Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

▶ **CHAPTER 3.1. EVOLUTIONARY SETTING.**

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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3.1. Evolutionary Setting

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1. Introduction

Following on from the initial phases of intensive biological investigations in the Southern Ocean we began to develop a concept of a distinctive benthic fauna with many unique characters. Clearly depauperate in certain key taxonomic groups such as gastropods, bivalves, decapod crustaceans and teleost fish, it seemed to be compensated by a proliferation of others such as peracarid crustaceans (i.e. isopods and amphipods), echinoderms, ascidians, pycnogonids and polychaetes (Nicol 1970, Hedgpeth 1971, Dell 1972). Infauna is notably depleted but in areas protected from intense ice scour distinctive three-dimensional assemblages of epifaunal, suspension-feeding sponges, sea anemones, soft corals, alcyonarians and other taxa developed (Dayton & Oliver 1977). These in turn provide extensive habitats for groups such as asteroids, ophiuroids, crinoids, bryozoans and brachiopods, and their abundance is often such as to give the benthos an archaic (or 'Palaeozoic') appearance (Aronson *et al.* 2007). Antarctica was viewed as a comparatively low diversity ecological refuge that had been at least partially isolated from the world ocean for as much as 30–40 million years, and its fauna as the product of intensive interactions between ecological and historical factors. Various models were developed as to how the marine fauna had accumulated over this time period, but in essence these can be resolved down to three main components: (i) a relict autochthonous fauna of essentially Late Mesozoic – Early Cenozoic origin; (ii) more recent evolutionary origins from adjacent deep-sea basins; (iii) more or less continuous shallow-water migration into and out of the Antarctic via the Scotia Arc (Lipps & Hickman 1982, Clarke & Crame 1989).

However, such has been the intensity of Southern Ocean research over the last two decades that we now know very much more about the nature and distribution of a wide variety of Antarctic marine organisms. Taxonomic and biogeographic research programmes conducted from both ships and bases, the advent of large databases (such as SCAR-MarBIN), and the rapid proliferation of molecular phylogeographic and phylogenetic techniques have all led to the accumulation of data sets that are beginning to call some of our cherished assumptions into question. It is the intention of this short review to revisit some of the basic tenets of Antarctic evolutionary biology and see how they have stood the test of time. Attention will be focused primarily on benthic marine invertebrates but it is hoped that at least some of the conclusions and inferences drawn here will have wider application.

2. How rich is the Southern Ocean fauna?

There has always been a distinct impression that species richness values are somewhat higher in the southern high-latitudes than their northern counterparts (Platnick 1992, Gaston 1996). And within the marine realm at least this would seem to be an entirely reasonable assumption to make, as there is demonstrably more high-latitude ocean in the south than the north (Clarke 1992). Recent support for such a concept has come from both the study of latitudinal gradients (Valdevinos *et al.* 2003, Kiel & Nielsen 2011) and the compilation of existing biogeographic data sets within online analytical databases such as SCAR-MarBIN (De Broyer *et al.* 2011). Building on the important survey by Clarke & Johnston (2003) that recorded in excess of 4100 shallow marine species, the SCAR-MarBIN Register of Antarctic Marine Species (RAMS) now lists over 8800 species from all depths; this in turn is approximately half of a grand total derived from various theoretical estimates (Gutt *et al.* 2004). Access to these new databases has been instrumental in promoting a critical reassessment of levels of endemism and taxonomic diversity in the Antarctic fauna (Griffiths *et al.* 2009a, Griffiths 2010, Hogg *et al.* 2011).

3. Latitudinal gradient in taxonomic diversity

One of the most striking examples of a reverse latitudinal gradient, where the number of species actually increases into the Antarctic, occurs in the sea spiders, or Pycnogonida. This is an essentially shelf-depth taxon (i.e. <1000 m in the Antarctic context) whose 270 species represent approximately 20% of the global total (Griffiths *et al.* 2009b). The same is also true of the bryozoans where a recent re-analysis of the distribution of 1681 species south of 30°S showed no obvious latitudinal gradient at either species or genus level (Barnes & Griffiths 2008). This trend is particularly clear in the well-studied South Atlantic and may well be repeated in other common Southern Ocean groups such as polychaetes, sponges, isopods, amphipods and ascidians (Griffiths 2010, De Broyer *et al.* 2011).

