae), Prosobranchia, Opisthobranchia, Polyplacophora, Bivalvia, Cirripedia (Balanidae, rare and Scalpellidae), Scleractinia (solitary), Turbellaria, Nemertinea and Pterobranchia. The sparse infauna includes: Polychaeta, Bivalvia, Prosobranchia, Echiurida, Priapulida, Sipunculida, irregular Echinoidea, Scaphopoda and Solenogastres (Arntz et al., 1994; Fogg, 1998; Gutt et al., 2000, 2004). The dominant taxa can vary over short distances (Teixidó et al., 2002), and this pattern is largely determined by iceberg scour (Gutt and Starmans, 1998). In the Weddell Sea this community ranges over depths from ca. 70 m down to about 400 m, and lives well within the zone of iceberg scour. These benthic communities display a key characteristic that differentiates them from most other shelf ecosystems extant today in that they are dominated by sessile suspension feeders living mostly on soft substrata.

The principal difference between the faunal assemblages of modern Antarctic continental shelves and those in other oceans is that these three-dimensional communities cover large sections of the Antarctic continental shelves, whereas elsewhere they are found only on rocky substrata or are confined to specific areas such as deep coral banks (Mortensen and Buhl-Mortensen, 2004). In recent years, detailed studies carried out in the Weddell Sea and other regions of the high-Antarctic continental shelf have demonstrated clearly the richness and high degree of heterogeneity of communities dominated by sessile suspension feeders, many of which extend continuously over kilometres (Gutt, 2000; Teixidó et al., 2002).

1.2. High-Antarctic communities at shallower and deeper depths

True shallow-water communities are missing in those parts of the high-Antarctic where ice shelves cover all shallow-water sites. This is true for the Weddell and Lazarev Sea coasts, and to a lesser degree for the Ross Sea coast. Here, however, there are sites within diving depths (e.g. around McMurdo Sound: Dayton et al., 1974, and Terra Nova Bay: Cattaneo-Vietti et al., 2000). The shallowest site in

the high-Antarctic Weddell Sea is the unique *Four Seasons Bank,* which reaches as shallow as 60 m below the sea surface (Raguá-Gil et al., 2004). The community at this site, which is exposed to strong currents, is also dominated by suspension feeders but on very coarse sand, gravel and boulders. The fauna includes dense populations of Hydrozoa and Stolonifera together with a motile epifauna mainly of regular echinoids, small gastropods and peracarid crustaceans (Gili et al., 1999; Raguá-Gil et al., 2004) (Fig. 1). This is somewhat similar to the extremely dense soft-bottom infaunal/shallow epifaunal community of McMurdo East Sound,

described by Dayton and Oliver (1977), which has a canopy of only a few centimetres.

Below the archaic community in the high-Antarctic Weddell Sea there is a level-bottom community dominated numerically by ophiuroids, which, surprisingly, have their highest species numbers (15–17) between 300 and 350 m, at the same depth as the asteroids (19–21 species; Arntz et al., 2005). Truly archaic species (such as the stalked crinoid *Bathycrinus aldrichianus*, see Macurda and Meyer, 1976) have been collected only on the Antarctic deep slope (1500 m) (D. Gerdes, personal observation).
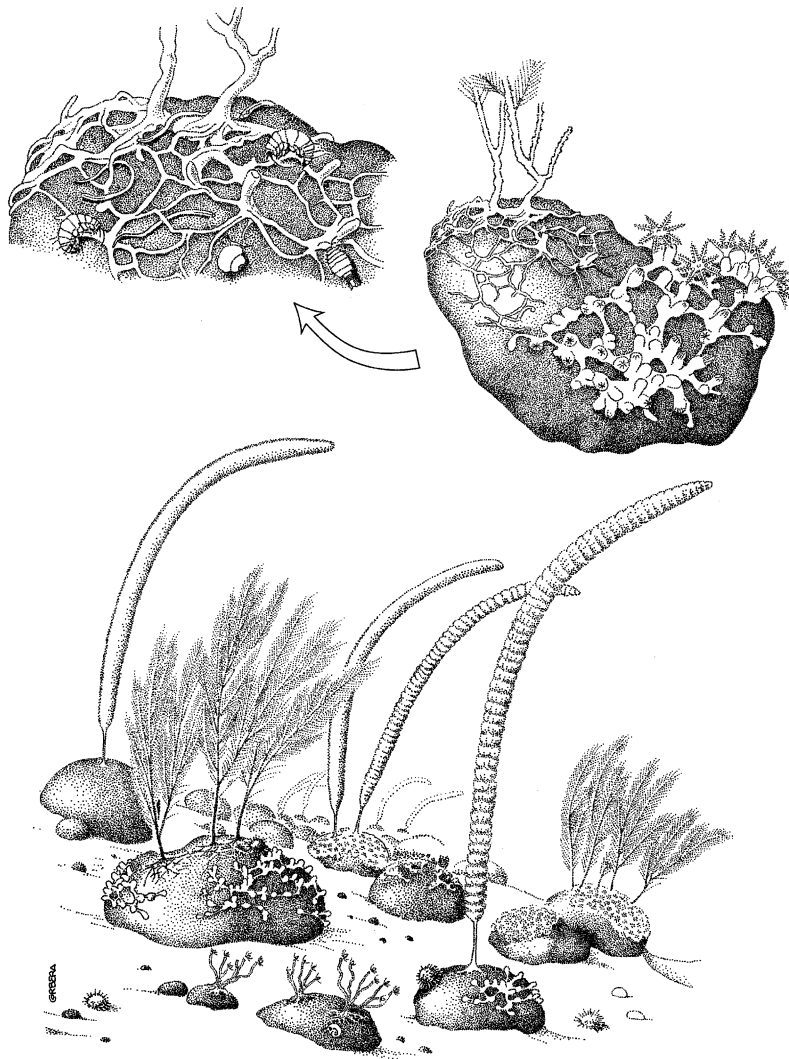

Fig. 1. Epibenthic assemblage on hard substratum at the 60–70 m deep hilltop of Four Seasons Inlet (East of the Weddell Sea) (drawing by Jordi Corbera Barcelona).

1.3. Other macrofaunal benthic communities in the Antarctic

A traditional view of Antarctic benthic marine communities is that densities and biomasses of macrobenthos are high both on hard and soft bottoms, especially in comparison with the Arctic (Dayton, 1990). However, a long history of comparative studies in shelf and shallow areas, mainly on soft bottom areas (e.g. Mühlenhardt-Siegel, 1988, 1989; Gerdes et al., 1992; Galerón et al., 1992; Arntz et al., 1994, 2005; Klöser et al., 1994; Gutt and Starmans, 1998; Arntz and Gili, 2001; Barnes, 2005) have shown that there are also communities that exhibit greatly reduced vertical structures, which are typically dominated by a single group such as ascidians or pennatulaceans. Macroalgae are important in the shallower areas and these are often dense infaunal populations of modern bivalves or polychaetes (e.g. Gallardo, 1987; Gambi et al., 1997; Mercuri et al., 1998). Thus within the Antarctic (even in the high Antarctic) there are typical modern communities, suggesting that there must be specific reasons why apparently archaic communities survive on the high-Antarctic shelf.

2. Are there similar recent communities elsewhere in the world?

2.1. Shallow areas

In shallow Antarctic waters, assemblages of sponges, bryozoans, anthozoans and ascidians form benthic communities with complex three-dimensional structures (Fig. 2). These are similar to those found on rocky bottoms in temperate or tropical seas, such as coral reefs, or coralligenous hard-bottom communities of the Mediterranean (Gili and Coma, 1998; Witman and Dayton, 2001). Soft bottoms predominate on the continental shelves of the world's oceans, and sessile suspension feeders are commonly found there. However, the species richness and structural development of such communities are much less pronounced than in the Antarctic, and deposit-feeding or burrowing organisms tend to dominate instead (Lanihan and Micheli, 2001). Epibenthic communities of sessile suspension feeders are very rare on accumulations of fine-grained marine sediment, although individuals do occur on small-scale, cryptic surfaces of skeletal debris lying on the sediment surface (McKinney, 2003). Factors such as input of fine

sediment or the presence of bioturbating organisms can result in the clogging of filtering organs and/or instability of the substratum, and thereby interfere with the development of sessile suspension-feeding assemblages (Gili and Coma, 1998). Hemisessile or mobile suspension-feeding communities represent a totally different type of community, are typically composed of a few dominant species of bivalves, ophiuroids, or polychaetes, and are more common (Reise, 2002). In the high Antarctic, the presence of dense populations of sessile suspension feeders tends to increase the stability of the substratum through retention and consolidation of the sediment, thereby creating a favourable habitat for settlement of many other species.

In the NE Adriatic the soft-bottom associations have a species composition and structure characteristic of the modern fauna, being dominated mainly by molluscs and polychaetes; however, there are also communities that have a more Palaeozoic-like benthic ecology (McKinney, 2003). The latter are dominated by sessile epibenthic suspension feeders, sometimes with mobile epibenthic detritus feeders. Ophiuroids and comatulid crinoids constitute the mobile suspension-feeding guild in these communities, and, as in the modern Antarctic assemblage they climb up other erect organisms such as bryozoans, allowing them to feed higher in the water column. The structure and ecology of these communities is similar to those living in the post-Cambrian Palaeozoic, although species composition is entirely modern. This fauna is found in areas with low-nutrient water, low contents of suspended sediment, a low intensity of grazing and predation, and relatively few endobenthic bioturbators; these are conditions similar to those postulated for Palaeozoic seas (McKinney, 2003). A comparable situation has been reported for Caribbean ophiuroid-dominated and tropical Pacific benthic associations of coralline sponges and articulate brachiopods in oligotrophic waters (Thayer, 1989; Thayer et al., 1992).

2.2. Deep areas

The modern deep seas suffer the same (low) degree of bioturbation as Early Palaeozoic shelves, and harbour an immobile soft-substrate fauna reminiscent of Palaeozoic shallow seas: stalked crinoids, articulate brachiopods, hexactinellid sponges, and free-living immobile bryozoans. It has long been suggested that archaic Cambrian and

Palaeozoic faunas were displaced to deep-sea environments from shallow shelves (Wood, 1998). This Paleozoic similarity of deep-sea communities has been observed in many regions (McKinney, 2003) and could be extended to deep filter-feeding communities around the world (Roberts and Hirshfield, 2004).

Deep-sea benthic communities occur worldwide and have been studied at least since the *Challenger* expedition (Zibrowius, 1980). While the Cretaceous extinction (*K/T*) event obviously had profound impacts on most of the continental shelves, the bathyal and abyssal zones, canyons and seamounts may have been spared some of the impacts. It has

been speculated that these habitats could have served as a refuge for many species that could later recolonize shallower areas. What is not clear, however, is whether periodic anoxic events in the deep sea could have eradicated the deep-sea fauna entirely (Rogers, 2000). The biological communities in some deep-water habitats are characterized by great biogenic structure (e.g. cold coral banks: Fosså et al., 2002) and complex vertical heterogeneity (Thrush and Dayton, 2002). Studies of the biology and ecology of deep-coral communities have expanded only in the last decade (Freiwald et al., 1999) and are revealing systems that are more diverse and productive than previously thought (Gage et al., 1995). The very low continental sediment inputs, the slow bacterial turnover, the efficient use of carbon, and the lack of key groups of predators make some of these deep-sea communities strikingly reminiscent of those inhabiting the continental shelf of the Weddell and Ross seas.

