# Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf

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**Abstract:** The modern benthic fauna of the Antarctic continental shelf is characterized by the lack of active, skeleton-breaking (durophagous) predators such as crabs, lobsters and many fish, and the dominance in many areas of epifaunal suspension feeders. It has often been remarked that these ecological characteristics give the fauna a distinctly Palaeozoic feel, with the assumption that it may be an evolutionary relic. We now know that this is not so, and fossil evidence shows clearly that many of the taxa and life-styles that are absent now were previously present. The modern fauna has been shaped by a number of factors, important among which have been oceanographic changes and the onset of Cenozoic glaciation. Sea-water cooling, and periodic fragmentation of ranges and bathymetric shifts in distribution driven by variability in the size and extent of the continental ice cap on Milankovitch frequencies will all have caused both extinction and allopatric speciation. The modern glacial setting with relatively low terrestrial impact away from immediate coastal regions, and scouring by icebergs are the key factors influencing the ecology and population dynamics for the modern Antarctic benthos.

## Introduction

All faunas are shaped by both ecological and evolutionary factors. On the longer time scales faunal assemblages reflect the influence of macroevolutionary events, invasions, extinctions, tectonics and climatic change. On the shorter time scales the organisms comprising the fauna are subject to ecological factors such as predation, habitat and food supply. These two time scales are simply extremes of a continuum, across which there is a shifting balance between the relative importance of ecological and evolutionary factors (Clarke 2003a), and it is not always a simple matter to separate the two (Jablonski 2000).

The benthic marine fauna of Antarctica provides a unique opportunity to distinguish the various factors that influence the evolutionary history of a biota. Compared with many other marine areas the fauna is relatively well known (though sampling remains patchy: Clarke & Johnston 2003), has been isolated by the Antarctic Circumpolar Current for a long time, and inhabits an area with a well-defined tectonic, climatic and glacial history. Here we discuss the evolutionary history of the Antarctic benthic marine fauna and attempt to distinguish the various factors that have shaped this history. To do so we first summarize current systematic knowledge of the fauna and then examine the historical context for its evolution. Finally, we review the important outstanding questions, and attempt to provide answers to some of these.

### The modern Antarctic benthic marine fauna

*Sampling distribution and species richness*

Although many areas of the Antarctic continental shelf remain unexplored the benthic marine fauna of Antarctica is comparatively well known. The groundwork was laid by the pioneering work of HMS *Challenger* and the many naturalists working with expeditions of the Heroic Era of polar exploration. Although many of these important pioneers are commemorated in the scientific names of the polar fauna, it is doubtful that they will receive the credit their work deserves (Dayton 1990). More recently significant contributions have come from the work of the *Discovery* Investigations, a series of voyages by RV *Eltanin,* and work undertaken through many national Antarctic programmes and organised under the auspices of SCAR (the Scientific Committee on Antarctic Research).

The Antarctic benthic fauna currently comprises over 4000 described species (White 1984, Arntz *et al.* 1997, Clarke & Johnston 2003). The sample coverage is however extremely patchy. Areas such as South Georgia, the South Shetland Islands and the western Antarctic Peninsula have been well sampled. In addition the Ross Sea has been intensively covered by biologists from the United States,

**Table I.** Spatial variability in sampling intensity for Southern Ocean benthos. Data are number of sampling locations for which gastropod or bivalve data are available, divided by sector or depth. The depth strata are continental shelf (0–1000 m), continental slope (1000–3000 m) and deep sea (> 3000 m). Data are from the Southern Ocean Molluscan Database (Griffiths *et al.* 2003) and are reproduced courtesy of Huw Griffiths, Katrin Linse and Alistair Crame. Table reproduced from Clarke & Johnston (2003) and excludes data from the recent ANDEEP cruises.

| Sector | Continental shelf | Number of samples Continental slope | Deep sea |
|---|---|---|---|
| South Georgia, South Sandwich Islands and South Orkney Island | 209 | 24 | 16 |
| Weddell Sea, east to 10°W | 357 | 31 | 2 |
| Dronning Maud Land, 10°W to 65°E | 89 | 4 | 1 |
| Prydz Bay, 65°E to 80°E | 9 | 1 | 0 |
| Wilkes Land, 80°E to 170°E | 191 | 8 | 1 |
| Ross Sea, 170°E to 150°W | 408 | 18 | 5 |
| Bellinghausen and Amundsen seas, 80°W to 150°W | 2 | 0 | 6 |
| Western Antarctic Peninsula, 80°W to 50°W, including South Shetland Islands but excluding Weddell Sea | 231 | 12 | 5 |
| Total | 1490 | 98 | 36 |
| %Total samples | 92 | 6 | 2 |

New Zealand and Italy, and the eastern Weddell Sea has been well described by biologists working from the German RV *Polarstern.* Coverage of East Antarctica is far from complete and we know almost nothing of the benthic fauna of the largely inaccessible Bellingshausen and Amundsen seas (Table I). Gutt *et al.* (2004) have used a variety of extrapolation techniques to estimate that the total macrobenthic fauna of the Antarctic continental shelf may exceed 17 000 species. This would suggest that we have described only a quarter of the entire fauna to date.

Most of the samples come from the continental shelf; in common with most other areas of the world we know relatively little about the fauna of the continental slope or the deep sea (Hilbig 2001, Clarke 2003b). The recent ANDEEP cruises will, however, enhance considerably our knowledge of the Southern Ocean deep seas and their connection with the shallow water fauna (Fütterer *et al.* 2003).

As with all areas of the world, the species richness of Antarctic benthos varies widely between taxonomic groups (Table II). The most speciose groups of Antarctic benthos are the polychaetes, gastropods, amphipods, bryozoans, isopods and true sponges (that is, excluding hexactinellids). All of these are groups that are species rich in most areas of the world. An alternative pattern emerges, however, if the Antarctic fauna is viewed in terms of the representation of the world fauna. The area of continental shelf not beneath permanent ice shelves in Antarctica is about $3 \times 10^6$ km², which represents approximately 11% of the world's continental shelves (Walsh 1988, Clarke & Johnston 2003). A figure of 11% of the world's described fauna might thus be taken as indicative of *pro rata* representation in Antarctica. This approach is very crude, for it ignores any consideration of the species/area relationship which is typically non-linear; since the scaling exponent is frequently < 1, *pro rata* calculation may overestimate the species richness to be expected from the Antarctic continental shelf. It does suggest that many of the most speciose groups in Antarctica are simply reflecting their species richness in general, since in many the number of species described from Antarctica represents 8–12% of the world fauna. Some groups, however, appear to deviate from this trend: gastropods, isopods and true sponges appear to be markedly under-represented in the Antarctic fauna, and pycnogonids to be strikingly well represented (Table II). These comparisons must be viewed with care as they are crude, and may be distorted by factors such as the exceptionally high species richness of the Indo–West Pacific region.