Nevertheless it is important to bear in mind that some of the globally most diverse marine taxa show very strong regional diversity contrasts between the tropics and the poles. Shelled gastropods (60,000+ species globally), for example, average 1700+ species per province across six tropical provinces (JAC unpublished data) as compared with a grand total of ~450 species for the very much larger Antarctic province. Even then, the Indonesian – Philippines core of the Indo-West-Pacific Province is still very under-sampled, and recent estimates give a projected total of more than 10,000 species for this region

alone (Bouchet 2006, 2008). Of course, many of these species are tiny (<5 mm in length), many are rare, and most have yet to be formally described; but they are all from shallow shelf depths. Similar patterns of very strong tropical – polar contrasts can be demonstrated for the bivalves (10,000+ species globally), teleost fish (25,000) and decapod crustaceans (15,000) (Clarke & Crame 2010, JAC unpublished data).

What has to be remembered in the study of latitudinal gradients is that they are regional features that show considerable variation in form in both hemispheres (Gaston 2000). In a meta-analysis of 600 latitudinal gradients from both the marine and terrestrial realms, Hillebrand (2004) was unable to detect any significant differences between the northern and southern hemispheres; gradients in the north were neither steeper nor stronger than those in the south. In addition, there were no differences between marine and terrestrial organisms, active and passive dispersers, or ectotherms and endotherms. Latitudinal gradients between the tropics and the poles are widespread features in nature but, overall, the inequalities in the north balance out those in the south.

It is important to ask whether large-scale biodiversity patterns might be any different in the deep sea? Here, there were initial impressions of a marked asymmetry between North and South Atlantic latitudinal gradients (Rex *et al.* 1993), and these seemed to be amply confirmed by the three ANDEEP cruises to the Weddell Sea and adjacent areas (774–6348 m depth) (Brandt *et al.* 2007). Amongst the substantial levels of unrecorded biodiversity established by these cruises were 674 isopod species (585 new to science), 200 polychaete species (81 new), 158 foraminiferan species (nearly all new) and 100 ostracods (70 new). Using a rarefaction technique to standardise sample sizes, taxonomic diversity values for isopods, gastropods and bivalves from the Weddell and Scotia seas were shown to be similar to, or even higher than, those from many temperate and tropical slopes in the Southern Hemisphere (Brandt *et al.* 2007). This is indeed a striking result, but it has to be remembered that what is being considered here are samples of within-habitat (or alpha) diversity, and this metric alone does not necessarily change systematically with latitude (Clarke & Lidgard 2000, Gray 2001). Only when samples are collected over larger spatial scales can latitudinal diversity gradients be fully assessed. This is because regional (or gamma) diversity is the sum of alpha plus beta (or between-habitat) diversity and it is the latter that can vary substantially along environmental gradients. Beta diversity records the turnover of taxa between various habitats and the movement of species from regional to local species pools. In a recent re-assessment of Philippines biodiversity based on the MUSORSTOM expeditions, Bouchet (2008) estimated that there could be as many as 20,000 deep sea mollusc species, i.e. in addition to the 12–15,000 estimated from shelf depths. There is thus a strong suspicion that regional deep sea diversity values, at least in molluscs, must increase dramatically from the poles to the tropics, although this still needs to be fully demonstrated along a single, clearly defined latitudinal gradient.

4. Two important evolutionary models

Two global models with significant implications for the origin and evolution of polar marine biotas have recently received considerable attention. The first of these is linked essentially to shallow-marine (i.e. shelf-depth) habitats and the second to the deep sea (i.e. bathyal and abyssal depths).

4.1. Out of the Tropics (OTT) model

There has always been a distinct impression that many groups of marine organisms originated in the tropics and then expanded their distributions polewards through time. The primary impetus for this finding comes from palaeontology where it could be demonstrated that the tropics were characterised by a higher proportion of geologically young genera and families, and thus a higher rate of turnover (or net diversification) (Stehli *et al.* 1969, Flessa & Jablonski 1996). The latitudinal gradient in taxonomic diversity is in effect matched by a parallel gradient in rates of origination (Map 1).