Many deep-dwelling coral communities comprising sponges, gorgonians, and other groups of sessile filter feeders are located on the edges of the continental shelves, for example on the Scandinavian and British deep shelf and slope. This region appears to mark the maximum extension of glaciation during the last ice age (Clark et al., 1996). When the ice sheets receded, the inability of these communities to recolonize the inner shelf may be explained by the increased flux of terrigenous sediments from the continental land mass following deglaciation (Arthur and Garrison, 1986). Input of
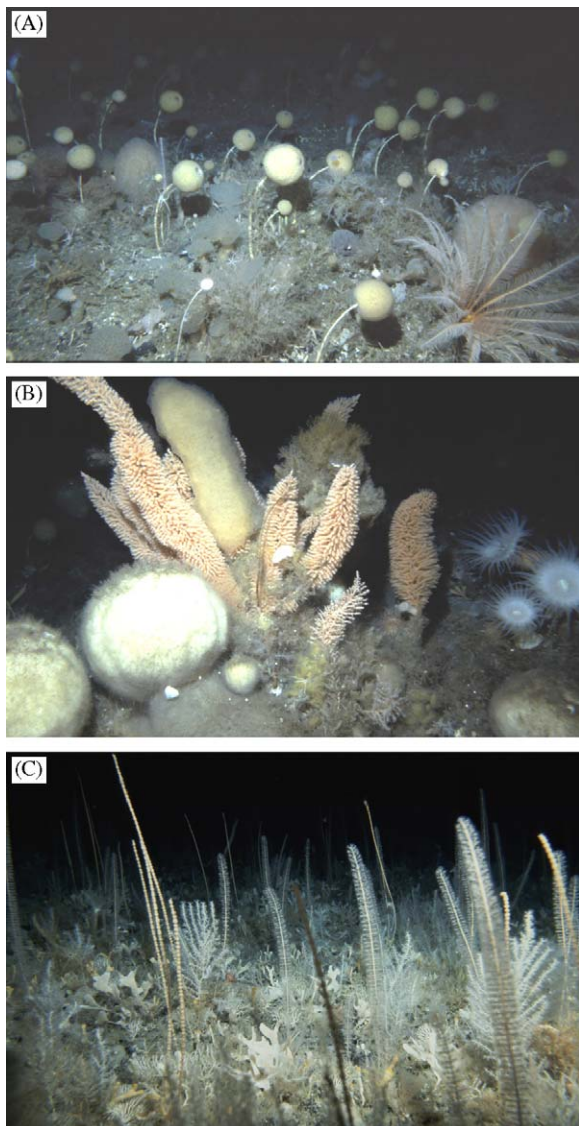
Fig. 2. Three views of Antarctic benthic communities in the Weddell Sea dominated by sessile suspension feeders. The three pictures are representative of the three-dimensional, highly diversified benthic communities growing on soft-bottom substrata, comparable only to hard-bottom communities in tropical and temperate seas. (A) Dense aggregation of *Stylocordyla* sp. accompanied by the crinoid *Promachocrinus kerguelensis,* several soft bryozoans, and a colonial ascidian (*Synoicum adereanum*) covering the sea floor on the continental shelf in the Weddell Sea at a depth of 189-193 m. (B) Communities dominated by round yellow-brown sponges (*Cinachyra barbata*) and the pink bottle brush gorgonian (*Dasystenella acanthina*), smaller colonies of *Thouarella* sp., and white anemones (*Hormathia* sp.) on the shelf at depths between 136 and 152 m. (C) Communities dominated by different species of bryozoans and gorgonians such as the rigid species of yellow *Cellarinella* sp. and *Systenopora contracta*, the rigid species of white *Hornea* sp. (Cyclostomata), *Reteporella* sp., *Smittina antarctica*, colonies of the unbranched gorgonian *Primnoella* sp., and the white bottle brush colonies of *Primnoisis antarctica* covering the sea floor on the shelf between 193 and 218 m (photographs by Julian Gutt, AWI, Bremerhaven).

food to the bottom may thus be one of the most important differences between what may have happened in the regions inhabited by deep-dwelling corals and the Antarctic shelves. In the cold-water coral communities input of particulate food can sometimes be substantial, but is typically sporadic (Duineveld et al., 2004). In contrast, the continental shelves off Antarctica are fertilized every spring and summer by an enormous amount of food sedimenting to the bottom, produced by ice thaw and the activity of planktonic organisms. Accordingly, the combination of a very reduced influx of inorganic sediment coupled with an abundant supply of food may well have supported the development of communities of suspension feeders from ancestral species that survived below the Antarctic shelf edge. There would thus seem to be a certain similarity between the deep-dwelling coral communities and the Antarctic communities with respect to both their origin and environmental conditions.

3. Are high-Antarctic assemblages one of oldest marine benthos shelf communities in the world?

The composition of the high-Antarctic communities has been attributed both to ecological and historical factors (Dell, 1972; Dayton, 1990; Arntz et al., 1994; Teixidó et al., 2002; Clarke et al., 2004). While the overall importance of historical factors such as variation in the extension of the ice shelf is well recognized within the Tertiary, it is now clear that some elements of the present Antarctic fauna can be traced back to the Mesozoic (Clarke and Crame, 1989; Clarke, 1996). We therefore may speculate that the ancestral species at the end of the Cretaceous, using the deep sea as a refuge, gave rise to species that recolonized the high-Antarctic shelf when the environmental conditions changed in a way that facilitated this colonization process. These species, together with Palaeozoic elements and others that later colonized from the deep-sea habitats, constitute the recent benthic communities in the high Antarctic. As a result, the marine Antarctic benthos possesses characteristics reminiscent of Palaeozoic marine communities together with components of modern deep-sea fauna (Aronson and Blake, 2001). Ecological evidence thus suggests that the benthic communities of the high Antarctic, such as the Weddell Sea, exhibit what has been termed a retrograde community structure, reminiscent of general Palaeozoic characteristics. The similarity in structures and life styles of present-day Antarctic communities with those of the Palaeozoic is thus a convergent development, consequent upon a similar environmental setting. To see how this convergence has occurred, we need to look back into history.

4. From the Cambrian to the present

4.1. Faunal change in the Phanerozoic

Sepkoski (1981) partitioned the skeletonized marine fauna into three broad temporal associations that he termed evolutionary faunas: (a) *Cambrian Fauna*, characterized by Trilobita, Brachiopoda Inarticulata, Polychaeta (including some old worm groups), Monoplacophora, Hyolitha, and Pogonophora. (b) *Palaeozoic Fauna*: characterized by the radiation of the shelly fauna, and the presence of Brachiopoda Articulata, stalked Crinoidea, Ostracoda, Cephalopoda, Anthozoa, Ophiuroidea, together with, to a lesser extent, Bryozoa Stenolaemata, Gastropoda, Asteroidea, Bivalvia. There was a high diversity of epifaunal suspension feeders, increasing in dominance until the end of the Palaeozoic era. The major extinction event at the end of the Permian caused a rapid turnover in faunas, and the final decline of the Palaeozoic fauna appears to begin in Late Cretaceous, continuing into the Cenozoic. (c) *Modern Fauna*, important from latest Permian/earliest Triassic, and characterized by the dominance of Mollusca, primarily Gastropoda and Bivalvia, and to a lesser extent Cephalopoda. Other important groups include Osteichthyes, Malacostraca, Echinoidea, Bryozoa Gymnolaemata, Demospongia and Hexactinellida, Chondrichthyes, Polychaeta and Stelleroidea (Asteroidea and Ophiuroidea).

The dominant components of the Modern Fauna during the Early Jurassic were siphonate and partly mobile (pectinid) bivalves, together with sessile oysters, which in shallow waters replaced the brachiopods. There were also gastropods, ammonoid and coleoid (belemnite) cephalopods, and the diversifying decapods, such as thalassinoids. There still were stalked crinoids and many articulate brachiopods, but these were found increasingly in deep water. Towards the end of the Jurassic, benthic communities came to resemble more and more aspects of recent assemblages, although articulate brachiopods and stalked crinoids were still much more abundant (McKerrow, 1978). Infaunal space was used to a much higher degree than before.

If the Triassic was still essentially Palaeozoic in marine community organization and skeletal architecture, the Late Cretaceous was already of essentially modern aspect (Vermeij, 1983). There were, however, aspects of the Cretaceous fauna that resembled very much that of the previous era. There were new ammonite families, the rudist bivalves appeared, and the inoceramid bivalves increased in importance and grew much larger. Molluscs (cephalopods, bivalves, gastropods) dominated, and on soft bottoms at intermediate depths demosponges were common. In comparison to preceding periods, however, epifaunal communities showed less marked tiering because of the dominance of bivalves and other molluscs, which built low canopies and were often partly buried. Stalked crinoids seem to have disappeared entirely from shallow water, but articulate brachiopods were still common. Infaunal ecospace was used to a much greater extent than in preceding eras (McKerrow, 1978).

Sepkoski's (1981) study of 91 metazoan classes during the last 650 Ma shows that the roots of most Recent faunal elements extend far into the past. Almost two-thirds of the modern classes made their appearance in the Vendian and Cambrian, and very few first appeared in the Permian or later. With few exceptions such as the Trilobita, which became extinct at the end of the Palaeozoic, most major clades originated in the Palaeozoic, expanded in the Mesozoic and Cenozoic and persist to the present (Bambach, 1985). For example, hexactinellids, demosponges, bivalves and malacostracans, all characteristic of the Modern Fauna, appeared already in the Early Cambrian (Sepkoski, 1984). Change after the Palaeozoic was typically within existing clades, in which new designs and capabilities evolved, and in the ecological character of the communities rather than by the evolution of new clades (Sepkoski 1981, 1984).

4.2. Escalation: the sequence of evolutionary innovation

There had been major faunal changes during the Palaeozoic, but what has become known as the *Mesozoic Marine Revolution* brought unprecedented changes to benthic communities (Vermeij, 1987). The Late Triassic marks a time of important changes: the attainment of intense bioturbating capacity in arenicolid annelids and glyphaeoid decapods, the appearance of drilling predators,

and the evolution of potentially shell-crushing palinurids, reef-building scleractinian corals, rock-boring bivalves and bioeroding sea urchins.

The Early Jurassic witnessed the origin of shell-preying asteroids, intensely bioturbating sea urchins and thalassinid shrimps, and the diversification of shell-crushing elasmobranchs. By the Middle Jurassic, antipredatory features had developed strongly in bivalves and gastropods, and gastropods vulnerable to crushing diminished. Conchicolous hermit crabs developed, as did bioeroding bivalves, grazing-resistant encrusting coralline algae, and calcareous operculate structures in cephalopods; the diversification of mineralized plankton (foraminiferans, radiolarians, coccolithophores, and the first diatoms) was enhanced, and scleractinian corals assumed hermatypic habits.

The most important evolutionary innovation in the Cretaceous, however, was, the origin of flowering plants (angiosperms) during the Barremian. They increased greatly in diversity on land, but also invaded the sea: unconsolidated shallow water marine bottoms became colonized by a highly productive community whose primary producers were angiosperms. Other innovations were the diversification of predatory gastropods, many of them drillers, and of sessile barnacles with calcareous lateral and opercular plates. Operculate cheilostome bryozoans became abundant, highly integrated bryozoan colonies diversified, rudist bivalves and several groups of foraminiferans developed the hermatypic habit; stalked crinoids and most brachiopods disappeared from shallow-water communities, many families of shell-breaking predators developed, deeply excavating burrowers and bioturbators evolved, and the incidence of repaired shell damage in gastropods rose to modern levels.

The unprecedented changes in the Mesozoic Marine Revolution coincided with a large-scale increase in organic diversity. During the post-Ordovician Palaeozoic, the number of marine animal families was broadly constant, being exceeded only in the Late Cretaceous, when the diversification of modern groups such as gastropods, bivalves, forams, fish and decapods was well under way.

4.3. Displacement of older communities

The three evolutionary faunas occupied different environments during the post-Cambrian portion of

the Palaeozoic era, with mollusc-rich communities in nearshore environments, brachiopod-rich environments in more offshore shelf environments, and trilobite-rich communities in deepwater environments (Sepkoski, 1981). Changes in dominance involved nearshore–offshore expansion of new community types. Each successive fauna appeared onshore of the others and then successively displaced elements of the previous fauna further offshore. As a broad generalization, predation was lower and community structure was more archaic in offshore, deep-water habitats compared to nearshore, shallow-water habitats (Aronson and Blake, 2001). The process of displacement has been going on over tens to hundreds of million years, and it is likely that competitive replacement of onshore taxa caused the observed patterns (Sepkoski and Miller, 1985; Aronson, 1994; Aronson and Blake, 2001). Epifaunal suspension-feeder communities on shallow-water soft substrata were predominant throughout much of the Palaeozoic and into the Mesozoic, but have been far more restricted in their distribution since the end of the Mesozoic. At least four phyla have played key roles in such palaeocommunities at different times in geological history, so their decline is not a simple correlate of a single taxon (Jablonski and Bottjer, 1983).

In the early Mesozoic there still was a permanence of various guilds and remarkable evolutionary stability of morphotypes, with pedunculate brachiopods and epibyssate bivalves dominating. "Cemented forms" contained rudist bivalves (which, contrary to former belief, may have been sediment dwellers, Gili et al., 1995; Skelton et al., 1995) and certain orders of sponges and bryozoans. From the Jurassic onward, epifaunal suspension feeders on soft substrata were increasingly replaced by infaunal and more mobile epifaunal suspension feeders, giving nearshore soft-bottom communities their modern, bivalve-dominated ecology with increasing importance of heterodont siphonate bivalves (Aberhan, 1994; Aronson and Blake, 2001). In the Palaeozoic most animals in benthic communities had been low in biomass, whereas in the modern type they were, and are, high (Bambach, 1983). The last extensive occurrence of epifaunal suspension-feeding palaeocommunities was in the Late Cretaceous.