Patterns of relative importance of different taxa can also be assessed by comparing species richness between Antarctica and elsewhere on earth. To do this requires a reasonably complete species inventory for the areas under comparison, and remarkably few of these exist. Any such

**Table II.** Benthic marine invertebrate taxa exhibiting the highest species richness in the Southern Ocean. Colloquial names are used as the various groups represent different taxonomic levels (phylum, class or order). Taxa are ranked according to the total number of species so far described, with a threshold for inclusions of 100. Species richness can only be approximate because of unresolved taxonomic difficulties and undescribed or undiscovered species. Also included are estimates of the percentage of the world fauna for that taxonomic group. Data from Clarke & Johnston (2003).

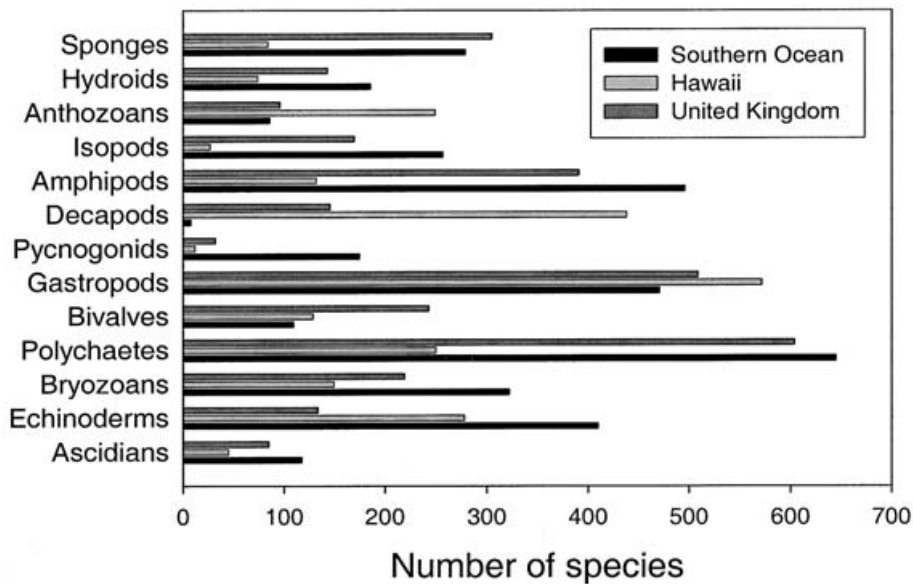| | Number of described species | Percentage of world species |
|---|---|---|
| Polychaetes | 645 | 12 |
| Gastropods | 530 | <1 |
| Amphipods | 496 | 8 |
| Bryozoans | 322 | 6–8 |
| Isopods | 257 | 3 |
| True sponges* | 250 | 3–6 |
| Hydrozoans (benthic forms only) | 186 | nd |
| Pycnogonids | 175 | 18 |
| Ophiuroids | 119 | 6 |
| Ascidians | 118 | 6–9 |
| Bivalves | 110 | 6 |
| Asteroids | 108 | 7 |
| Holothurians | 106 | 9 |

*excludes hexactinellids

**Fig.1.** Comparison of species richness for selected benthic marine invertebrate groups in the Southern Ocean with Hawaii and north-western European waters around UK. Redrawn from Clarke & Johnston (2003), with data from Eldredge & Miller (1995), Hayward & Ryland (1995) and Howson & Picton (1997).

inventory needs to be reasonably complete and there are statistical problems in comparing areas with differing proportions of unknown taxa (Gutt *et al.* 2004). Comparison can be made, however, with regions such as Hawaii and the north-west Atlantic around UK (Fig. 1). This comparison indicates that for many groups, species richness is broadly comparable between the Antarctic and UK. In many cases the lower values for Hawaii can probably be ascribed to the smaller area of continental shelf and its great isolation from sources of colonisation. The comparison does, however, emphasise the markedly low diversity of decapods and the apparent richness of pycnogonids in the Antarctic fauna.

Statistically significant polar–equatorial gradients in taxonomic diversity have now been established in a number of shallow and deep-sea taxa (summarized in Crame in press). It is apparent that in almost all instances investigated to date significantly higher richness has been observed in the Antarctic than Arctic regions, and hemispheric asymmetry may be a persistent feature of global marine diversity (Gray 2001). This in turn suggests a significant difference in the evolutionary history of the two Polar Regions (Crame in press).

*Characteristics of the modern Antarctic benthic fauna*

Away from the deeper soft sediment habitats, the modern Antarctic benthic fauna is very much an epifauna of sessile filter and particle feeders associated with coarse grained glacial substrates. At its most abundant, it is typified by dense, stratified communities of sponges, anemones, ascidians, gorgonians, hydroids, bryozoans, cirripedes, crinoids and corals that often form a three-dimensional framework at intermediate depths (50–30 m) below the influence of sea ice and anchor ice formation (Arntz *et al.* 1994, 1997, Gutt 2000, Catttaneo-Vietti *et al.* 2000, Gambi *et al.* 2000). Associated with these sessile forms is an errant

fauna of ophiuroids, asteroids, echinoids, pycnogonids, isopods, amphipods, nemerteans and gastropods. Trophic relationship among these various groups have yet to be fully established, but certain predators, such as the nemertean worms and buccinoidean gastropods, are known to be highly omnivorous, taking a wide range of live and dead prey (Arnaud 1974, Gibson 1983). Detailed analyses of groups such as amphipods are providing new insights into the complex habitat use of the continental shelf benthos (De Broyer *et al.* 2001).

One of the most important features of the Antarctic benthic fauna is the lack of durophagous (skeleton-breaking) predation, which is so characteristic of shallow waters elsewhere. Crabs, lobsters and sharks are essentially absent, and there is only a very limited diversity of teleosts and skates (Aronson & Blake 2001). The strikingly depauperate decapod fauna of Antarctica has long attracted attention. There are now known to be fewer than a dozen benthic caridean shrimps in the Southern Ocean (Gorny 1999) and although a number of anomuran crabs are known from the deeper waters of the continental slope (Thatje & Arntz 2004), there are no lobsters or brachyuran crabs. The reason for their absence is not clear although recently a physiological explanation has been advanced, centred on the inability of the brachyurans and astacids to maintain a suitable ionic balance for activity at low temperatures (Frederich *et al.* 2001).