In the full development of the OTT model it is emphasised that the vast majority of those taxa expanding from the low- to high-latitudes maintain their tropical distributions and thus, in time, a diversity peak is developed (Jablonski *et al.* 2006). An empirical test of the model using an extensive Late Cenozoic bivalve data set showed that tropical first occurrences significantly exceeded extra-tropical ones, and that median bivalve age did indeed increase with latitude (Jablonski *et al.* 2006, Krug *et al.* 2009a). It is important to emphasise that OTT does not exclude extra-tropical origination but it is likely that most extra-tropical species belong to lineages that originated in the tropics. Examples of comparatively shallow-water taxa that have radiated extensively in Antarctica would include notothenioid fish, buccinoidean gastropods and ctenocidarine echinoids (Briggs 2003, Pearse & Lockhart 2004) but the ultimate origins of all these groups is still uncertain (see also, below). The OTT model has served to reinforce the concept of the tropics as a macroevolutionary source and the poles as corresponding sinks, but it still needs to be refined using further specific examples (Krug *et al.* 2009a).
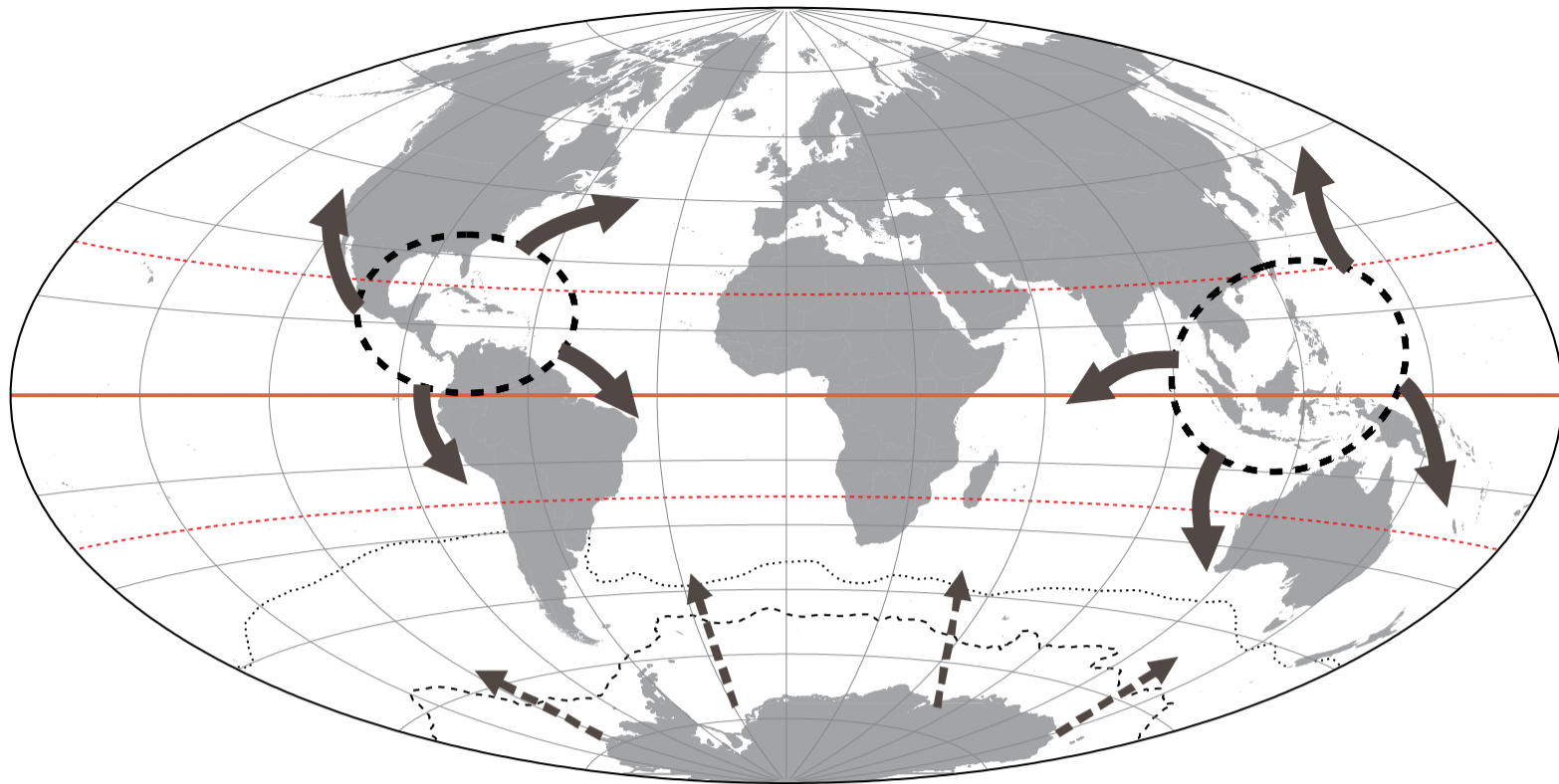
Evolutionary Setting Map 1 Centres of evolutionary radiation in the shallow and deep sea. Schematic representation of radiation into higher latitudes from two shallow water, tropical centres of origin: the Indo-West Pacific and Atlantic – Caribbean – East Pacific. Radiation into the deep sea from Antarctica is represented by the broken arrows. Also shown are the Equator, Tropics of Cancer and Capricorn, and around Antarctica the Subtropical Front (dotted line) and Polar Front (dashed line). Evolutionary centres superimposed on the present day configuration of continents and oceans but they can be traced back through considerable periods of geological time.