Sessile suspension feeders such as sponges of the genera *Doryderma*, *Siphonia*, and *Hallirhoa*, together with species of bivalve molluscs, bryozoans,

and corals, dominated Cretaceous communities (Kennedy, 1978) (Fig. 3). These communities spread widely over the continental shelves, which were broader and shallower than modern continental shelves, giving rise to wide, shallow epicontinental seas. The dominant species in these Cretaceous seas exhibited morphological characteristics similar to those of modern Antarctic species. The Cretaceous fauna was dominated by epifaunal and infaunal suspension feeders (Ausich and Bottjer, 1982; Bambach, 1983; Stilwell, 1997). For example, in many parts of the ocean, erect or massive highly branched forms, or stalked articulated forms, have been losing ground, though they can still be found in the deep sea (Etter and Mullineaux, 2001). Bryozoans and other sessile invertebrates in the Southern Ocean have generally followed the evolutionary trends for the groups overall, but a fraction of the dominant forms remain strongly reminiscent of ancestral forms. For instance, a predominance of large erect, branching forms and of tubular forms has been reported from high-Antarctic continental-shelf bryozoans (McKinney et al., 2001).

The Cretaceous was an important period of change in that archaic communities were still present, but a striking modernisation of faunas was underway (Jablonski and Bottjer, 1983). The more archaic epifauna-rich communities were mostly restricted to relatively offshore habitats, while soft substrata nearshore already had been occupied primarily by deposit-feeding and infaunal suspension-feeding communities that were relatively modern in structure and composition. Shelled infaunal taxa may have been present in offshore habitats as well, but it is here that the last prolific development of sessile epifaunal suspension feeders can be seen (Bottjer and Ausich, 1986). However, these offshore habitats were not inhabited by a suspension-feeding three-dimensional fauna of the typical Palaeozoic or recent high-Antarctic type (at least such a fauna does not appear in the fossil record), but by gryphaeid oysters, inoceramid and spondylid bivalves, scallops, gastropods, and echinoids. Many of the brachiopods and bivalves used the "snowshoe" (floating on the soft mud) or "iceberg" strategy (half buried in the mud: Thayer, 1975; Jablonski and Bottjer, 1983; Aberhan, 1994). Infauna appears to have been extremely rare in these soft sediments. The epifauna also showed particular adaptations: small adult size; larval settlement on relatively large hard substrata or on very small substrata followed by expanded or
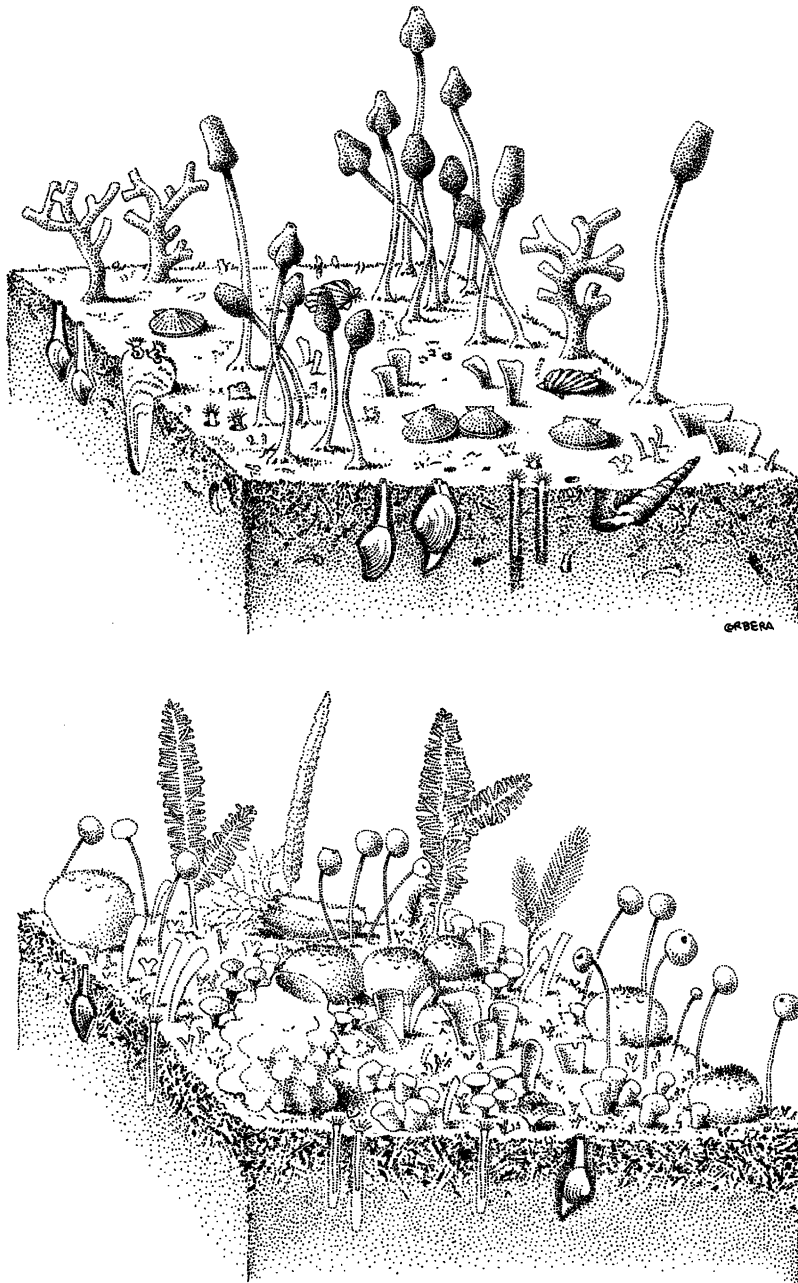
Fig. 3. Schematic view of two examples of benthic communities dominated by Cretaceous (modified from Kennedy, 1978) and present-day sessile suspension-feeder communities. The Cretaceous community is dominated by sponges of the genera *Doryderma*, *Siphonia* and *Hallirhoa*, and the Weddell Sea community is dominated by "lollipop" sponges (*Stylocordyla* sp.) and gorgonians *(Thouarella* sp.) together with other bryozoan and ascidian species (drawing by Jordi Corbera, Barcelona).

inflated free-living adults. Modern brachiopods and many scallops are usually dependent on islands of hard substrate for recruitment on soft bottoms. The chalk faunas, inhabitants of Cretaceous offshore soft substrata, were thus archaic not in their species or generic level composition, but in their adaptive

types and trophic structures (Jablonski and Bottjer, 1983).

In contrast to shallow-water biological communities that have become progressively more monotonous since the Cretaceous, the modern high-Antarctic shelf benthic communities are highly

diversified and heterogeneous (Jackson and McKinney, 1990). Studies of the functional morphology of bryozoans have indicated changes in the proportion of colonies of branching, encrusting or erect forms occurred since the Late Cretaceous as well as in the nature of ecological interactions such as antipredator defenses and bioturbation (Thayer, 1979, 1983). These trends are remarkably resistant to episodes of mass extinction, including that at the end of the Cretaceous. These macroevolutionary trends do not imply that geologically more recent organisms are any better adapted now than their predecessors were before, but that adaptation has proceeded over millions of years in a directional manner (Jackson and McKinney, 1990).

5. What drove the changes induced by the Mesozoic Marine Revolution?

5.1. Abiotic factors

The Mesozoic Marine Revolution (Vermeij, 1977) is characterized by a great many faunal innovations including the increased use of ecospace and the evolution of powerful consumers and well-protected prey. The Mesozoic was a special time in history, although only a handful of geological and climatic events were responsible for the background environmental changes and faunal escalation. In the Permian the different continental pieces had joined in the supercontinent Pangaea. This resulted in a severe reduction of shallow marine areas, increasing competition on the remaining shallow shelves of the oceans (McKerrow, 1978). Continental breakup began in the Jurassic, under generally benign climatic conditions (there were no ice caps on the poles) with little latitudinal differentiation (Clarke, 1990). Breakup increased in the Late Cretaceous with the final disintegration of Gondwana in the Tertiary. The gradual steepening of the latitudinal climate gradient and increasing climate variation, which continued and increased in the Cenozoic, resulted in the creation of new biogeographic provinces, driven by the raising and lowering of barriers, geographical isolation and contact, all of which favoured differentiation and speciation (Vermeij, 1977, 1983; McKerrow, 1978; Aberhan, 1994). Regional differentiation culminated with the glaciation and isolation of Antarctica, together with the rapid succession of glacial and interglacial periods that continues up to the present day. As a consequence of icecap formation at the poles, ocean circulation increased and deep-water exchange was improved (Martin, 1996).

Sea level was variable during this period (Bambach, 1983). From the Late Permian and Triassic low-stand sea levels generally rose during the Jurassic and Cretaceous and then fell during the Cenozoic, but there also were periods of higher sea level during the Eocene, between the Late Oligocene and Middle Miocene, and in the Pliocene (Vermeij, 1983). High sea-level stands generally mean larger areas for occupation by marine life and the presence of extensive shallow, epicontinental seas. These transgressions reached their maximum in the Late Jurassic, with a limited withdrawal towards the end of the era (McKerrow, 1978), and in the Cretaceous (Vermeij, 1983). Sea-level rise and the resultant increase in water-column stratification and habitat availability may have been a major cause for the diversification of marine plankton in the Mesozoic and Tertiary (Lipps and Hickman, 1982; Martin, 1996).

The formation of shallow, epicontinental seas was accompanied by increased runoff and nutrient input from land and the onset of intense pelagic sedimentation. An increased accumulation rate of chalk created soft, soupy substrates, which triggered the evolution of specific faunal adaptations (Vermeij, 1977; McKerrow, 1978; Bambach, 1983; Aberhan, 1994; Martin, 1996). In many parts of the Late Mesozoic world detrital input from the continents to the deep sea was low (Leckie et al., 2002). This was partly because the land vegetation tended to retain the subsoil, but also a result of the extensive continental shelves, which protected areas beyond the shelf break from significant detrital influxes. From the Palaeozoic, when the plankton was dominated by calcareous nanoplankton and dinoflagellates, different groups of eukaryotic phytoplankton have alternately dominated (Falkowski et al., 2004). It is possible that the increase in phytoplankton during the Cretaceous was what allowed the development of large communities of benthic filter-feeding organisms as has been lately documented (Dame, 1996).

The East Antarctic ice sheet probably first developed at the Eocene/Oligocene border, about 36 Ma ago (Barker and Thomas, 2004), when a thermohaline oceanic circulation pattern similar to that existing today began to form (Matthews and Poore, 1980). The onset of this circulation pattern may have driven the diatoms to flourish as opposed, for instance, to the more mobile dinoflagellates

(Margalef, 1978). The proliferation of diatoms in all oceans since the Eocene has allowed active suspension feeders such as bivalves to thrive (Dame, 1996), but has also favoured other groups, particularly in the Antarctic. At some point in the Cenozoic, the respective dates of which are still under discussion, the ocean gateways between Antarctica and Australia, and also the Drake Passage opened and deepened to the extent that a vigorous Antarctic Circumpolar Current (ACC) could develop (Beu et al., 1997; Barker and Thomas, 2004). Unlike other continental shelves, the process in the Antarctic was characterized by the development of a thick ice cap (whose causal connection to the ACC is still under discussion, Barker and Thomas, 2004), and present-day environmental conditions began to emerge. The ice shield inhibited river runoff in most of the Antarctic continent. Although glaciers can supply locally important sediment inputs, ice shelves containing very reduced sediment load extend over large areas of the Antarctic continental shelf, delivering relatively light continental sediment inputs at the ice shelf edge located over those shelves. Thus, in this sense, the situation is similar to the conditions that existed at the end of the Cretaceous. Coupled with Antarctica's isolation by deep sea and the circumpolar currents, this may also have resulted in a process of speciation of sessile benthic suspension feeders in the Antarctic.

The Antarctic continental shelf possesses particular features in being deeper (up to 600 m, in some areas up to 1400 m) than most of today's continental shelves (Anderson and Molina, 1989). This is the result of isostatic depression caused by the weight of the continental ice sheet. There is also considerable topographic relief on the shelf as a result of previous glacial action, with an unusual landward bathymetric gradient. This relief, and the coastal currents flowing along the shelf, combine to hold sediment particles delivered from glaciers and the seston from the water column on the continental shelf (Elverhoi, 1984). It is likely that ice advance over the continental shelf seabed during previous glacial maxima eliminated benthic communities (Clarke and Crame, 1989; Clarke et al., 2004), but portions of the populations survived at greater depths (or possibly in continental shelf refugia) and were able to recolonize the shelves during interglacial periods (Brey et al., 1996). Local eradication and subsequent recolonization, although on much shorter time scales, also can be observed today where icebergs scrape the bottom and act as one of

the most important mechanisms defining assemblages of sessile benthic organisms (Gutt et al., 1996).