The benthic fish fauna of Antarctica is no less remarkable in its taxonomic balance. With the exception of a small number of rays known from deeper waters around South Georgia, there are no selachians in the Southern Ocean. Furthermore many teleost groups are almost completely absent and the fauna is dominated by striking radiations in two groups: the nototheniioids, principally on the continental shelf and the lipariids in the deeper waters of the continental slope (Eastman 1993, Eastman & Clarke 1998).
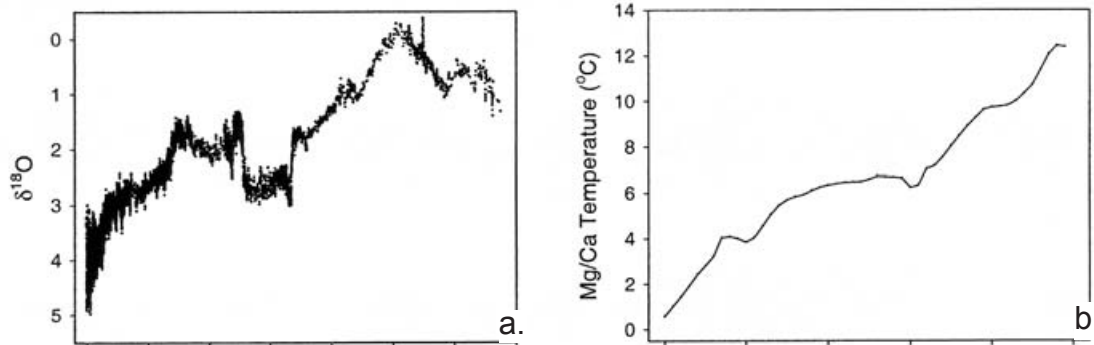
**Fig. 2. a.** Globally averaged paleotemperature curve for the deep sea environment. These data are averaged from 47 cores collected in three ocean basins but provide a broad measure of Antarctic bottom temperatures through the Cenozoic though the raw oxygen isotope signal is confounded with ice volume (Zachos *et al.* 2001a). **b.** Mg/Ca temperature curve from the Southern Ocean (Lear *et al.* 2000).

a variety of reasons. In addition to the Cenozoic increase in durophagous predators (at least initially), it is possible that many suspension-feeding groups were unable to cope with a pulsed food supply linked to the onset of glaciation and coarse grained glacial substrates may have proved inimical to many taxa (Crame 2000).

*Further evidence from the La Meseta Formation*

The La Meseta Formation has yielded a wide variety of other invertebrates and vertebrates which are crucial to deciphering the evolutionary history of the modern Antarctic marine fauna. All known Antarctic Cenozoic fish fossils come from this unit and include a diverse array of chondrichthyans including sharks, saw sharks, rays and ratfish. Teleosts are represented only by a variety of fragmented and unidentifiable spines, vertebral centra and jaw bones (Eastman & Grande 1989, Eastman 1993). There are records of both crabs and lobsters (Feldman & Zinsmeister 1984b, Feldmann & Tshudy 1989), and a surprisingly rich assemblage of echinoderms includes asteroids, ophiuroids and both comotulid and isocrinid crinoids (Meyer & Oji 1993, Aronson *et al.* 1997, Blake & Aronson 1998).

The Eocene fauna contrasts with that inhabiting the continental shelves of Antarctica today, most strikingly in the lack of lobsters, brachyuran crabs, sharks, all but a few batoid skates and rays, and most of the teleost fishes. This represents a significant loss of predatory taxa from the shallow water community, and especially of durophagous taxa (Aronson *et al.* 1997, Aronson & Blake 2001). Although the La Meseta Formation either immediately predates or is associated with the late Eocene/early Oligocene environmental change, we do not know whether this change actually caused the shift in community composition. What fossils we do have, however, suggest that at least some elements survived until relatively recently. Thus although lobsters and brachyuran crabs are now absent from Antarctica, there was at least one species of crab in the

Miocene (Förster *et al.* 1987) and lobsters are known from as late as the Pliocene (Feldmann & Quilty 1997, Feldmann & Crame 1998). It is not known when the Eocene fish fauna was lost from Antarctica, but molecular evidence dates the base of the notothenioid radiation to the middle Miocene (Cheng & Chen 1999). This notothenioid radiation is characterized by a single evolutionary event, the acquisition of antifreeze (Clarke & Johnston 1996), and is coincident with the sharp drop in temperature which may well have marked the first onset of freezing sea-water temperatures. Non-notothenioid fish in Antarctica also have antifreezes, and these have different evolutionary origin (Cheng & Chen 1999).

*A living Palaeozoic fauna?*

It has long been remarked that the lack of several key predator groups, coupled with the dominance of suspension feeders and the presence of dense ophiuroid beds and crinoid populations give the modern Antarctic benthic marine fauna a more than passing resemblance to Palaeozoic assemblages (Dell 1972, Aronson *et al.* 1997). The fact that this community composition arose during the Cenozoic from a more typical modern assemblage poses the question of whether the modern fauna reflects an ecological and evolutionary response to the loss of predators, or is an adaptation to the glacial-marine environment of the Antarctic continental shelf, or some combination of these.

*Temperature, oceanography and glaciation*

The overall thermal history of oceanic bottom temperatures during the Cenozoic is now well established from oxygen isotope analyses of foraminifera from deep sea sediment cores (see Zachos *et al.* 2001a for a recent summary). These data provide a broad indication of bottom temperatures in Antarctica throughout the Cenozoic, and indicate two periods of sharp change in isotopic signature (Fig. 2a): at the end of the Eocene and in the middle of the Miocene.

The association of lipariids with the continental slope is interesting, as this is also where lithodid crabs are mostly found in the Southern Ocean (Thatje & Arntz 2004). In the Arctic liparids of the genus *Careproctus* have long been known to lay their eggs either on, or in the branchial chambers, of lithodids (Somerton & Donaldson 1998) and similar relationships have recently been noted at South Georgia (Yau *et al.* 2000). The warmer waters of the Upper Circumpolar Deep Water also bring a range of other midwater fish to the continental slope of Antarctica (Eastman 1993).

One result of the low benthic predation pressure has been the development of dense populations of suspension feeders such as crinoids and ophiuroids, although the low level of fine grained terrigenous sediment will also play a role. This gives the modern benthic fauna a distinct 'Palaeozoic' appearance (Aronson *et al.* 1997). The unusual composition of the Antarctic benthic marine fauna poses a number of questions concerning its origin and evolution. In this paper we explore three inter-related themes:

1. How has the fauna changed through geological time and in particular during the Cenozoic era (the last 65 Ma)?

2. What was the relationship between Antarctic climate change and both speciation and extinction rates?

3. What happened to the benthic fauna during glacial maxima, and subsequently?

**The historical context**

Although the fossil record is far from complete, there is growing evidence to suggest that distinctive, temperate, shallow marine faunas have characterized the southernmost high latitudes since at least the late Palaeozoic (Crame 1992). Such faunas, which were not necessarily continuous through time, show two consistent features: they are invariably less diverse than their lower latitude counterparts (Crame 2001), and they are characterized by bipolar elements (Shi & Grunt 2000). The lower taxonomic diversity of these faunas is important because it hints at an underlying difference in evolutionary rates on the grandest of geographical and temporal scales. Reduced rates of speciation or enhanced rates of extinction (or both) may not just be a feature of the recent past in Antarctica. In addition, the occurrence of bipolar faunas through time indicates that temperate taxa were repeatedly able to cross the intervening tropical ocean, probably using a variety of different dispersal mechanisms and routes.