4.2. The "Thermohaline Expressway"

Whereas the predominant flow of taxa is from the low- to the high-latitudes in the OTT model, almost exactly the reverse process seems to occur in the deep sea. This is particularly so in the Southern Hemisphere where Antarctica is the primary source of cold bottom waters in the world ocean. As the continent became progressively thermally isolated by the formation of the Antarctic Circumpolar Current and continental ice sheets built up (Table 1), cold, saline bottom waters formed close to the continental margins before descending and moving northwards into all the major ocean basins. It would seem only logical to conclude that as they did so they carried shallow-water Antarctic marine organisms with them to populate abyssal and hadal sea floors at lower latitudes. Such a biological process has been termed both 'polar submergence' and the 'thermohaline expressway' (Vinogradova 1997, Briggs 2003, Strugnell et al. 2008) (Map 1).

Perhaps the most important examples of Antarctica acting as a centre of origin for deep sea organisms occur within the isopods, and in particular in families such as the Antarcturidae, Serolidae, Munnidae, Stenetriidae and Paramunnidae (Kussakin 1973, Brandt 1992). Early cladistic biogeographic studies confirmed this trend and these have now been reinforced by a series of molecular phylogenetic investigations that point to multiple colonisation events within both the Serolidae and Acanthopsidiidae (Brandt et al. 2007, Raupach et al. 2009). Other taxa that appear to have used the thermohaline expressway to colonise the deep sea include octopuses (Strugnell et al. 2008), foraminiferans (Pawlowski et al. 2007), elasipodid holothurians (Gebruk 1994), polychaetes, and hexactinellid sponges (Brandt et al. 2007). Movement in the opposite direction (= polar emergence) does occur, most notably in isopod families such as the Desmosomatidae, Ischnomesidae and Munnopsidae, but it is unlikely that this is on a scale such as to counterbalance the phenomenon of isothermal submergence (Briggs 2003, Brandt et al. 2007).

5. How old is the Antarctic marine fauna?

There is an understandable tendency to link the origin of the bulk of the Antarctic marine fauna to the thermal isolation of Antarctica and onset of major continental glaciations (Clarke & Crame 1989, Lörz & Held 2004). This in turn is usually attributed to the Eocene–Oligocene boundary (34 Ma) (Table 1), an interval when global mean oceanic temperature fell by 4°–5°C and then continued to decline, more or less uniformly, through to the present day (Zachos et al. 2008). Nevertheless it is important to bear in mind that there are also some substantially older elements within the fauna and it is apparent that these must have adapted successfully to the gradual onset of glacial conditions (Clarke & Crame 1989). Perhaps the most striking example in this category occurs within the Pycnogonida where a Silurian fossil from Herefordshire, U.K. (~425 Ma) shows a striking resemblance to certain modern Antarctic taxa, and plots close to the base of the pycnogonid crown group in a morphological cladogram (Siveter et al. 2004). If this analysis is correct, then it implies that the crown group (i.e. a monophyletic group containing living taxa plus the fossils that nest within them) had arisen by the Silurian (Table 1)! Schweglerella strobli Polz is a crown group sphaeromatid isopod showing close affinities to the modern Southern Ocean families Bathynataliidae and