The presence of dense calcareous deposits on the outermost continental shelf and upper slope in the Weddell Sea (Elverhoi, 1984) and other areas of the Antarctic continental shelf (Anderson et al., 1984) is important evidence of previous glacial activity. These calcareous accumulations were deposited in glacial times, and while they have been found in other regions of the world covering the whole shelf (Anderson and Molina, 1989), on the Antarctic shelves, in contrast, they are concentrated at the shelf edge. It is likely that they were created by the deposition of organisms displaced to the edge of the shelf during previous glacial maxima. Some of the benthic fauna also may have been preserved by migrating towards greater depth on the slope, especially during major glaciations (Hsü, 1986; Brey et al., 1996), later recolonizing the continental shelves in the Antarctic during interglacials (Fig. 4). In contrast, recolonization of the continental shelves by sessile suspension feeders did not take place in most other oceans, because influxes of detritus and sediment from rivers continued.

High-resolution stratigraphic studies suggest that polar ecosystems show the least change and most rapid recovery following mass extinction in comparison to tropical and temperate ones (Kauffman and Erwin, 1995). Many groups that were important components of Late Cretaceous biota suffered only slight to moderate levels of extinction. These groups became quickly re-established in the Palaeocene and continued their radiation during the Cenozoic, being formed predominantly of trophic and habitat generalists (Kauffman, 1984). One good example of this partial extinction and rapid recuperation is the mollusc family Tellinidae, which is common today in the Antarctic Ocean (Freydoun, 1969). The Late Cretaceous biotic crisis was caused by environmental factors that affected mainly shallow tropical habitats (Kauffman and Erwin, 1995). Because of the high structural complexity of the high-Antarctic epibenthic communities, their full reestablishment may take as long as 2 million years, but probably less (Jablonski, 1989). As elsewhere ecological generalists probably drive community recovery after partial extinction.

The onset of continental East Antarctic glaciation was probably in the Early Oligocene, approximately 36 Ma ago (Ehrmann and Mackensen, 1992), a
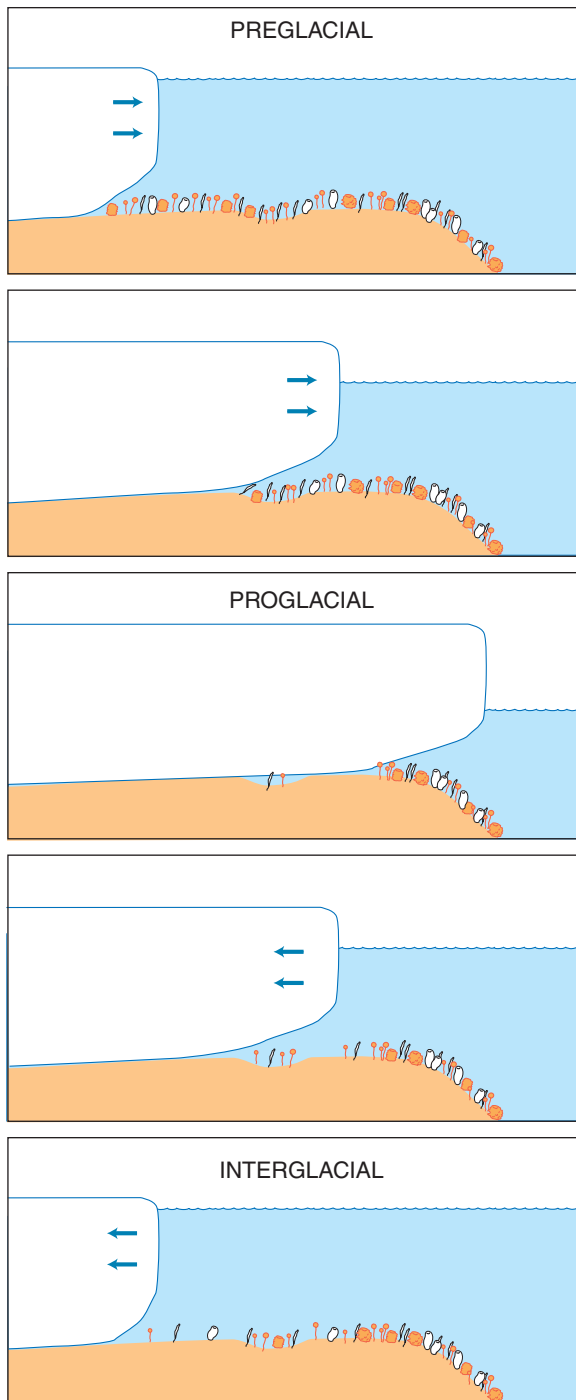
Fig. 4. Diagram of shifts in the ice sheet during glacial and interglacial periods showing the special form of the Antarctic shelf as a result of both the weight of the ice and scouring by icebergs and glaciers. The different episodes reflect the theory that benthic suspension-feeder communities colonize the shelf, are destroyed, and then recolonize the shelf from remnants surviving at the shelf edge or in large troughs beyond the reach of glacial ice (after Hannes Grobe, AWI, Bremerhaven).

process which largely reduced continental runoff, and which may thus have helped reduce the extinction of benthic sessile organisms. Since then, advances and retreats of the ice shelves, together with changes in bottom currents, have determined sedimentation patterns around Antarctica (Anderson et al., 1984; Grobe and Mackensen, 1992). Glaciomarine sedimentation prevailed during glacial episodes, when the sedimenting material exhibited an increase in opal and a decrease in carbonate (Ehrmann and Mackensen, 1992; Ehrmann, 1998). During interglacial intervals sedimentation rates increased by an order of magnitude, at least during the Late Quaternary, driven by intense calving processes, which delivered larger volumes of clay and fine silt (Grobe and Mackensen, 1992). However, even under interglacial conditions sediment input is minimal compared to other continents because of the lack of aeolian and riverine input.

During the last glacial maximum (LGM, 18,000–21,000 years BP), the eastern Weddell Sea was ice-covered and the grounding line of the ice margin largely coincided with the continental shelf edge (Grobe and Mackensen, 1992). During the mid-Holocene climate warming, beginning approximately 9500 years BP, the ice started to retreat (Gingele et al., 1997), and sedimentation on the continental shelf increased once again in areas where the ice shelves had disappeared. The present-day sedimentary environment on the Antarctic continental margin follows the same pattern as in former interglacial periods, in that ice is the main source of terrigenous sediment (Grobe and Mackensen, 1992). In regions such as the Weddell Sea, thermohaline circulation promoted weak bottom currents, which allowed the accumulation of silty sediments on the continental shelf (Anderson et al., 1982).

Modern sediments on the Antarctic continental shelf of the Weddell Sea exhibit unusual features as compared to the sediments in other parts of the world (Isla et al., 2006). The content of fine particles is mainly from 3% to 30%, but can be up to 50%, and the sediments are very rich in organic matter. The inorganic fraction is almost exclusively of glacial origin, and the organic fraction comes from planktonic organisms in the water column (Hense et al., 2003). The biological component of these sediments undergoes relatively slow decomposition because of the very low temperatures (Bathmann et al., 1991).

5.2. Biotic factors

After over 300 million years of essentially unaltered life style, in which the marine benthos was dominated by epifaunal or semi-infaunal elements, important changes in life habits took place, which fundamentally altered the interactions between marine organisms in shallow-water communities. These changes began in the Jurassic, accelerated during the Cretaceous, and continued in the Cenozoic, being only temporarily delayed by the end-Cretaceous extinction (Vermeij, 1977). Although many details of these biotic changes have been enumerated by various authors, they can be summarized under a few headings, following Bambach (1983), Vermeij (1983) and Martin (1996). Many of these evolutionary innovations and adaptations occurred over considerable periods of time and cannot always be assigned to a specific limited period; some even had their roots in the Late Palaeozoic and Early Mesozoic.

5.2.1. Eutrophication

Palaeozoic communities were poor in nutrients, and oligotrophic waters and low nutrient content seem to be a prerequisite for retrograde Palaeozoic-type communities (McKinney, 2003). Catastrophic declines in nutrient levels appear to coincide with a number of mass (and minor) extinctions (Vermeij, 1987). Following the end-Permian extinctions, there was a return to oligotrophic Early Palaeozoic conditions in the Early Mesozoic (Triassic) (Martin, 1996). On the whole, however, the supply of nutrients and food increased across the whole spectrum of marine habitats during the Phanerozoic. In the Triassic, productivity was enhanced through expansion of pelagic habitats following sea-level rise. Continental runoff and erosion also seem to have increased in this era, and nutrient cycling on the shelves may have accelerated in response to increased bioturbation (Martin, 1996). Angiosperm development on land in the Cretaceous gave rise to a higher input of particulate and dissolved organic matter into the sea (Vermeij, 1977), stimulating productivity in coastal marine settings and in the open ocean, where the abundance and diversity of phytoplankton increased (Bambach, 1983). Diversification of phytoplankton, which has continued steadily from the Early Jurassic to the Present, resulted in a general enhancement of marine primary and secondary production (Martin, 1996). Dinoflagellates occurred earlier in the Mesozoic,

whereas the modern dominant, planktonic diatoms, appeared only in the Cretaceous (Vermeij, 1977) and developed rapidly from the Miocene (Martin, 1996). The ensuing increase of biomass and production extended from the level of primary production across the whole food chain. Thus rising nutrient levels, largely from decaying angiosperm litter from land, and increasing marine productivity seem to have fuelled the secular increase in marine biomass and diversity through the Phanerozoic (Martin, 1996; Aronson and Blake, 2001). Sea-grass beds and mangrove swamps, with roots to stabilize the sediment and provide shelter for other organisms, only developed in the Late Cretaceous (Vermeij, 1977).

5.2.2. Improved use of ecospace

Another important process characterizing the Mesozoic Marine Revolution was the increased exploitation of ecospace, as a response both to the more rigorous and variable physical conditions (Aberhan, 1994) and the diversification of the benthic fauna, accompanied by increased predation and competition. The post-Cambrian soft-bottom fauna of the Palaeozoic, replacing the Cambrian trilobites and the sedentary or creeping epifaunal surface deposit feeders, grazers or suspension feeders, included species with a broad range of solitary or colonial epifaunal habits (Anthozoa, Bryozoa, Brachiopoda, Isocrinida, and others). Tiering (stratification) above the soft substratum was added to the benthic structure by these groups (Bambach, 1985). During the Palaeozoic fenestrate bryozoans, isocrinid echinoderms, graptolites, and sponges mainly established a tier of considerable height, whereas in the post-Palaeozoic corals, sponges, alcyonarians and others maintained a lower tier (Ausich and Bottjer, 1985). The more diverse fauna of the Mesozoic, with increasing infauna, included classes with highly varied life styles from deep infaunal to active pelagic habits (Bambach, 1985). The Cenozoic was typically dominated by infaunal tiering (Ausich and Bottjer, 1985).

From the Cambrian to the end of the Jurassic, the uppermost level of tiered epibenthic communities was maintained by stalked crinoids, from the Cretaceous to the present by alcyonarians and sponges. Crinoids in the Silurian attained a height of 100 cm; after the Jurassic the maximum level in soft substrata has been about 50 cm. Infaunal tiering reached ~100 cm twice, during the Early

Permian by anomalodesmatan bivalves and possibly burrowing arthropods, and by at least the Cenozoic by siphonate heterodont bivalves (Ausich and Bottjer, 1985). The diversification of the Modern Fauna during the Mesozoic and Cenozoic resulted in full scale exploitation of deep infaunal modes of life, together with the continued occupation of epifaunal, shallow infaunal (and pelagic) modes of life (Bambach, 1983). Both epifaunal and infaunal tiering increased the number of niches, thus raising the potential diversity threshold (Ausich and Bottjer, 1985). Because the epifaunal stratification had been largely exploited since the Palaeozoic, the Mesozoic Marine Revolution has been characterized primarily by infaunalization.