In a recent molecular phylogenetic investigation of the shallow marine gastropod subfamily Littorininae, Williams *et al.* (2003) established a sister-group relationship between the genera *Littorina* (northern Pacific) and *Afrolittorina* (southern Africa and southern Australia); an estimated divergence time of 66–108 Ma (i.e. essentially late Cretaceous) matched that for antitropical patellid limpets (Koufopanou *et al.* 1999). These examples can be added to that of gastropod family Struthiolariidae to suggest that at least some elements of the modern Antarctic benthic fauna have a late Cretaceous ancestry (Zinsmeister 1984, Zinsmeister & Feldmann 1984, Clarke & Crame 1989). Such 'palaeoaustral' elements within the fauna are not necessarily confined to molluscs, as a recent palaeontological discovery has indicated that the ancestry of the Antarctic isopod family Serolidae can be traced back to the Late Jurassic (150 Ma; Brandt *et al.* 1998). Briggs (2003) recently summarized evidence to suggest that the Antarctic had been one of two great centres of origin within the temperate marine realm (the other being the North Pacific) throughout the Cenozoic to Recent.

By the Late Cretaceous the Antarctic shallow marine fauna formed part of a distinctive Weddellian Province that could be traced around the southern Gondwana margins from Patagonia, through West Antarctica, to New Zealand and south-eastern Australia (Zinsmeister 1984). There is no doubt that it was affected by the mass extinction event at the end of the Cretaceous, but to precisely what extent is still uncertain. At least nine benthic molluscan taxa actually crossed the K–T boundary in Antarctica, and it is clear that a number of these would have been deposit feeders well able to cope with a major collapse in the benthic ecosystem (Stilwell 2003). Nevertheless, a prominent, large suspension feeding bivalve, *Lahillia*, crosses the K–T boundary in strength, and of the 26 molluscan taxa in the beds directly above the boundary, 15 have been assigned to new species in surviving genera (Stilwell 2003).

Although there was undoubtedly an overall reduction in marine diversity in the early Palaeocene (i.e. earliest Cenozoic) this was to some extent mitigated by the global expansion of a number of key benthic groups. Prominent amongst these were the neogastropods and it is interesting to note that bucciniform taxa underwent a pronounced radiation in Antarctica at this time (Oleinik & Zinsmeister 1996). Indeed, one of the new genera to appear in the early Paleocene, *Probuccinum*, still has a circum-Antarctic distribution at the present day.

The late Paleocene–early Eocene fossil record of Antarctica is incomplete, but by the Middle Eocene it is apparent that benthic molluscan diversity had more than recovered to its pre-mass extinction levels. The prolific middle–late Eocene La Meseta Formation of Seymour Island has now yielded in excess of 170 molluscan taxa, with more than half of these being bivalves (Stilwell & Zinsmeister 1992). Thereafter shallow-marine benthic molluscan diversity was substantially reduced to its present day levels but whether this was a gradual process or perhaps punctuated by further mass extinctions is unknown. Bivalves appear to have been particularly badly hit in the intervening 35 m.y. and it is possible that this happened for

Debate continues over the relative contribution of ice volume and temperature to these two events, but it seems likely that the early Oligocene marked the onset of continental glaciation, and the mid-Miocene the onset of rapid cooling (Lear *et al.* 2000). A second palaeotemperature proxy, Ca $^{2+}$ in foraminiforal skeletons, is unaffected by ice volume and provides a lower resolution picture of sea-water temperature during the Cenozoic (Fig. 2b: Lear *et al.* 2000).

Bottom temperatures are driven principally by large scale oceanography and glacial processes at high latitudes, and it has long been recognised that a key event in the evolution of Antarctic oceanography was the opening of the Drake Passage. This allowed the onset of a circum-Antarctic current system and was almost certainly an important factor in the overall cooling of high latitudes (Clarke & Crame 1989 and references therein). Recent advances in our understanding of Scotia Sea tectonics suggest that this critical event occurred in the earliest Oligocene (approximately 35 Ma BP). This work has focussed on both the Shackleton Fracture Zone, a major submarine ridge running diagonally from Tierra del Fuego to the Antarctic Peninsula, and certain tectonic blocks in the eastern Scotia Sea (Eagles 2003). The configuration of these features is now thought to have allowed the ingress of deep bottom waters through this region in the earliest Oligocene and thus completed the thermal isolation of Antarctica. A deep water gateway across the South Tasman Rise may be of a very similar age (Lawver & Gahagan 2003).

Although the broad history of continental glaciation in Antarctica is reasonably well established (Barrett 1996, 2001), the details which are important to an understanding of the evolution of the Antarctic marine fauna are still lacking. Continental glaciation was probably initiated about 35 Ma BP, and the individual ice-sheets almost certainly fluctuated in size in response to orbital variations on Milankovitch frequencies (Barrett *et al.* 1987, Fielding *et al.* 2000, Powell *et al.* 2000, Naish *et al.* 2001, DeConto & Pollard 2003). As the continental ice-sheet grew in size it probably became less sensitive to Milankovitch frequency climatic cycles but would still have responded to fluctuations in sea level (Barrett 2001). The sharp cooling in the mid-Miocene marked a major growth in the continental ice sheet, but quite what drove this is unknown.

The important question in terms of the evolutionary history of the Southern Ocean shallow water marine fauna is to what degree fluctuations in sea level, and the extent of the continental ice-sheet, have driven changes in the depth and area of habitat on the continental shelves around Antarctica (Clarke & Crame 1989). Although there is clear geophysical evidence for extensions of the ice-sheet having reduced considerably the area of continental shelf at least once in the past, we cannot yet say how often this has occurred in the past or how widespread they might have been.

## The modern fauna: habitat

The modern Antarctic benthic marine fauna inhabits a relatively atypical continental shelf environment. The shelf around Antarctica is unusually deep as a result of scouring from ice shelves at previous glacial maxima and depression by the enormous mass of continental ice (Clarke 1996, Clarke & Johnston 2003). Continental shelves elsewhere in the world are typically 100–200 m deep and average 75 km in width (Walsh 1988); those around Antarctica average 450 m in depth, and in places they extend to over 1000 m. The deepest areas are trenches and basins scoured by ice flow, and the outer edge of the shelf is typically somewhat shallower. In contrast to all other continental shelves (including those of the Arctic) there is essentially no riverine input. Mudflats are rare and estuaries almost non-existent; almost all terrestrial input comes via glacial processes or, in a few places, wind. Most of the coastline is ice, with only 14% being rock (Clarke & Johnston 2003). This rocky coastline is subject to intense scour from floating ice and is consequently largely devoid of the traditional intertidal fauna.