Serolidae (Brandt et al. 1999, Brandt & Poore 2003). However, it is a fossil from the Early Tithonian (~150 Ma) Plattenkalk of Solnhofen, southern Germany where it inhabited a Tethyan coral reef environment. There are other examples too, which indicate that some elements of the Antarctic marine fauna may in fact have a long and complex evolutionary history (Crame 1994). We cannot discount the possibility that some modern Antarctic clades are diverse simply because they are extremely old.

It is becoming clearer that a major global event to have had a significant effect on the composition of modern biotas was the mass extinction at the Cretaceous–Paleogene (K–Pg) boundary (Table 1). It is estimated that at this time up to 70% of species were lost in both the marine and terrestrial realms and the ensuing ecological vacuum acted as a primary trigger for a significant burst of evolutionary diversification (Miller & Sepkoski 1988, Jablonski 2005, 2008). At least part of the process involved here is the removal of incumbent taxa and subsequent diversification of formerly marginal groups; these in turn became the direct ancestors of many living species. In a key study based on the fossil record of modern marine bivalves, Krug et al. (2009b) were able to show that a large and permanent increase in origination rates occurred immediately after the K–Pg boundary and continued through to the present day. Moreover, there was a strong geographical component to this diversification event with tropical rates being significantly higher than those at the poles. Not only was a marked acceleration in origination rates continued throughout the Cenozoic, but it was also very much stronger in the tropics than at the poles (Krug et al. 2009b). The Cenozoic era was a time of marked increase in tropical marine diversity and accentuation of the slope of latitudinal diversity gradients, but the precise reasons for this are still unclear.

A second global event that could well have had a significant effect on the composition of the Antarctic marine fauna was a marked pulse of global warming at the Paleocene–Eocene boundary (55 Ma) when high-latitude sea surface temperatures were raised by 4°–6°C in <0.01 million years (Kennett & Stott 1991). This abrupt and short-lived spike in global temperatures, which has come to be known as the Paleocene–Eocene Thermal Maximum (PETM) (Table 1), occurred when the earth was already in a greenhouse phase and represents the acme of Cenozoic warmth (Zachos et al. 2008). It triggered a period of major biotic restructuring and in particular the largest recorded extinction of benthic foraminifera, with an estimated loss of 30–50% of all species (Thomas 2007). Such a large and rapid extinction is unusual in the deep sea as most species are cosmopolitan and typically rapid colonisers. It has led to speculation that there could have been an almost total collapse of ecosystems in the deep sea at this time, and this in turn implies subsequent recolonisation from shallow-water refugia such as Antarctica (Jacobs & Lindberg 1998). The causes of this extinction pulse are not altogether clear but are probably linked to the production of uniformly warm, low oxygen, corrosive bottom waters; this was probably a time of intense ocean acidification (Sluijs et al. 2007, Thomas 2007). Planktonic organisms showed a rapid evolutionary turnover at the PETM but no major extinction event. Many plant taxa were subject to pronounced range shifts and it was a time of profound modernisation of the terrestrial mammal fauna (Berggren et al. 1998, Sluijs et al. 2007). Global changes in the nature and distribution of Paleocene marine invertebrate faunas are currently under intense investigation.