This was not a straightforward process; increased sedimentation and accumulation rates caused fine-grained carbonate soft bottoms in outer shelf habitats from the Late Jurassic to the Late Cretaceous, which infaunal organisms were apparently unable to occupy. These habitats were colonized by epifaunal and semi-infaunal elements, especially inoceramid bivalves and oysters, which developed specific adaptations to cope with the sediment characteristics (Thayer, 1975). This created a low-tier community structure at the sediment-water interface, which lasted until the Late Cretaceous, though only in offshore habitats (Jablonski and Bottjer, 1983; Aberhan, 1994).

The process of true infaunalization appears to have been driven largely by a rise in Mesozoic predation and grazing pressure (see below), which favoured all kinds of burrowing and sediment-reworking organisms (some of which were known since the Early Palaeozoic: Aronson, 1994) and culminated with the enormous success of siphonate heterodont bivalves in the Late Cretaceous (Vermeij, 1977, 1983). Besides bivalves, the modern fauna constituents of these burrowers, bioturbators and bioeroders were thalassinid shrimp, irregular echinoids, and gastropods (Vermeij, 1977; Bambach, 1983; Aronson, 1994; Wood, 1998), joining older constituents such as polychaetes and other worm groups of which we know little because they do not fossilize well. As these bioturbators inhibit or exclude other, mostly immobile epifaunal, organisms (*trophic group amensalism:* Rhoads and Young, 1970), they contributed to the displacement of the older groups towards deep, cold and dark waters (Vermeij, 1983; Sepkoski and Miller, 1985). However, even in the Late Cretaceous some of these communities survived at specific sites in shallow water, as was the case with the demosponge community of the Upper Greensands in Southern England (Fig. 2; McKerrow, 1978). This community reveals a marked epifaunal stratification, but also contains many infaunal bivalves of the heterodont type and even thalassinid burrows, indicating change was underway.

5.2.3. Trophic changes in the plankton

The most recent of the big five mass extinction events occurred at the end of the Cretaceous, coinciding with a series of events that caused important changes in the pelagic and the benthic systems. Planktonic communities seem to have been largely affected by these changes, at least with regard to the major taxa of phytoplankton (Officer et al., 1987). It has been suggested that the impact of a large bolide, which marks the K/T boundary, may have resulted in a substantial reduction of primary production, which caused the partial extinction of the dominant groups of coccolithophores and dinoflagellates (Zachos et al., 1989; Rhodes and Thayer, 1991). The feeding structures of Cretaceous filter feeders were not so different from those of today; hence it was probably not the filtering mechanisms themselves but rather changes in the quantity and quality of suspended matter that affected these organisms. Furthermore, it seems highly unlikely that the entire marine food chain should have collapsed everywhere at the same time. Species of phytoplankton extant today, similar to those found in the fossil record, have been shown to be dependent on temperature for survival (Griffiths and Chapman, 1988). Consequently, when the dust cloud cleared and light increased again to levels suitable for growth, recovery of populations subjected to lower temperatures may have been favoured (Milne and McKay, 1982). Other authors have argued that the extinction event responsible for devastating most major groups of Cretaceous plankton did not affect diatoms because resting spore formation may have supported their survival (Harwood, 1988).

The fate of the phytoplankton in the course of evolution of Antarctic ecosystems since the Cretaceous and Palaeozoic is of great importance in the light of recent data on the feeding ecology of Antarctic suspension feeders (Gili and Coma, 1998). Various groups of plankton are essential to the diets of different species of both active filter feeders such as molluscs (Ahn, 1993) and ascidians (Tatián et al., 2002) and passive filter feeders such as gorgonians

(Orejas et al., 2003) throughout the year. Some suspension feeding taxa continue feeding into winter, when the continental shelves are entirely covered by sea ice (Barnes and Clarke, 1995). Benthic suspension feeders in the Antarctic depend strongly on primary production in the water column reaching the bottom following spring blooms. For large parts of the year they are able to feed on this same material resuspended from the sediment and advected by currents, which thus provides year-round sources of food (Gili et al., 2001), a situation that is likely to have existed also on the broad, shallow continental shelves during the Cretaceous. The ability to adapt to whatever type of food sources that are dominant in the habitat, above all the portion referred to as the small plankton communities (Orejas et al., 2001), may well have enabled Antarctic benthic suspension feeders to survive periods of critical food shortage even during glacial periods.

5.2.4. Predation and defensive architectures

The development of infaunal, burrowing and bioturbating forms was not the only reason for the displacement of the archaic communities into deep water. The Mesozoic Marine Revolution (Vermeij, 1977) is also recognized by the preferential survival of powerful consumers, both predators and grazers, and well-armed prey. This increase in predation was probably triggered by the increase in biomass and production at the base of the food chains (Bambach, 1983).

Increases in the capabilities of crushing predators and defensive architecture in prey as seen in the Mesozoic were not a totally new evolutionary invention. Although less extreme than in the Mesozoic, they may already have developed in the mid-Palaeozoic (Aronson, 1994). However, a major episode of benthic diversification of powerful predators with shell- and skeleton-breaking capacities began in the Jurassic and continued into the Cretaceous and Tertiary. Brachyuran crabs and palinurid spiny lobsters arose in the Early Jurassic. Among cephalopods, the first calcified jaws had appeared in the Middle Triassic, whereas nautilids and ammonoids originated in the Early Jurassic. Other major shell-breaking taxa with Jurassic origins include true stomatopods, batoid rays, and pycnodont holostean fish. In the Early Cretaceous, there was an explosive diversification of shell-breaking crabs and of acanthopterygian fish, which developed many perciform fishes (labrids, and

others). Triggerfishes arose in the Oligocene. Most of these groups have survived to the present (Vermeij, 1983).

Durophagous predators also contributed to the elimination of epifaunal, suspension-feeding populations from onshore soft-substratum habitats. This may have removed most ophiuroid beds, stalked crinoids and other constituents of the Palaeozoic sessile suspension-feeding epifauna from shallow water. From the Triassic to the mid-Cretaceous, these forms were successively replaced by infaunal and more mobile epifaunal suspension feeders such as the swimming shallow-water comatulid crinoids (Aronson, 1987, 1994; Aronson and Blake, 1997). Arm-regeneration studies showed that low-predation ophiuroid assemblages became very rare after the Jurassic, just when durophagous predators increased (Aronson, 1994), and the incidence of repaired breakage-related shell damage in gastropods was much higher than before the Mesozoic Marine Revolution. Drilling predators also increased as agents of mortality in gastropods, bivalves, and barnacles (Vermeij, 1983).

The Mesozoic Marine Revolution also involved the origin and diversification of many groups of grazers. Among them were modern teleost fish, which originated in the Triassic but probably perfected their grazing abilities in the Late Cretaceous or Early Tertiary; and echinoids, a much older group that became common in shallow environments in the Cretaceous, as did grazing chitons, limpets and other gastropods. The Aristotle's lantern was perfected only in the Late Cretaceous (Vermeij, 1977, 1983; Aronson, 1994; Wood, 1998). Herbivory was probably of minor importance in the Palaeozoic (Vermeij, 1977); modern macrophyte–herbivore relationships are another product of the Mesozoic Marine Revolution, and like predator–prey relationships they may have been driven by increased productivity (Aronson and Blake, 2001).

Besides developing increasingly infaunal habits, Mesozoic prey responded to increased predation and grazing by adopting a number of new defensive strategies (Vermeij, 1977). Armour evolved in gastropods, cephalopods, bivalves, barnacles, epifaunal echinoids, encrusting calcareous algae, and stemmed Palaeozoic echinoderms (Vermeij, 1983). Compound plates in echinoids appeared in the Middle Triassic and increased in complexity until the Late Cretaceous. Chitons developed increasing overlap and articulation of valves, bivalves evolved valves that closed tighter and strengthening

sculptures. Snail-shell sturdiness began to increase in the Cretaceous. Other architectural changes in the fauna included the foliated calcitic structure of the pectinids which, like the comatulids, tended towards greater mobility. The reasons for further changes such as the loss of peduncles in brachiopods or the development of byssus in bivalves are not quite clear (Vermeij, 1977, 1983). The development of armour and defensive architecture contributed to faunal evolution not only in the context of predation but also in competitive interactions (Vermeij, 1983). The combination of the increase of predators and defensive morphologies in prey was probably the most dramatic process during the Mesozoic Marine Revolution (Aronson, 1994; Aronson and Blake, 2001), promoting coevolution and coadaptation, and speeding up major adaptive breakthrough and speciation (Vermeij, 1977).

The proliferation of dense populations of echinoderms, especially ophiuroids, in Antarctic communities has been attributed to the decline in predators such as crabs, sharks and many teleosts (Aronson and Blake, 1997), and this could also explain the predominance of groups of sessile organisms. However, these predator groups do not ordinarily prey on such sessile organisms as sponges, cnidarians, and bryozoans. This means that the lack of large predators is probably not a major factor explaining the make-up of the sessile Antarctic fauna today (although it may have been decisive in the diversification of some groups such as the peracarid crustaceans). Certain echinoderms, fish, and arthropods (such as pycnogonids) are known to prey on sessile organisms at lower latitudes (Day and Osman, 1981; Harwell and Suchanek, 1987; Dunlap and Pawlik, 1996), and some of these taxa are common on the seabed in the Antarctic. In any event, the scarcity of herbivores and predators, together with the lack of terrigenous sediment input and the paucity of bioturbators, may have combined to help create the singular character of the modern Antarctic benthos.

5.2.5. Energetics

The epifaunal or shallow-infaunal passive life style of Palaeozoic sessile suspension feeders contrasts markedly with the active life habits (deep burrowing, swimming or walking, predation or grazing) of the modern fauna (Bambach, 1983). During and after the Mesozoic Marine Revolution escalation included an increase of the level of metabolic activity in response to more energetic modes of life (Bambach, 1983). A higher metabolic rate in suspension-feeding invertebrates, echinoderms, and vertebrates, and an increased emphasis on locomotion in mobile animals, including gastropods, cephalopods, bivalves, echinoderms, and fish, are among the best-documented trends that indicate escalation. The modern species developed a higher capability to cope with competitors or predators despite the fact that the oceans had changed from a low-energy to a high-energy environment (Vermeij, 1987).

Marine diversity has increased almost continuously through the Cenozoic in parallel with a general energetic change in the oceans (Sepkoski, 1997). The increase of primary production, organic detritus, consumers and predators suggests that the supply of food increased across all spectra of marine habitats during the Phanaerozoic (Bambach, 1993). A significant part of this general trend is because of the increase of production on land and its transfer to the coastal oceans via river run-off, which thereby links the diversity and biomass of marine communities with the development of land vegetation through the Phanaerozoic (Bambach, 1999). These land-sea interactions decreased strongly during the Cenozoic in the Antarctic because of the development of continental ice. This phenomenon is especially important in the older East Antarctic continent (Crame, 1994); a different pattern of glaciation has been followed in West Antarctica, with permanent continental ice not reaching the coastal and shelf waters (Poole et al., 2005).

5.2.6. Role of extinctions

Major biological crises (mass extinctions) occurred in the Late Ordovician, Late Devonian, Late Permian, Late Triassic, and Late Cretaceous. The Palaeozoic fauna, which was to dominate during the next 250 Ma (Sepkoski, 1981), originated during the Ordovician radiation. It was marked by a transition from trilobite to brachiopod dominated communities in shallow soft sediments and addition of new megaguilds, such as pelagic predators and epifaunal mobile suspension feeders.

Whereas the first two mass extinction events did not interrupt the establishment of the Palaeozoic Fauna, the end-Permian extinction was the greatest mass extinction in the history of life. As much as 96% of all marine species may have gone extinct, megaguilds were lost, and the transition from brachiopod-dominated to mollusc-dominated shelf communities was completed (Droser et al., 1997).

After this event, global diversity was low and benthic communities were markedly depauperate (Sepkoski, 1984). However, only 4 of 91 classes became extinct, and 3 of these had been on the decline before the event (Sepkoski, 1981). Moreover, the extinction was selective (McKerrow, 1978). After the event, some classes, especially Brachiopoda Articulata and Crinoidea, never regained their former dominance, others contracted but reexpanded (Cephalopoda, Anthozoa), and yet others showed only moderate (Demospongia, Gastropoda) or no response to the event (Bivalvia, Malacostraca, Asteroidea, Ophiuroidea) (Sepkoski, 1981; Sepkoski and Hulver, 1985; Aronson and Blake, 1997). In any case, the Permian extinction opened the way for the diversification of modern predators and other innovations of the Mesozoic Marine Revolution by providing many empty niches (Aronson and Blake, 2001), and these changes in life habits were largely unaffected, or only temporarily delayed by the extinction at the end of the Cretaceous (Vermeij, 1977; Crame et al., 1996).