The unusual depth and topography of the Antarctic continental shelf mean that many habitats typical of shelves elsewhere are missing from Antarctica. These include most of the shallow water habitats which traditionally support rich and diverse communities. The soft sediment habitats are characterised by poorly sorted glacial-marine sediments, with an increasing incidence of drop-stones towards shore (Clarke 1996). In the shallower regions benthic habitats are disturbed by scour from icebergs. The intensity and frequency of these scours are major features dictating assemblage structure and population dynamics in the Antarctic continental shelf benthos (Gutt 2000, 2001, Gutt & Starmans 2001, Gutt & Piepenburg 2003).

The sea-water temperature is typically very low and although water column production can be very intense close to shore this productivity is markedly seasonal and influenced by ice dynamics (Clarke & Leakey 1996, Smith *et al.* 1998). Much of the summer production is dominated by larger diatoms, although colonial haptophytes can be important at times, and can result in a significant flux of phytodetritus to the continental shelf.

### Predation in the modern Antarctic benthic marine fauna

Despite the absence of typical active durophagous predators, the Antarctic marine benthos involves many trophic interactions typical of modern seas. Examples include chemical defences against other invertebrates (McClintock 1994, McClintock & Baker 1997, 1998), consumption of algae by regular urchins (Brockington *et al.* 2001), and drilling by naticid and muricid gastropods (Harper & Peck 2003). Thus, although the Antarctic shallow water benthos has a Palaeozoic feel to it, the taxa

themselves are not archaic. Many are recently derived and many aspects of the food web dynamics are distinctly modern (Aronson & Blake 2001). Nevertheless, the assemblages are frequently dominated by suspension feeders and the benthic food web is unusual in the large fraction of overall biomass concentrated in the first consumer trophic level (Jarre-Teichmann *et al.* 1997). The top trophic level is dominated by asteroids (Dayton *et al.* 1974, Fratt & Dearborn 1984, McClintock & Baker 1997), and the large predatory nemertean *Parborlasia corrugatus* is important in shallow water habitats close to shore (Gibson 1983).

### What factors drove the evolution of the current fauna?

The question of where the Antarctic marine fauna came from is a deceptively simple one, but it has no simple answer. This is because no complex fauna has a single time or place of origin. Knox & Lowry (1977) have suggested that the present Southern Ocean fauna as a whole comprises four main components:

1. A relict autochthonous fauna which has always been there, and which has evolved *in situ*

2. A fauna derived from adjacent deep-water basins

3. A fauna dispersing from South America along the Scotia Arc

4. A fauna which has spread in the opposite direction from Antarctic northwards along the Scotia arc.

Nearly three decades of systematic, biogeographic and molecular evolutionary research have not changed this basic framework, though we may have altered our view of the relative importance of the various components. The one factor not dealt with in this classification, however, is extinction. This process will have affected all four components, but primarily the autochthonous fauna.

### *Cenozoic extinction in the Antarctic benthic marine fauna*

The fossil record of the Antarctic marine fauna is sufficient to indicate that several groups of organisms have been lost, but not good enough to suggest precisely when or why these extinctions occurred.

One major faunal change is that of the fish fauna from which almost all the groups present in the late Mesozoic and early Cenozoic have subsequently vanished. In their place are two radiations which show many feature of species flocks and radiation into vacant niches (Eastman 1993, Eastman & Clarke 1998). This suggests that extinction of the Eocene fauna preceded the notothenioid and liparid radiations. It seems likely that key factors in this extinction were loss of many traditionally fish-rich nearshore habitats, and climatic cooling. The notothenioid radiation is coincident with the sharp cooling in the middle Miocene, and appears to be related to a single key physiological innovation, the evolution of a glycopeptide antifreeze (Eastman & Clarke 1998, Cheng & Chen 1999). This would suggest that the success of the notothenioid clade was not related to any particular ecological feature possessed by the basal stock, but rather to the evolution of antifreeze. Indeed in many ways the basal notothenioid would appear to be ill adapted in the lack of a functional swim-bladder (Eastman 1993). Although the notothenioid radiation has been characterised by some trophic specialization (Eastman & DeVries 1997), no lineages have evolved durophagy.

The loss of lobsters and crabs is equally striking, although here the fossil record does show that these groups existed around Antarctica well into the glacial era. They do not survive today, however, when sea-water is permanently around freezing. It seems likely that in this case extinction was related to an inability to adapt physiologically to the very low temperatures (Frederich *et al.* 2001).

### *Evolutionary radiations in Antarctica*

Although the notothenioid radiation has attracted most attention, the Southern Ocean fauna contains several other groups which have clearly radiated during the Cenozoic. These include predatory gastropods, isopods (Brandt 1991, 2000, Brandt *et al.* 1999), amphipods (Watling & Thurston 1989) and pycnogonids (Clarke & Johnston 2003). It is likely that each of these radiations reflects a different set of ecological circumstances, though it is tempting to link the radiations of isopods and amphipods to the relative absence of decapods. Brandt (2000) has also proposed that the isopod radiation in Antarctica may be related to that of notothenioid fish. Until relatively recently, radiations were recognised on the basis of highly speciose lineages in particular taxa. Modern molecular techniques are, however, starting to demonstrate the presence of cryptic species in many taxa (Held 2000, 2001, 2003, Page & Linse 2002), indicating that species richness of the Antarctic benthos may be significantly greater than previously thought.

The Antarctic ice cap has responded to orbital variability on Milankovitch frequencies by regular increases and decreases in size. Although the ice core record indicates that the switch between glacial and interglacial conditions matches the 100 ka eccentricity variation, spectral analysis of oxygen isotopes from foraminfera in deep-sea cores (Zachos *et al.* 2001b) and physical properties of cores (Florindo *et al.* 2003) often reveal a dominant signal from the 41 ka obliquity variation.

Clarke & Crame (1989, 1992) have proposed that periodic extensions and retreat of the Antarctic ice cap on Milankovitch frequencies may have been an important factor in driving speciation of the continental shelf fauna. As the ice-sheet extended out over the shelf, distributions would have been fragmented with allopatric populations

confined to refugia or even driven down the continental slope. Following retreat of the ice-sheet, previously isolated populations would have mingled once more. The extent to which such cycles could have driven speciation depends on a number of factors, such as the time scale needed for genetic isolation to occur, the degree of isolation of, and geneflow between, refugia and the population sizes in those refugia. None of these can be estimated, though it is certain that there have been a great many cycles of ice-sheet growth and retreat during the Cenozoic glaciation.