Table 1 Key events in the evolution of the Southern Ocean marine fauna

11. Pleistocene glacial cycles, 2.6 Ma – 11.7 ka	A critical period for the Antarctic marine fauna; how did it survive repeated glacial advances across the continental shelf; eleven major glacial events plus many minor ones identified. Full extent of sea ice fluctuation during cycles largely unkown.
10. Pliocene, 5.3–2.6 Ma	A mid-Pliocene phase of global warming may be reflected in a series of circum-Antarctic faunas. These have yielded taxa such as scallops, decapod crustaceans and dolphins absent from the continent today and may indicate that certain groups were able to expand and contract their ranges in concert with climate change.
9. Middle – Late Miocene cooling, ~15 Ma	An abrupt cold phase linked to rapid expansion of the East Antarctic Ice Sheet and associated cooling of high-latitude waters. Some evidence to suggest fjord-like conditions existed around the fringes of the ice sheet from the Late Miocene into the Quaternary (Siegert & Florindo 2009).
8. Oligocene – Miocene boundary, 23 Ma	Small dynamic ice sheets of the Oligocene rapidly expanded to continental scale in the Early Miocene (Glaciation Mi 1). A period of Early Miocene global warming (~23–17 Ma) coincides with the development of a distinctive marine fauna in the South Shetland Islands; although closely linked to coeval glacial deposits, this contains elements, such as decapod crustaceans and euheterodont bivalves, missing from the modern fauna (Clarke & Crame 2010).
7. Eocene – Oligocene boundary, 34 Ma	Further opening of Drake Passage and almost complete thermal isolation of the Antarctic continent; surface and bottom waters may have decreased by as much as 4°C in 75–100 ka (Zachos *et al.* 2008). Development of first Antarctic Ice Sheet and an important expansion of ice volume (Siegert & Florindo 2009); probable formation of first major sea ice.
6. Late Middle Eocene, 41 Ma	Marked change in the nature of both vertebrate and invertebrate marine faunas recorded in the uppermost levels of the La Meseta Formation, Seymour Island; this is widely interpreted as marking the change from cool to cold waters and the onset of glacial conditions (Aronson *et al.* 2007, 2009). For the first time a clear link is established between polar shelf faunas and the deep sea.
5. Early Eocene, ~50 Ma	Full deep water separation of South Tasman Rise leads to the almost complete isolation of Antarctic continental shelves (Exon *et al.* 2004).
4. Paleogene period, ~63–43 Ma	An approximately 20 my period of global greenhouse warmth (~63–43 Ma) can be detected in Antarctica. A remarkable temperature excursion of some 5°–7°C at the Paleocene–Eocene boundary (Paleocene – Eocene Thermal Maximum, PETM) was first detected in Antarctica; cool subtropical waters were probably introduced into Antarctica at this time (Stott *et al.* 1990). Some distinctive modern Southern Ocean elements (gastropods, bivalves, corals etc) begin to be recognised in the Southern Ocean fossil record (Beu 2009). PETM at 55 Ma and a second Early Eocene Thermal Maximum (ETM2) at 53 Ma may have been times of significant mass extinction events in the deep sea (Zachos *et al.* 2008).
3. K–Pg mass extinction event, 66 Ma	Likely to have been just as severe in Antarctica as anywhere else in the world; ~50% genera and 70% species may have become extinct at shelf depths globally at this time (Krug et al. 2009a). In some way that is still not fully understood the K-Pg extinction event resets the evolutionary clock and leads to a subsequently faster net rate of speciation in the tropics than at the poles (Krug et al. 2009b). It is likely that LDGs steepened significantly throughout the Cenozoic era.
2. Mesozoic Era, ~250–66 Ma	There is evidence to suggest that the southern margins of the Gondwana supercontinent were at least intermittently covered by a distinct temperate faunal province; this is often referred to as the Weddellian Province (Zinsmeister 1982). Some modern Southern Ocean taxa, such as the gastropod family Struthiolariidae, can be traced back to probable mid- to Late Cretaceous origins; at the same time some formerly cosmopolitan taxa were beginning to be restricted to the Weddellian Province (Clarke & Crame 1989).
1. Early – Middle Devonian, ~390 Ma	Antarctic continent assumes mid- to high-latitude position in the Southern Hemisphere; it has essentially maintained this ever since. Cool temperate Malvinokaffric Province faunas detected (Briggs 2003).Some stem taxa to modern Southern Ocean clades (e.g. pycnogonids, certain echinoderms and mollusks) may well date back to at least the Late Palaeozoic era.