The end-Cretaceous extinction led to the disappearance of many faunal elements that had only originated in the Mesozoic, such as ammonites, rudist and inoceramid bivalves, and many previously dominant gastropods. Brachiopods decreased considerably in importance, and many echinoid taxa and corals disappeared that had been abundant in the Cretaceous (McKerrow, 1978). On the other hand, evolutionary innovations of predator and prey continued into the Cenozoic (Aronson and Blake, 2001), and many benthic groups that had appeared gradually in the Cretaceous showed an explosive development after the mass extinction event: these included predatory gastropods, many polychaetes, heterodont bivalves such as the Veneracea and Tellinacea, and reef-building corals (McKerrow, 1978).

6. The Antarctic in the Cenozoic: a special case?

The development of the shallow water marine fauna around Antarctica is likely to have been similar to that of other oceans at least up to the Eocene/Oligocene boundary, when the process of high-latitude cooling and isolation began. Following the Mesozoic Marine Revolution and the end-Cretaceous mass extinction, stomatopods and brachyurans, already well developed in the Jurassic and Cretaceous, developed shell-breaking limbs. At the same time, crushing habits evolved in many acanthopterygian and elasmobranch fish. Scleractinian corals and cheilostome bryozoans developed very high levels of colonial integration during the Eocene and especially during the Miocene, and balanomorph barnacles evolved calcareous bases and thick tubiferous walls during the Oligocene (Vermeij, 1983). The Antarctic should have shared these developments, at least to the end of the Eocene. So the question is why did faunal development then take such a different course on the high-Antarctic shelf?

At the end of the Cretaceous high-latitude waters around Gondwana were temperate, and the gradient between the equator and the poles was much less steep than today. Cooling since the Eocene was a slow process, although there may have been periods of more rapid temperature change (Zachos et al., 2001). Global cooling started with the rapid opening of the Atlantic Ocean and the Norwegian Sea, and closure of the Tethys Sea (Moore et al., 1978; Mackensen, 2004). Antarctic glaciation began at the Eocene–Oligocene boundary, probably in connection with the opening of the Tasman ocean gateway (Moore et al., 1978; Barker and Thomas, 2004). The next major cooling event was connected with the opening of Drake Passage in the Miocene, possibly about 23 Ma (Barker and Thomas, 2004), followed by a third steep decline at the Pliocene/Pleistocene border (Zachos et al., 2001). The Pliocene still had considerable warmer intervals, during which major parts of East Antarctica may have been covered again by epicontinental seas (Quilty, 1990).

Fossils from Seymour and James Ross Islands show that in the Late Cretaceous and Eocene a rich shallow-water fauna existed around at least some parts of Gondwana. This fauna included elements of the modern fauna (solitary corals, polychaetes, bivalves, gastropods, scaphopods, crabs, echinoids, asteroids, ophiuroids and fish: Clarke, 1990). On the whole, the fossil record from Seymour Island does not show the dominance of the passive suspension feeders found in the high Antarctic today, nor of its archaic structure; this specific fauna must have colonised the Antarctic shelf later. However, there is also a considerable evolutionary legacy (Crame, 1997) of the end-Cretaceous or Early Tertiary Gondwana fauna, including the gastropod families Buccinidae (the genus *Pareuthria*), Naticidae, Turridae. Some modern Patagonian bivalves (the genera *Aulacomya, Mysella, Gaimardia, Cyclocardia*) have

ancestors in the La Meseta Formation (Crame, 1997). Despite their relatively high species number in the Antarctic and their success elsewhere, neither gastropods nor bivalves are a dominant group in the high Antarctic (unpublished data from Ecology of Antarctic Sea Ice Zone cruises on board of R/V *Polarstern*: Gutt et al., 2000, 2004).

The modern fauna indicates that many epifaunal taxa have adapted well to the coarse-grained glacial sediments, with sessile filter and particle feeders being especially prominent (Crame, 1997). Unfortunately fossilized remains of epifaunal suspension feeders are rare, so it is difficult to compare the modern fauna directly with the fossil record. The high Antarctic benthic communities could be habitat refuges such as have been observed in the North Atlantic where the diversity reduction and extinction began in the deep ocean while some forms survive during the Neogene in the Norwegian-Greenland Sea (Kaminski, 1987). These extinction processes were linked with the transition from a warm sluggishly circulating, low-oxygen deep-sea environment to a more oxygenated, thermohaline-driven circulation caused by the influence of polar cooling (Thomas, 1992).

In high southern latitudes, current evidence suggests that the Early Tertiary fauna became extinct around the Eocene-Oligocene transition. Crabs and sharks disappeared in association with Late Eocene cooling trends although one crab survived until the Early Miocene (Feldmann and Crame, 1998; Aronson and Blake, 2001). Passive suspension feeding and epifaunal life habits are Palaeozoic traits which contrast with the modern lifestyles of deep-burrowing, swimming and predation (Bambach, 1983). Echinoderms are well represented and include populations of ophiuroids in shallow water (Aronson and Blake, 1997). Infauna however is poorly represented; infaunal tiering is mostly low. Epifaunal tiering in high-Antarctic communities is as tall as in the Palaeozoic. The occurrence of dense populations of ophiuroids, comatulid crinoids, and regular modern echinoids in shallow water suggests a community structure where skeleton-crushing predation is low. This is confirmed by the absence of sharks, brachyuran and lithodid crabs (Thatje et al., 2005), and the low occurrence of batoid rays and skates. The main predatory activity comes from slower-moving invertebrates that do not crush hard-shelled prey; these include asteroids, ophiuroids, nemerteans, anthozoans, pycnogonids, large isopods, and some

shell-drilling gastropods (Aronson and Blake, 2001). As far as we know, abundant populations of articulated brachiopods are confined to large dropstones; on soft bottoms they are relatively rare.

In the Mesozoic communities studied by Aberhan (1994), 5 broad community types are distinguished; however, the type we find in the high-Antarctic is missing. The closest guild, is the free-lying epifaunal suspension feeders on soft bottoms, would probably correspond to a mixture of shallow shelf and mid to outer shelf communities identified in the Weddell Sea. This means that throughout the Mesozoic, epifaunal passive suspension feeder communities of the Palaeozoic type found in the high-Antarctic today never played an important role.

Rates of speciation are not necessarily lower in cold, polar waters, nor are rates of extinction higher (Crame, 1999), and no simple relationship exists between the onset of glaciation and the extinction in the Antarctic marine fauna (Clarke et al., 2004). The level of species endemism of many groups of sessile benthic organisms has been shown to be very high (Clarke and Johnston, 2003), indicating a significant period of evolutionary isolation on the Antarctic shelf. Though fragmentary, the fossil record for certain groups of benthic marine invertebrates can shed some light on the origin and diversification of the Antarctic fauna. Gorgonian octocorals are a case in point, with high-Antarctic benthic assemblages being dominated by two families, Primnoidae and Isididae (Alderslade, 1998). Other families such as Chrysogorgiidae, Acanthogorgiidae, and Subergorgiidae are found only at lower latitudes in the Southern Ocean, mainly in the Scotia arc. Fossil remains ascribable to primnoids and isidiids have been found in Cretaceous deposits, whereas the other families are considered to have evolved more recently (Bayer, 1956). A Cretaceous fauna dominated by primnoids and isidiids could represent the origin of the present Antarctic fauna, with subsequent isolation resulting in a level of endemism reaching 50% at the genus level among primnoids (López-González et al., 2002). The presence of other gorgonian families in the southern segment of the Scotia arc probably represents more recent recolonization from the surrounding oceans. The pattern observed for gorgonians is typical of the trends observed for other groups (Clarke and Johnston, 2003), and a Cretaceous origin for the present-day fauna is also suggested, for example, for the hexactinellid (glass) sponges, one of the most

significant groups of Antarctic benthic fauna in terms of biomass and abundance (Barthel et al., 1991). Siliceous hexactinellid sponges dominated the earth's continental shelves during the Mesozoic but underwent significant extinction during the Late Cretaceous and beginning of the Tertiary (Maldonado et al., 1999). It is only on the continental shelves of Antarctica that hexactinellid sponges remain an important component of the fauna; in all other parts of the world ocean they are essentially a deep-sea group. In fact, there is evidence that some sessile groups once believed to have disappeared in the Mesozoic survive in the deep sea, for example, on Tasmanian seamounts (Richer de Forges et al., 2000).

The high level of endemism that has been reported for many Antarctic marine taxa (Arntz and Brey, 2003) is explained by the continent's prolonged period of isolation, dating back to before the Cretaceous (Clarke and Crame, 1989). At that time, Antarctica was part of Gondwana (Crame, 1994). Hence the origin of part of the extant fauna has been postulated to date from that period, a hypothesis substantiated by investigations on biodiversity and zoogeography of vagile fauna, such as gastropods (Clarke, 1990) and isopods (Brandt, 1991). If the changes in environmental conditions in Antarctica were gradual, they likely resulted in emigration of fauna rather than in the mass extinction of species (Clarke, 1990). At all events, the present Antarctic ecosystem is probably some 35 Ma old, and the high level of isolation has gone hand in hand with speciation (Watling and Thurston, 1989). Within that general frame, some recently discovered benthic cnidarians (López-González and Gili, 2001; Gili et al., 2006) may represent a relict stock that arose from a common ancestor, when the Antarctic island group and surrounding shelves were still located close to the Asiatic plate within the Gondwana continent (Crame, 1994). Similar phenomena and evidence are given by the species of the wide spread genus *Laternula* with congeneric species in the Red Sea, Indian Ocean, Antarctica and Australia (Dell, 1972), and other groups with links between Antarctica and Australia (Koltun, 1970; Knox and Lowry, 1977; Long, 1994; Schmidt and Bone, 2003).

The existence of a set of ancestral species, mainly sessile fauna such cnidarian and sponges, of late Eocene and early Miocene taxa has been postulated, with certain groups being found earlier in the Antarctic than in other oceans (Briggs, 2003).

7. Conclusions: what factors are responsible for the archaic character of the high-Antarctic suspension feeder communities?

The sporadic occurrence of dense ophiuroid assemblages in the Late Eocene/Early Oligocene shallow marine deposits in Antarctica (Aronson and Blake, 1997) and of isocrinids in southern South America (Malumián and Olivero, 2005) suggests reduced predation pressure in those communities. In combination with the low rates of bioturbation observed in the La Meseta Formation, these observations suggest a local and/or short-term switch from a typical Cenozoic (high predation, mollusc-dominated) to a Palaeozoic-type (low predation, ophiuroid-dominated) system. Unfortunately the poor fossil record in Antarctica means that we cannot be certain how widespread or long-term these archaic-looking communities were. The conditions favouring what Aronson and Blake (1997) have termed retrograde ecologies remain to be elucidated, but we can say that the modern Antarctic high-latitude communities are unique and deserving of special attention.

Several aspects of the modern high-latitude glacial environment are comparable with what we know of the Palaeozoic. These include the lack of riverine sediment input and oligotrophic waters (outside the period of the short summer phytoplankton bloom). The benthic community also has a Palaeozoic aspect with the lack of durophagous predators, reduced bioturbation, and a dominance of sessile or slow-moving taxa. However, there are also aspects that are clearly different from those in the Palaeozoic. These include the rich zooplankton community, which mediates transfer of phytoplankton to the benthos, severe iceberg disturbance, a significant mobile fauna (including amphipods and isopods), and taxa that were apparently absent from Palaeozoic seas (for example, ascidians).

Overall we must conclude that the archaic appearance of the modern high-Antarctic benthic communities is partly an illusion, in that key aspects of the environment and many aspects of the fauna differ from those in the Palaeozoic. Nevertheless there are undoubtedly old elements within the modern fauna, and many ecological similarities with Palaeozoic communities. It would appear that a community dominated by sessile suspension feeders will evolve wherever rates of inorganic sedimentation are low, and active durophagous predators are absent. Such communities are rare,

and on the spatial scale of the high-Antarctic continental shelf, unique. They deserve conservation.

Acknowledgements

References

Aberhan, M., 1994. Guild-structure and evolution of Mesozoic benthic shelf communities. Palaios 9, 516–545.

Ahn, I.Y., 1993. Enhanced particle flux through the biodeposition by the Antarctic suspension-feeding bivalve *Laternula elliptica* in Marian Cove, King George Island. Journal of Experimental Marine Biology and Ecology 171, 75–90.

Alderslade, P., 1998. Revisionary systematics in the gorgonian family Isididae, with description of numerous new taxa (Coelenterata, Octocorallia). Records of the Western Australian Museum Supplement 55, 1–359.