One refugium likely to have been of great importance at previous glacial maxima is the continental slope. The unusual depth and the low temperature of the Antarctic continental shelf since the development of an extensive ice-sheet means that the shelf fauna was physiologically adapted to at least moderate depths, and migration into the deeper waters of the slope may have been less problematic evolutionarily than for a true shallow water fauna. Evidence for the role of the continental slope as a major refugium of glacial maxima comes from the diversity peak in notothenioid fish at the shelf break (Andriashev 1987), the close evolutionary connections between shelf, slope and deep sea isopod faunas in Antarctica (Brandt 1991), the apparent evolution of a number of deep sea taxa in shallow Antarctic waters (Zinsmeister & Feldmann 1984), and the unusually wide bathymetric range of many Antarctic marine invertebrates (Brey *et al.* 1996).

## Concluding remarks

The benthic fauna of the Antarctic continental shelf is distinctive in the lack of active durophagous predators such as crabs, lobsters and many fish, and in the predominance of epifaunal suspension feeding groups. Some of these features give a Palaeozoic appearance to the fauna but this is a recent change rather than an evolutionary relic. Many of the groups characteristic of the Mesozoic marine revolution (Vermeij 1977) were present previously but became extinct during the tectonic changes and glaciation that have characterized the Cenozoic of Antarctica.

The absence of predators characterstic of continental shelves elsewhere has allowed the persistence of assemblages sensitive to predation. The glacial environment has also favoured epifaunal suspension feeding, which is the dominant trophic guild over large areas of continental shelf. The current composition of the fauna cannot therefore be ascribed to any one factor, any more than it can be said to have a single origin. Extinctions and radiations have both been important historically, and the modern glacial-marine setting with frequent disturbance by iceberg scouring are key factors structuring the modern assemblages.

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## References

ANDRIASHEV, A.P. 1987. A general review of the Antarctic bottom fish fauna. *In* KULLANDER, S.O. & FERNHOLM, B., *eds. Fifth Congress of European Ichthyologists, proceedings, Stockholm, 1985.* Stockholm: Swedish Museum of Natural History, 357–372.

ARNAUD, P.M. 1974. Contribution à la bionomie marine benthique des régions Antarctiques et Subantarticques. *Tethys*, **6**, 465–656.

ARNTZ, W.E., BREY, T. & GALLARDO, V.A. 1994. Antarctic zoobenthos. *Advances in Marine Biology*, **32**, 241–304.

ARNTZ, W.E., GUTT, J. & KLAGES, M. 1997. Antarctic marine biodiversity: an overview. *In* BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., *eds. Antarctic communities: species, structure and survival.* Cambridge: Cambridge University Press, 3–14.

ARONSON, R.B. & BLAKE, D.B. 2001. Global climate change and the origin of modern benthic communities in Antarctica. *American Zoologist*, **41**, 27–39.

ARONSON, R.B., BLAKE, D.B. & OJI, T. 1997. Retrograde community structure in the late Eocene of Antarctica. *Geology*, **25**, 903–906.

BARRETT, P.J. 1996. Antarctic palaeoenvironment through Cenozoic times. A review. *Terra Antartica*, **3**, 103–119.

BARRETT, P.J. 2001. Climate change - an Antarctic perspective. *New Zealand Science Review*, **58**, 18–23.

BARRETT, P.J., ELSTON, D.P., HARWOOD, D.M., MCKELVEY, B.C. & WEBB, P.-N. 1987. Mid-Cenozoic record of glaciation and sea-level change on the margin of the Victoria Land basin, Antarctica. *Geology*, **15**, 634–637.

BLAKE, D.B. & ARONSON, R.B. 1998. Eocene stellaroids (Echinodermata) at Seymour Island, Antarctic Peninsula. *Journal of Paleontology*, **72**, 339–353.

BRANDT, A. 1991. Colonization of the Antarctic shelf by the Isopoda (Crustacea, Malacostraca). *Berichte zur Polarforschung*, **91**, 1–240.

BRANDT, A. 2000. Hypotheses on Southern Ocean peracarid evolution and radiation (Crustacea, Malacostraca). *Antarctic Science*, **12**, 269–275.

BRANDT, A., CRAME, J.A., POLZ, H. & THOMSON, M.R.A. 1998. Late Jurassic Tethyan ancestry of Recent southern high-latitude marine isopods (Crustacea, Malacostraca). *Palaeontology*, **42**, 663–675.

BRANDT, A., LINSE, K. & MÜHLENHARDT-SIEGEL, U. 1999. Biogeography of Crustacea and Mollusca of the Subantarctic and Antarctic regions. *Scientia Marina*, **63** (Supplement 1), 383–389.

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.

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

BROCKINGTON, S., CLARKE, A. & CHAPMAN, A.L.G. 2001. Seasonality of feeding and nutritional status during the austral winter in the Antarctic sea urchin *Sterechinus neumayeri*. *Marine Biology*, **139**, 127–138.

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 Terra Nova Bay. *In* FARANDA, F.M., GUGLIELMO, L. & IONORA, A., *eds. Ross Sea ecology.* Berlin: Springer, 503–514.

CHENG, C.H.C. & CHEN, L.B. 1999. Evolution of an antifreeze glycoprotein. *Nature*, **401**, 443–444

CLARKE, A. 1996. Benthic marine habitats in Antarctica. *Antarctic Research Series*, **70**, 123–133.

CLARKE, A. 2003a. Evolution, adaptation and diversity: global ecology in an Antarctic context. *In* HUISKES, A.H.L., GIESKES, W.W.C., ROZEMA, J., SCHORNO, R.M.L., VAN DER VRIES, S.M. & WOLFF, W.J., *eds. Antarctic biology in a global context.* Leiden: Backhuys Publishers, 3–17.

CLARKE, A. 2003b. The polar deep seas. *In* TYLER, P.A., *ed. Ecosystems of the deep oceans.* Amsterdam: Elsevier, 239–260.

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. Geological Society of London Special Publication*, No. 47, 253–268.

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

CLARKE, A. & JOHNSTON, I.A. 1996. Evolution and adaptive radiation of Antarctic fishes. *Trends in Ecology & Evolution*, **11**, 212–218.

CLARKE, A. & JOHNSTON, N.M. 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology: an Annual Review*, **41**, 47–114.

CLARKE, A. & LEAKEY, R.J.G. 1996. The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore Antarctic marine ecosystem. *Limnology & Oceanography*, **41**, 1281–1294.

CRAME, J.A. 1992. The evolutionary history of the polar regions. *Historical Biology*, **6**, 37–60.

CRAME, J.A. 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas. *Paleobiology*, **26**, 188–214.

CRAME, J.A. 2001. Taxonomic diversity gradients through geological time. *Diversity and Distributions*, **7**, 175–189.

CRAME J.A. In press. Pattern and process in marine biogeography: a view from the poles. *In* LOMOLINO, M.V. & HEANEY, L., *eds. Modern biogeography: new directions in the geography of nature.* Cambridge: Cambridge University Press.

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

DAYTON, P.K., 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.