6. Stages of Cenozoic reduction and extinction of the marine fauna

Palaeontological studies on Seymour Island have indicated that a pronounced change occurred in the marine fauna in the late Middle Eocene (~41 Ma) (Table 1), more or less coincident with the onset of global cooling on the northern Antarctic Peninsula (Ivany *et al.* 2008, Anderson *et al.* 2011). At this time there was a very marked reduction in the numbers of durophagous (i.e. shell-breaking) predators, such as various teleost fish, rays, neoselachian sharks and decapod crustaceans, followed by the introduction of dense assemblages of slow-moving/sedentary, epifaunal asteroids, ophiuroids, crinoids, bryozoans and brachiopods. The sudden reduction in shell-crushing predators in the colder waters allowed the communities to regress to an archaic state such as is found today in the deep sea or in the past in the Palaeozoic era (Aronson *et al.* 2007, 2009). These changes were almost certainly reinforced by the switch to glacio-marine conditions of coastal sedimentation.

Unfortunately, the post-Eocene fossil record of Antarctica is very incomplete and we are left with only a few tantalising glimpses of how the marine fauna responded to the onset of widespread continental glaciation. Whereas a number of key elements have undoubtedly been lost from Antarctica since the mid- to late Eocene (i.e. last 40 million years), these would appear to represent predominantly regional rather than global extinctions. One striking example here occurs within the Euheterodonta, the largest of the modern bivalve clades comprising predominantly infaunal, siphonate burrowers. The globally most common euheterodont family, the Veneridae, is virtually absent from Antarctica today but in the Early – Late Eocene La Meseta Formation of Seymour Island it is particularly common, with the genus *Retrotapes* being a prolific component of the characteristic shell beds (Stilwell & Zinsmeister 1992, Beu 2009). Although now absent from Antarctica, *Retrotapes* is a common element of southernmost South American faunas at the present day (Del Rio 1997) and this distribution pattern is such as to suggest that it may simply have been displaced northwards across the Polar Frontal Zone. Very similar distribution patterns can be demonstrated for ribbed scallops of the genus *Austrochlamys* (Pectinidae) and various decapod crustaceans, and both these groups can be traced intermittently in the Antarctic fossil record from the Paleocene to the Pliocene (Feldmann & Crame 1998, Berkman *et al.* 2004). What we do not know with any degree of certainty is whether these northward displacements occurred only once (i.e. post- mid-Pliocene, approximately 2.5 Ma) or perhaps represent a series of migrations; southwards during periods of climatic amelioration, and northwards during climatic deterioration. The former of these explanations would imply a considerable regional extinction event approximately 2 Ma (Berkman & Prentice 1996) and the latter would highlight the importance of the Scotia Arc as a serial migration route (Table 1).

This leads directly to a consideration of how the Antarctic marine fauna survived multiple glaciations, particularly over the last 15 million years since the marked expansion of the East Antarctic ice sheet (Zachos *et al.* 2008). Some idea of the intensity of these glaciations can be obtained from the recent results of the ANDRILL programme where a 600 m core beneath the north-west part of the Ross Ice Shelf revealed no fewer than 38 glacio-marine cycles within the last 5 million years (Naish *et al.* 2009). There is good geological evidence to suggest that during each glacial maximum grounded ice sheets advanced to more or less the shelf edge, and even on the upper slope submarine mass wasting processes such as slides, debris flows and turbidity currents must have had a catastrophic effect on the benthos (Thatje

et al. 2005). However, there is also some evidence to suggest that asymmetric advance and retreat of ice across the shelf meant that some areas were left unglaciated, and thus it is possible that there were two types of refugium: isolated pockets of open water on the shelf; and the lower slope and abyssal regions (Dayton & Oliver 1977, Clarke & Crame 1989, Thatje *et al.* 2005, Convey *et al.* 2009). It has been suggested that the existence of both these types was very strongly linked to the presence of polynyas which in effect became productivity hotspots (Thatje *et al.* 2008). Within the areas of open waters which were likely developed at a number of sites towards the shelf edge, periods of primary productivity would have been significantly enhanced, and thus the availability of food to higher trophic levels. This would have been at a level that was such as to maintain numerous discrete populations on the shelf and export excess detritus to the deep sea (Thatje *et al.* 2008) (Table 1).