Anderson, J.B., Molina, B.F., 1989. Short Course in Geology, vol. 9. American Geophysical Union, Washington, pp. 1–126.

Anderson, J.B., Brake, C., Myers, N., 1984. Sedimentation on the Ross Sea continental shelf, Antarctica. Marine Geology 57, 295–333.

Anderson, J.B., Kurtz, D., Weaver, F., Weaver, M., 1982. Sedimentation on the West Antarctica Continental Margin. In: Craddock, C. (Ed.), Antarctic Geoscience. The University of Wisconsin Press, Madison, pp. 1003–1012.

Arntz, W.E., Brey, T., 2003. The expedition Antarktis XIX/5 (LAMPOS) of RV "Polarstern" in 2002. Berichte zur Polarforschung 462, 1–120.

Arntz, W.E., Gili, J.M., 2001. A case for tolerance in marine ecology: let us not put out the baby with the bathwater. Scientia Marina 65 (Suppl. 2), 283–299.

Arntz, W.E., Brey, T., Gallardo, V.A., 1994. Antarctic zoobenthos. Oceanography and Marine Biology: An Annual Review 32, 241–304.

Arntz, W.E., Thatje, S., Gerdes, D., Gili, J.-M., Gutt, J., Jacob, U., Montiel, A., Orejas, C., Teixidó, N., 2005. The Antarctic–Magellan conection: macrobenthos ecology on the shelf and upper slope, a progress report. Scientia Marina 69 (Suppl. 2), 237–269.

Aronson, R.B., 1987. Predation on fossil and recent ophiuroids. Paleobiology 13, 187–192.

Aronson, R.B., 1994. Scale-independent biological processes in the marine environment. Oceanography and Marine Biology Annual Review 32, 435–460.

Aronson, R.B., Blake, D.B., 1997. Evolutionary palaeoecology of dense ophiuroid populations. Paleontological Society Papers 3, 107–119.

Aronson, R.B., Blake, D.B., 2001. Global climate change and the origin of modern benthic communities in Antarctica. American Zoology 41, 27–39.

Aronson, R.B., Blake, D.B., Oji, T., 1997. Retrogade community structure in the late Eocene of Antarctica. Geology 25, 903–906.

Arthur, M.A., Garrison, R.E., 1986. Cyclicity in the Milankovitch band through geological time: an introduction. Paleoceanogaphy 1, 369–372.

Ausich, W.A., Bottjer, D.J., 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. Science 216, 173–174.

Ausich, W.I., Bottjer, D.J., 1985. Phanerozoic tiering in suspension feeding communities on soft substrata: implications for diversity. In: Valentine, J.W. (Ed.), Phanerozoic Diversity Patterns. Princeton University Press, Princeton, NJ, pp. 255–274.

Bambach, R.K., 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In: Tavesz, M.J.S., McCall, P.M. (Eds.), Biotic Interactions Between Recent and Fossil Benthic Communities. Plenum, New York, pp. 719–746.

Bambach, R.K., 1985. Classes and adaptive variety: the ecology of diversification in marine faunas during the Phanerozoic. In: Valentine, J.W. (Ed.), Phanerozoic Diversity Patterns. Princeton University Press, Princeton, NJ, pp. 191–253.

Bambach, R.K., 1993. Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. Paleobiology 19, 372–397.

Bambach, R.K., 1999. Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere. GEOBIOS 32, 131–144.

Barker, P.F., Thomas, E., 2004. Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. Earth-Science Review 66, 143–162.

Barnes, D.K.A., 2005. Changing chain: past, present and future of Scotia Arc's shallow benthic communities. Scientia Marina 69 (Suppl. 2), 65–89.

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

Barthel, D., Gutt, J., Tendal, O.S., 1991. New information on the biology of Antarctic deep-water sponges derived from underwater photography. Marine Ecology Progress Series 69, 303–307.

Bathmann, U., Fischer, G., Müller, P.J., Gerdes, D., 1991. Short-term variations 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.

Bayer, F.M., 1956. Octocorallia. In: Moore, C. (Ed.), Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas Press, pp. 166–231.

Beu, A.G., Griffin, M., Maxwell, P.A., 1997. Opening of Drake Passage gateway and late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence

from New Zealand and Argentina. Tectonophysics 281, 83–97.

Bottjer, D.J., Ausich, W.I., 1986. Phanerozoic development of tiering in soft subdtrata suspension-feeding communities. Paleobiology 12, 400–420.

Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M., Arntz, W.E., 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? Antarctic Science 8, 3–6.

Brandt, A., 1991. Zur Besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopoda (Crustacea, Malacostraca). Berichte zur Polarforschung 98, 1–240.

Briggs, J.C., 2003. Marine centres of origin as evolutionary engines. Journal of Biogeography 30, 1–18.

Cattaneo-Vietti, R., Chiantore, M., Gambi, M.C., Albertelli, G., Cormaci, M., Di Geronimo, I., 2000. Spatial and vertical distribution of benthic littoral communities. In: Faranda, F., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer, Berlin, pp. 503–514.

Clark, P.U., Alley, R.B., Keigwin, L.D., Licciardi, J.M., Jonshen, S.J., Wang, H., 1996. Origin of the first global meltwater pulse following the last glacial maximum. Paleoceanography 11, 563–577.

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. Springer, Berlin, pp. 9–22.

Clarke, A., 1996. Distribution of Antarctic marine benthic communities. American Geophysical Union, Antarctic Research Series 70, 219–230.

Clarke, A., Crame, J.A., 1989. The origin of the Southern Ocean marine fauna. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota. The Geological Society, London, pp. 253–268.

Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. Oceanography and Marine Biology: An Annual Review 41, 47–114.

Clarke, A., Aronson, R.B., Crame, J.A., Gili, J.M., Blake, D.B., 2004. Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf. Antarctic Science 16, 559–568.

Crame, J.A., 1994. Evolutionary history of Antarctica. In: Hempel, G. (Ed.), Antarctic Science—Global Concerns. Springer, Berlin, pp. 188–214.

Crame, J.A., 1997. An evolutionary framework for the polar regions. Journal of Biogeography 24, 1–9.

Crame, J.A., 1999. An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. Scientia Marina 63, 1–14.

Crame, J.A., Lomas, S.A., Pirrie, D., Luther, A., 1996. Late Cretaceous extinction patterns in Antarctica. Journal of the Geological Society of London 153, 503–506.

Dame, R.F., 1996. Ecology of Marine Bivalves. An Ecosystem Approach. CRC Press, Boca Raton, FL.

Day, R.W., Osman, R.W., 1981. Predation by Patiria miniata (Asteroidea) on bryozoans: prey diversity may depend on the mechanism of succession. Oecologia 51, 300–309.

Dayton, P.K., 1990. Polar benthos. In: Smith, Jr., W.O. (Ed.), Polar Oceanography Part B Chemistry, Biology, and Geology. Academic Press, San Diego, pp. 631–685.

Dayton, P.K., Oliver, J.S., 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. Science 197, 55–58.

Dayton, P.K., Robilliard, G.A., Paine, R.T., Dayton, L.B., 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecological Monographs 44, 105–128.

Dearborn, J.H., 1977. Food and feeding characteristics of Antarctic asteroids and ophiuroids. In: Llano, G.A. (Ed.), Adaptations within Antarctic Ecosystems. Gulf Publication, Houston, pp. 293–326.

Dell, R.K., 1972. Antarctic benthos. Adances in Marine Biology 10, 1–216.

Dingle, R.V., Lavelle, M., 2001. Late Cretaceous–Cenozoic climatic variation of the northern Antarctic Peninsula: new geochemical evidence and review. Palaeogeography Palaeoclimatology Palaeoecology 141, 215–232.

Droser, M.L., Bottjer, D.J., Sheehan, P.M., 1997. Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life. Geology 25, 167–170.

Duineveld, G.C.A., Lavaleye, M.S.S., Berghuis, E.M., 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). Marine Ecology Progress Series 277, 13–23.

Dunlap, M., Pawlik, J.R., 1996. Video-Monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. Marine Biology 126, 117–123.

Ehrmann, W., 1998. Implications of late Eocene to early Miocene clay mineral assemblages in McMurdo Sound (Ross Sea, Antarctica) on paleoclimate and ice dynamics. Palaeogeography Palaeoclimatology Palaeoecology 139, 213–231.

Ehrmann, W.U., Mackensen, A., 1992. Sedimentological evidence for the formation of an East Antarctic ice sheet in Eocene/Oligocene time. Palaeogeography Palaeoclimatology Palaeoecology 93, 85–112.

Elverhoi, A., 1984. Glaciogenic and associated marine sediments in the Weddell Sea, fjords of Spitsbergen and the Barents Sea: a review. Marine Geology 57, 53–88.

Etter, R.J., Mullineaux, L.S., 2001. Deep-sea communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Inc., Sunderland, pp. 367–393.

Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. Nature 305, 354–360.

Feldmann, R.M., Crame, J.A., 1998. The significance of a new nephropid lobster from the Miocene of Antarctica. Palaeontology 41, 807–814.

Fogg, G.E., 1998. The Biology of Polar Habitats. Oxford University Press, Oxford.

Fosså, J.H., Mortensen, P.B., Furevik, D.M., 2002. The deep-sea coral Lophelia pertusa in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471, 1–12.

Freiwald, A., Wilson, J.B., Henrich, R., 1999. Grounding Pleistocene icebergs shape recent deep-water coral reefs. Sedimentary Geology 125, 1–8.

Freydoun, A., 1969. Taxonomic revision of the superspecific groups of the Cretaceous and Cenozoic Tellinidae. GSA Memoir 119, 1–215.

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

Gambi, M.C., Castelli, A., Guizzardi, M., 1997. Polychaete populations of the shallow soft bottom off Terra Nova Bay (Ross Sea, Antarctica): distribution, diversity and biomass. Polar Biology 17, 199–210.

Gage, J.D., Lamont, P.A., Tyler, P.A., 1995. Deep-sea macro-benthic communities at contrasting sites off Portugal. Preliminary results: 1. Introduction and diversity comparisons. Internationale Revue der gesamten Hydrobiologie 80, 235–250.

Galerón, 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.

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

Gili, E., Masse, J.-P., Skelton, P.W., 1995. Rudists as gregarious sediment-dwellers, not reef-builders, on Cretaceous carbonate platforms. Palaeogeography Palaeoclimatology Palaeoecology 118, 245–267.

Gili, J.M., Arntz, W.E., Filipe, P., López, P., Orejas, C., Ros, J., Teixidó, N., Dijkstra, J., 1999. Study of the hard-bottom fauna on an underwater hilltop at 60–70 m depth. In: Arntz, W., Gutt, J. (Eds.), The Expedition ANTARKTIS XV/3 (EASIZ II) of RV "Polarstern" in 1998. Berichte zur Polarforschung, vol. 301, pp. 30–83.

Gili, J.M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends in Ecology and Evolution 13, 316–321.

Gili, J.M., Coma, R., Orejas, C., López-González, P.J., Zavala, M., 2001. Are Antarctic suspension feeding communities different from those elsewhere in the world? Polar Biology 24, 473–485.

Gili, J.M., López-González, P.J., Bouillon, J., 2006. A new Antarctic association: The case of the hydroid Sarsia medelae (new sp) associated with gorgonians. Polar Biology 29, 624–631.

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

Griffiths, K., Chapman, D.J., 1988. Survival of plankton under prolonged darkness: implications for the Cretaceous/Tertiary boundary darkness hypothesis. Palaeogeography Palaeoclimatology Palaeoecology 67, 305–314.

Grobe, H., Mackensen, A., 1992. Late Quaternary climatic cycles as recorded in sediments from the Antarctic Continental Margin. In: Kernet, J.P., Warnke, D.A. (Eds.), The Antarctic Paleoenvironment: a Perspective on Global Change. Antarctic Research Series. American Geophysical Union, Washington, pp. 349–376.

Gutt, J., 2000. Some "driving forces" structuring communities of the sublittoral Antarctic macrobenthos. Antarctic Science 12, 297–313.

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

Gutt, J., Sirenko, B.I., Arntz, W.E., Smirnov, I.S., De Broyer, C., 2000. Biodiversity of the Weddell Sea: macrozoobentic species (demersal fish included) sampled during the expedition ANT XIII/3 (EASIZ I) with RV Polarstern. Berichte zur Polarforschung 372, 1–103.

Gutt, J., Sirenko, B.I., Smirnov, I.S., Arntz, W.E., 2004. How many macrozoobenthic species might inhabit the Antarctic shelf? Antarctic Science 16, 11–16.