DE BROYER, C., SCAILTEUR, Y., CHAPELLE, G. & RAUSCHERT, M. 2001. Diversity of epibenthic habitats of gammaridean amphipods in the eastern Weddell Sea. *Polar Biology*, **24**, 744–753.

DECONTO, R.M. & POLLARD, D. 2003. Rapid Cenozoic glaciation of Antarctic induced by declining atmospheric $CO_2$. *Nature*, **421**, 245–249.

DELL, R.K. 1972. Antarctic benthos. *Advances in Marine Biology*, **10**, 1–216.

EAGLES, G. 2003. Tectonic evolution of the Antarctic-Phoenix plate system. *Earth and Planetary Science Letters*, **217**, 97–109.

EASTMAN, J.T. 1993. *Antarctic fish biology: evolution in a unique environment.* San Diego, CA: Academic Press, 322 pp.

EASTMAN, J.T. & CLARKE, A. 1998. A comparison of adaptive radiations of Antarctic fish with those of non-Antarctic fish. *In* DI PRISCO, G., PISANO, E. & CLARKE, A., *eds. Fishes of Antarctica: a biological overview.* Berlin: Springer, 3–26.

EASTMAN, J.T. & DEVRIES, A.L. 1997. Biology and phenotypic plasticity of the Antarctic notothenioid *Trematomus newnesi* in McMurdo Sound. *Antarctic Science*, **9**, 27–35

EASTMAN, J.T. & GRANDE, L. 1989. Evolution of the Antarctic fish fauna with emphasis on the recent notothenioids. *In* CRAME, J.A., *ed. Origins and evolution of the Antarctic biota. Geological Society Special Publication*, No.47, 241–252.

ELDREDGE, L.G. & MILLER, S.E. 1995. How many species are there in Hawaii? *Bishop Museum Occasional Papers*, **41**, 1–18.

FELDMANN, R.M. & TSHUDY, D.M. 1989. Evolutionary patterns in macrurous decapod crustaceans from Cretaceous to early Cenozoic rocks of the James Ross Island region, Antarctica. *In* CRAME, J.A., *ed. Origins and evolution of the Antarctic biota. Geological Society Special Publication*, No.47, 183–195.

FELDMANN, R.M. & CRAME, J.A. 1998. The significance of a new nephropid lobster from the Miocene of Antarctica. *Palaeontology*, **41**, 807–814.

FELDMANN, R.M. & QUILTY, P.G. 1997. First Pliocene decapod crustacean (Malacostraca: Palinuridae) from the Antarctic. *Antarctic Science*, **9**, 56–60.

FELDMANN, R.M. & ZINSMEISTER, W.J. 1984a. First occurrence of fossil decapod crustaceans (Callianassidae) from the McMurdo Sound region, Antarctica. *Journal of Paleontology*, **58**, 1041–1045.

FELDMANN, R.M. & ZINSMEISTER, W.J. 1984b. New fossil crabs (Decapoda, Brachyura) from the La Meseta Formation (Eocene) of Antarctica: paleogeographic and biogeographic implications. *Journal of Paleontology*, **58**, 1046–1061.

FIELDING, C.R., NAISH, T.R., WOOLFE, K.J. & LAVELLE, M.A. 2000. Facies analysis and sequence stratigraphy of CRP-2/2A, Victoria Land Basin, Antarctica. *Terra Antartica*, **7**, 323–338.

FLORINDO, F., CLAPS, M., NIESSEN, F. & DINARÈS-TURELL, J. 2003. Spectral analysis of physical property periodicities in fine-grained sediments from the CRP-3 drillhole, Ross Sea, Antarctica. *Terra Antartica*, **10**, 17–26.

FÖRSTER, R., GAZDZICKI, A. & WRONA, R. 1987. Homolodromid crabs from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica. *Palaeontologia Polonica*, **49**, 147–161.

FRATT, D.B. & DEARBORN, J.H. 1984. Feeding biology of the Antarctic brittle star *Ophionotus victioriae* (Echinodermata, Ophiuroidea). *Polar Biology*, **3**, 127–139.

FREDERICH, M., SARTORIS, F.J. & PÖRTNER, H.O. 2001. Distribution patterns of decapod crustaceans in polar areas: a result of magnesium regulation? *Polar Biology*, **24**, 719–723.

FÜTTERER, D.K., BRANDT, A. & POORE, G.C.B. 2003. The expeditions ANTARKTIS-XIX/3-4 of the research vessel Polarstern in 2002. *Berichte zur Polar- und Meeresforschung*, **470**, 1–174.

GAMBI, M.C., BUIA, M.C., MAZZELLA, L., LORENTI, M. & SCIPIONE, M.B. 2000. Spatio-temporal variability in the structure of benthic populations on a physically controlled system off Terra Nova Bay: the shallow hard bottoms. *In* FARANDA, F.M., GUGLIELMO, L. & IONORA, A., *eds. Ross Sea ecology.* Berlin: Springer, 527–538.

GIBSON, R. 1983. Antarctic nemerteans: the anatomy, distribution and biology of *Parborlasia corrugatus* (McIntosh, 1876) (Heteronemertea, Lineidae). *Antarctic Research Series*, **39**, 289–316.

GORNY, M. 1999. On the biogeography and ecology of the Southern Ocean decapod fauna. *Scientia Marina*, **63**, 367–382.

GRAY, J.S. 2001. Antarctic marine benthic biodiversity in a world-wide latitudinal context. *Polar Biology*, **24**, 633–641.

GRIFFITHS, H.J., LINSE, K. & CRAME, J.A. 2003. SOMBASE - Southern Ocean Mollusc Database: a tool for biogeographic analysis in diversity and ecology. *Organisms, Diversity & Evolution*, **3**, 207–213.

GUTT, J. 2000. Some 'driving forces' structuring communities of the sublittoral Antarctic macrobenthos. *Antarctic Science*, **12**, 297–313.

GUTT, J. 2001. On the direct impact of ice on marine benthic communities: a review. *Polar Biology*, **24**, 553–564.

GUTT, J. & PIEPENBURG, D. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology Progress Series*, **254**, 77–83.

GUTT, J. & STARMANS, A. 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea. *Polar Biology*, **24**, 615–618.

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.

HARPER, E.M. & PECK, L.S. 2003. Predatory behaviour and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biology*, **26**, 208–217.

HAYWARD, P.J. & RYLAND, J.S. 1995. *Handbook of the marine fauna of north-west Europe*. Oxford: Oxford University Press, 811 pp.

HELD, C. 2000. Phylogeny and biogeography of serolid isopods (Crustacea, Isopoda, Serolidae) and the use of ribosomal expansion segments in molecular systematics. *Molecular Phylogenetics and Evolution*, **15**, 165–178.

HELD, C. 2001. No evidence for slow-down of molecular substitution rates at subzero temperatures in Antarctic serolid isopods (Crustacea, Isopoda, Serolidae). *Polar Biology*, **24**, 497–501.