We are fortunately now in the position of being able to test some of these assumptions about the nature of refugia through the use of various molecular techniques. Investigation of haplotype diversity at the population level should give a good indication of viable population sizes that were able to withstand glacial periods, and also indicate possible colonisation routes (Convey *et al.* 2009). Recent phylogeographic studies in the northern high latitudes are already pointing to the existence of hitherto cryptic refugia where various temperate terrestrial taxa clearly survived long glacial intervals (Stewart *et al.* 2010).

7. Synopsis

Although we still lack accurate quantitative comparisons based on a standardised sampling protocol, there is a distinct impression that taxonomic diversity in the polar regions has always been somewhat lower than in the tropics. Indeed, such an imbalance may have persisted through the greater part of the Phanerozoic eon (i.e. the last 542 million years) (Valentine & Jablonski 2010) (Table 1). Latitudinal diversity gradients have varied in form over this time but reverse gradients would still seem to be the exception rather than the rule in both hemispheres. This is particularly so when we consider the distribution of the largest taxonomic groups over regional scales. At least in shelf-depth waters, latitudinal gradients would in turn appear to be underpinned by an OTT macroevolutionary dynamic. On geological timescales there is some justification for regarding tropical high diversity hotspots, such as the Indo-West Pacific and Atlantic – Caribbean – East Pacific (Map 1), as evolutionary sources and the poles as evolutionary sinks.

There is currently an intense research interest in the large-scale taxonomic diversity patterns of the Late Cretaceous – Early Cenozoic greenhouse world (~75–40 Ma). There is good evidence to suggest that for much of this time the tropics/subtropics reached much higher latitudes (50°+, or even higher) and the polar regions were correspondingly significantly reduced in size. Nevertheless, polar/sub-polar faunas are present in localities such as Seymour Island and Nûgssuaq, West Greenland, and these can be used to make direct and quantitative comparisons with various lower latitude localities. This work is not yet complete but there are indications that the latitudinal gradient, when viewed across both hemispheres, was much more in the form of a low dome than a steep-sided, bell-shaped curve (Archibald *et al.* 2010). The transition from the former to the latter must have occurred sometime after the late Middle Eocene (~40 Ma) and involved both a substantial increase in tropical diversity and a smaller-scale reduction at the poles.

Certain Antarctic marine crown group taxa may be considerably older

than the onset of enhanced global cooling at 34 Ma. There is evidence to suggest that both the mass extinction at the K–Pg boundary (65 Ma) and the brief but intense burst of global warming at the PETM (55 Ma) reset the global evolutionary stage, including both polar regions. Certain taxa have managed the transition to life in cold water extremely successfully and radiated secondarily in the cold but constant environmental conditions (e.g. notothenioid fish, peracarid crustaceans, buccinoidean gastropods). The OTT model does not preclude secondary radiations in this way but hints at ultimate tropical origins for most groups (Jablonski *et al.* 2006). There is no simple link between low temperature and extinction in marine invertebrates (i.e. ectotherms) (Clarke & Gaston 2006). The primary response to a reduction in ambient temperatures is a shift in geographical ranges, and it is possible that a number of marine taxa moved in and out of Antarctica repeatedly as climates fluctuated through the later Cenozoic (Table 1).

The evolutionary link between Antarctica and the deep sea is an enduring one that is worthy of further extensive investigation using molecular phylogenetic techniques. By definition, the thermohaline expressway must postdate substantial thermal isolation of Antarctica and massive extension of the continental icesheets. It is likely to have been an important process throughout the Neogene (i.e. the last 23 million years) and thus may have had a profound effect on total deep-sea biodiversity levels. The role of refugia in general and polynyas in particular over the last 15 million years has been crucial in helping the Antarctic marine fauna survive the most intense periods of glaciation.

Acknowledgements

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

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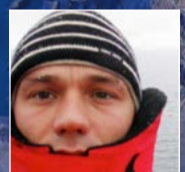
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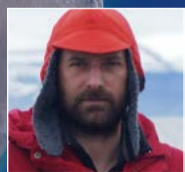
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