Harwell, C.D., Suchanek, T.H., 1987. Partial predation on tropical gorgonians by Cyphoma gibbosum (Gastropoda). Marine Ecology Progress Series 38, 37–44.

Harwood, D.M., 1988. Upper Cretaceous and lower Palaeocene diatom and silicoflagellate biostratigraphy of Seymour Island, eastern Antarctic Peninsula. Memories of the Geological Society of America 169, 55–129.

Hense, I., Timmermann, R., Beckmann, A., Bathmann, U.V., 2003. Regional and interannual variability of ecosystem dynamics in the Southern Ocean. Ocean Dynamics 53, 1–10.

Hsü, K.J., 1986. Cretaceous/Tertiary boundary event. American Geophysical Union, Geodynamics Series 15, 75–84.

Isla, E., Rossi, S., Palanques, A., Gili, J.M., Gerdes, D., Arntz, W.E., 2006. Biochemical composition of marine sediments from the eastern Weddell Sea (Antarctica): high nutritive value in a high benthic-biomass environment. Journal of Marine Systems 60, 255–267.

Jablonski, D., 1989. The biology of mass extinction: a paleontological view. Philosophical Transactions of the Royal Society of London Series B 235, 357–368.

Jablonski, D., Bottjer, D.J., 1983. Soft-bottom epifaunal suspension-feeding assemblages in the Late Cretaceous: implications for the evolution of benthic paleocommunities. In: Taevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Press, New York, pp. 747–812.

Jackson, J.B.C., McKinney, F.K., 1990. Ecological processes and progressive macroevolution of marine clonal benthos. In: Ross, M., Allmon, W.D. (Eds.), Causes of Evolution. A Paleontological Perspective. The University of Chicago Press, pp. 173–205.

Kaminski, M.A., 1987. Cenozoic deep-water agglutinated Foraminifera in the North Atlantic. Ph.D. Thesis, MIT/WHOI 88-3, 1-262.

Kauffman, E.-G., 1984. The fabric of Cretaceous marine extinctions. In: Berggren, W.A., Van Couvering, J.A. (Eds.), Catastrophes and Earth History. Princeton University Press, Princeton, NJ, pp. 151–246.

Kauffman, E.G., Erwin, D.H., 1995. Surviving mass extinctions. Geotimes 40, 14–17.

Kennedy, W.J., 1978. Cretaceous. In: McKerrow, W.S. (Ed.), The Ecology of Fossils. Gerald Duckworth, London, pp. 280–322.

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

Koltun, V.M., 1970. Sponges of the Arctic and Antarctic: a faunistic review. Symposia of the Zoological Society of London 25, 285–297.

Knox, G.A, Lowry, J.K., 1977. A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and Polychaeta. In: Dunbar, M.J. (Ed.), Polar Oceans, Antarctic Institute, North America, pp. 423–462.

Lanihan, H.S., Micheli, F., 2001. Soft-sediment communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Sunderland, pp. 253–287.

Leckie, R.M., Bralower, T.J., Cashman, R., 2002. Oceanic anoxic events and plankton evolution: biotic response to tectonic forcing during the mid-Cretaceous. Paleoceanography 17.

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. Prentice-Hall, Englewood Cliffs, NJ, pp. 324–356.

Long, D.J., 1994. Quaternary colonization or Paleogene persistence—historical biogeography of skates (Chondrichthyes, Rajidae) in the Antarctic ichthyofauna. Paleobiology 20, 215–228.

López-González, P.J., Gili, J.M., 2001. *Rosgorgia inexpectata*, new genus and new species of Subergorgiidae (Cnidaria, Octocorallia) from off the Antarctic Peninsula. Polar Biology 24, 122–126.

López-González, P.J., Gili, J.M., Orejas, C., 2002. A new primnoid genus (Anthozoa: Octocorallia) from the Southern Ocean. Scientia Marina 66, 383–397.

Maldonado, M., Carmona, M.C., Uriz, M.J., Cruzado, A., 1999. Decline in Mesozoic reef—building sponges explained by silicon limitation. Nature 401, 785–788.

Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta 1, 493–509.

Matthews, R.W., Poore, R.Z., 1980. Tertiary δ^{18}O record and glacio-eustatic sea level fluctuations. Geology 8, 501–504.

McKerrow, W.S., 1978. The Ecology of Fossils. Duckworth & Co.; Geman edition "Ökologie der Fossilien", revised by F.T. Fürsich, Franckh-Kosmos, Stuttgart.

McKinney, F.K., 2003. Preservation potential and palaeoecological significance of epibenthic suspension feeder-dominated benthic communities (northern Adriatic Sea). Palaios 18, 47–62.

McKinney, F.K., Lidgard, S., Taylor, P.D., 2001. Macroevolutionary trends. Perception depends on the measured used. In: Jackson, J.B.C., Lidgard, S., MacKinney, F.K. (Eds.), Evolutionary Patterns. Growth, Form, and Tempo in the Fossil Record. The University of Chicago Press, Chicago, pp. 348–385.

Mackensen, A., 2004. Changing Southern Ocean palaeocirculation and effects on global climate. Antarctic Science 16, 369–386.

Macurda Jr., D.B., Meyer, D.L., 1976. The morphology and life habits of the abyssal crinoid *Bathycrinus aldrichianus* Wyville Thomson and its paleontological implications. Journal of Paleontology 50, 647–667.

Malumián, N., Olivero, E., 2005. Shallow-water late-middle Eocene crinoids from Tierra del Fuego: a new southern record of a retrograde community structure. Scientia Marina 69 (Suppl. 2), 349–353.

Martin, R.E., 1996. Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, and diversity of the marine biosphere. Palaios 11, 209–219.

Milne, D.H., McKay, C.P., 1982. Response of marine plankton communities to global atmospheric darkening. Geological Society of America Special Papers 190, 297–303.

Mercuri, G.K., Iken, K., Ledesma, B., Dubois, R.F., 1998. On the distribution patterns and density of the Antarctic infaunal bivalve *Laternula elliptica* in Poter Cove, King George Island, Antarctica. Berichte zur Polarforschung 299, 137–143.

Moore Jr., T.C., van Andel, T.H., Sancetta, C., Pisias, N., 1978. Cenozoic hiatuses in pelagic sediments. Micropalaeontology 24, 113–138.

Mortensen, P.B., Buhl-Mortensen, L., 2004. Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Marine Biology 144, 1223–1238.

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

Mühlenhardt-Siegel, U., 1989. Quantitative investigations of Antarctic macrozoobenthos communities in winter (May/June) 1986 with special reference to the sediment structure. Archiv für Fischereiwissenschaft 39, 123–141.

Officer, C.B., Hallam, A., Drake, C.L., Devine, J.D., 1987. Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions. Nature 326, 143–148.

Orejas, C., Gili, J.M., López-González, P.J., Arntz, W.E., 2001. Feeding strategies and diet composition of four species of Antarctic cnidarian species. Polar Biology 24, 620–627.

Orejas, C., Gili, J.M., Arntz, W.E., 2003. The role of small-plankton communities in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.). Marine Ecology Progress Series 250, 105–116.

Poole, I., Cantrill, D., Utescher, T., 2005. A multy-proxy approach to determine Antarctic terrestrial palaeoclimate during the Late Cretaceous and Early Tertiary. Palaeogeography Palaeoclimatology Palaeoecology 222, 95–121.

Quilty, P.G., 1990. Significance of evidence for changes in the Antarctic marine environment over the last 5 million years. In: Kerry, K.R., Hempel, G. (Eds.), Antarctic Ecosystems: Ecological Change and Conservation. Springer, Berlin, pp. 3–8.

Raguá-Gil, J.M., Gutt, J., Clarke, A., Arntz, W.E., 2004. Antarctic shallow-water mega-epibenthos: shaped by circumpolar dispersion or local conditions? Marine Biology 144, 829–839.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. Journal of Sea Research 48, 127–141.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Sea Research 28, 150–178.

Rhodes, M.V., Thayer, C.W., 1991. Mass extinctions: ecological selectivity and primary production. Geology 19, 877–880.

Richer de Forges, A., Koslow, J.A., Poore, G.C.B., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405, 944–947.

Roberts, S., Hirshfield, M., 2004. Deep-sea corals: out of sight, but no longer out of mind. Frontiers of Ecology and Environment 2, 123–130.

Rogers, A.D., 2000. The role of the oceanic oxygen minima in generating biodiversity in the deep sea. Deep-Sea Research, Part II 47, 119–148.

Schmidt, R., Bone, Y., 2003. Biogeography of Eocene bryozoans from the St Vincent Basin, South Australia. Lathaia 36, 345–356.

Sepkoski Jr., J.J., 1981. A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7, 36–53.

Sepkoski Jr., J.J., 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology 10, 246–267.

Sepkoski Jr., J.J., 1997. Biodiversity: past, present, and future. Journal of Paleobiology 71, 533–539.

Sepkoski Jr., J.J., Hulver, M.L., 1985. An atlas of Phanerozoic clade diversity diagrams. In: Valentine, J.W. (Ed.), Phaner-

ozoic Diversity Patterns. Princeton University Press, Princeton, pp. 11–39.

Sepkoski Jr., J.J., Miller, A.I., 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In: Valentine, J.W. (Ed.), Phanerozoic Diversity Patterns. Princeton University Press, Princeton, NJ, pp. 153–155.

Skelton, P.W., Gili, E., Vicens, E., Obrador, A., 1995. The growth fabric of gregarious rudist elevators (hippuritids) in a Santonina carbonate platform in the southern Central Pyrenees. Palaeogeography Palaeoclimatology Palaeoecology 119, 107–126.

Stilwell, J.D., 1997. Tectonic and palaeobiographic significance of the Chatham Islands, South Pacific, Late Cretaceous fauna. Palaeogeography Palaeoclimatology Palaeoecology 136, 97–116.

Tatián, M., Sahade, R., Kowalke, J., Kivatinitz, S.C., Esnal, G.B., 2002. Food availability and gut contents in the ascidian *Cnemidocarpa verrucosa* at Potter Cove, Antarctica. Polar Biology 25, 58–64.

Teixidó, N., Garrabou, J., Arntz, W.E., 2002. Spatial pattern quantification of Antarctic benthic communities using landscape indices. Marine Ecology Progress Series 242, 1–14.

Thatje, S., Anger, K., Calcagno, J.A., Lorich, G.A., Pörtner, H.O., Arntz, W.E., 2005. Challenging the cold: crabs reconquer the Antarctic. Ecology 86, 619–625.

Thayer, C.W., 1975. Morphologic adaptations of benthic invertebrates to soft substrata. Journal of Marine Research 33, 177–189.

Thayer, C.W., 1979. Biological bulldozers and the evolution of marine benthic communities. Science 203, 458–461.

Thayer, C.W., 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. In: Taevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Press, New York, pp. 479–625.

Thayer, C.W., 1989. Brachiopods and sclerosponges: Drop-outs from the evolutionary race? Geological Society of America, Abstracts with Programs 21, 252–253.

Thayer, C.W., Hall, J., Grage, K., Barrett, P., 1992. Oligotrophic refuge for living brachiopods; the Southern Hemisphere and fijords of New Zealand. Geological Society of America, Abstracts with Programs 24, 313.

Thomas, E., 1992. Middle Eocene—Late Oligocene bathyal benthic Foraminifera (Weddell-Sea): faunal changes and implications for ocean circulation. In: Prothero, D.R., Berggren, W.A. (Eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, NJ, pp. 245–271.

Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annual Review in Ecology and Systematics 33, 449–473.

Vermeij, G.J., 1977. The mesozoic marine revolution: evidence from snails, predators and grazers. Paleobiology 3, 245–258.

Vermeij, G.J., 1983. Shell-breaking predation through time. In: Tevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Communities. Plenum Press, New York, pp. 649–669.

Vermeij, G.J., 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press, Princeton, NJ.

Watling, L., Thurston, M.H., 1989. Antarctica as an evolutionary incubator: evidence from the cladistic biogeography of the amphipod family Iphimediidae. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota. Geological Society, London, pp. 297–313 (Geol Soc Spec Publ. 47).

Witman, J.D., Dayton, P.K., 2001. Rocky subtidal communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Sunderland, pp. 339–366.

Wood, R., 1998. The ecological evolution of reefs. Annual Review in Ecology and Systematics 29, 179–206.

Zachos, J.C., Arthur, M.A., Dean, W.E., 1989. Geochemical evidence for suppression of pelagic marine productivity at the Cretaceous/Tertiary boundary. Nature 337, 61–64.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 29, 686–693.

Zibrowius, H., 1980. Les scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Memories de l'Institut Oceanographique 11, 1–107.