HELD, C. 2003. Molecular evidence for cryptic speciation within the widespread Antarctic crustacean *Ceratoserolis trilobitoides* (Crustacea, Isopoda). *In* HUISKES, A.H.L., GIESKES, W.W.C., ROZEMA, J., SCHORNO, R.M.L., VAN DER VRIES, S.M. & WOLFF, W.J., *eds. Antarctic biology in a global context*. Leiden: Backhuys Publishers, 135–139.

HILBIG, B. 2001. Deep-sea polychaetes in the Weddell Sea and Drake Passage: first quantitative results. *Polar Biology*, **24**, 538–544.

HOWSON, C.M. & PICTON, B.E. 1997. *The species directory of the marine fauna and flora of the British Isles and surrounding seas*. Belfast and Ross on Wye: Ulster Museum and The Marine Conservation Society, 508 pp.

JABLONSKI, D. 2000. Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology*, **26**(4), 15–52.

JARRE-TEICHMANN, A., BREY, T., BATHMANN, U.V., DAHM, C., DIECKMANN, G.S., GORNY, M., KLAGES, M., PAGÉS, F., PLÖTZ, J., SCHNACK-SCHIEL, S., STILLER, M. & ARNTZ, W.E. 1997. Trophic flows in the benthic shelf community of the eastern Weddell Sea, Antarctica *In* BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., *eds. Antarctic communities: species, structure and survival*. Cambridge: Cambridge University Press, 118–134.

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 the Polychaeta. *In* DUNBAR, M.J., *ed. Polar oceans*. Calgary: Arctic Institute of North America, 423–462.

KOUFOPANOU, V., REID, D.G., RIDGWAY, S.A. & THOMAS, R.T. 1999. A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. *Molecular Phylogenetics and Evolution*, **11**, 138–156.

LAWVER, L.A. & GAHAGAN, L.M. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **198**, 11–38.

LEAR, C.H., ELDERFIELD, H. & WILSON, P.H. 2000. Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science*, **287**, 269–272.

McCLINTOCK, J.B. 1994. Trophic biology of Antarctic shallow-water echinoderms. *Marine Ecology Progress Series*, **111**, 191–202.

McCLINTOCK, J.B. & BAKER, B.J. 1997. A review of the chemical ecology of Antarctic marine invertebrates. *American Zoologist*, **37**, 329–342.

McCLINTOCK, J.B. & BAKER, B.J. 1998. Chemical ecology in Antarctic seas. *American Scientist*, **86**, 254–263.

MEYER, D.L. & OJI, T. 1993. Eocene crinoids from Seymour Island, Antarctic Peninsula: paleobiogeographic and paleoecologic implications. *Journal of Paleontology*, **28**, 250–257.

NAISH, T.R., WOOLFE, K.J., BARRETT, P.J., WILSON, G.S., ATKINS, C., BOHATY, S.M., BÜCKER, C.J., CLAPS, M., DAVEY, F.J., DUNBAR, G., DUNN, A.G., FIELDING, C.R., FLORINDO, F., HANNAH, M.J., HARWOOD, D.M., WATKINS, D.K., HENRYS, S.A., KRISSEK, L.A., LAVELLE, M., VAN DER MEER, J., McINTOSH, W.C., NIESSEN, F., PASSCHIER, S., POWELL, R.D., ROBERTS, A.P., SAGNOTTI, L., SCHERER, R.P., STRONG, C.P., TALARICO, F., VEROSUB, K.L., VILLA, G., WEBB, P.-N. & WONIK, T. 2001. Orbitally induced oscillations in the East Antarctic ice sheet at the Oligocene–Miocene boundary. *Nature*, **413**, 719–723.

OLEINIK, A.E. & ZINSMEISTER, W.J. 1996. Paleocene diversification of bucciniform gastropods on Seymour Island, Antarctica. *Journal of Paleontology*, **70**, 923–934.

PAGE, T.J. & LINSE, K. 2002. More evidence of speciation and dispersal across the Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biology*, **25**, 818–826.

POWELL, R.D., KRISSEK, L.A. & VAN DER MEER, J.J.M. 2000. Preliminary depositional environment analysis of CRP-2/2A, Victoria Land Basin, Antarctica: palaeoglaciological and palaeoclimatic inferences. *Terra Antartica*, **7**, 313–322.

SHI, G.R. & GRUNT, T.A. 2000. Permian Gondwana–Boreal antitropicality with special reference to brachiopod faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **155**, 239–263.

SMITH, R.C., BAKER, K.S., BYERS, M.L. & STAMMERJOHN, S.E. 1998. Primary productivity of the Palmer Long Term Ecological Research area and the Southern Ocean. *Journal of Marine Systems*, **17**, 245–259.

SOMERTON, D.A. & DONALDSON, W. 1998. Parasitism of the golden king crab, *Lithodes aequispinus*, by two species of snailfish, genus *Careproctus*. *Fishery Bulletin*, **96**, 871–884.

STILWELL, J.D. 2003. Patterns of biodiversity and faunal rebound following the K–T boundary extinction event in austral Palaeocene molluscan faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 319–356.

STILWELL, J.D. & ZINSMEISTER, W.J. 1992. Molluscan systematics and biostratigraphy. Lower Tertiary La Mesata Formation, Seymour Island, Antarctic Peninsula. *Antarctic Research Series*, **55**, 356–378.

THATJE, S. & ARNTZ, W.E. 2004. Antarctic reptant decapods: more than a myth? *Polar Biology*, **27**, 195–201.

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

WALSH, J.J. 1988. *On the nature of continental shelves*. San Diego, CA: Academic Press, 520 pp.

WATLING, L. & THURSTON, M. 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 Special Publication*, No. 47, 297–313.

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

WILLIAMS, S.T., REID, D.G. & LITTLEWOOD, D.T.J. 2003. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution*, **28**, 60–86.

YAU, C., COLLINS, M.A. & EVERSON, I. 2000. Commensalism between a liparid fish (*Careproctus* sp.) and stone crabs (Lithodidae) photographed *in situ* using a baited camera. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 379–380.

ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. 2001a. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.

ZACHOS, J.C., SHACKLETON, N.J., REVENAUGH, J.S., PÄLIKE, H. & FLOWER, B.P. 2001b. Climate response to orbital forcing across the Oligocene–Miocene boundary. *Science*, **292**, 274–278.

ZINSMEISTER, W.J. 1984. Late Eocene bivalves (Mollusca) from the La Meseta formation, collected during the 1974–1975 joint Argentine–American expedition to Seymour Island, Antarctic Peninsula. *Journal of Paleontology*, **58**, 1497–1527.

ZINSMEISTER, W.J. & FELDMANN, R.M. 1984. Cenozoic high-latitude heterochroneity of southern hemisphere marine faunas. *Science*, **224**, 281–283.