CHAPTER 3.1. EVOLUTIONARY SETTING.


THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN


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1. Introduction

Following on from the initial phases of intensive biological investigations in the Antarctic, 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 pteropod crustaceans (i.e. isopods and amphipods), echinoderms, ascidians, pycnogonids and polychaetes (Nicol et al. 1997; Hedgpeth 1971, Dell 1972).

Infusoria is notably depleted but in areas protected from intense ice scour, distinctive three-dimensional assemblages of epifauna, 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, ophiurids, crinoids, byzozooids and brachipods, and their abundance is often such as to give the benthos an archaic (or ‘Palaeeozic’) appearance (Arntzen et al. 2007).

Antarctica was viewed as a comparatively low diversity ecosystem of biological 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 long period. In essence these can be resolved down to three main components: (i) a relict autchothonous fauna of essentially Late Mesozoic – Early Cenozoic origin; (ii) more recent evolutionary origins from adjacent deep-sea basins; (iii) or more less continuous shallow-water migration into and out of the Antarctic via the Scotia Arc (Lips & 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 evolutionary history 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-latitude than their northern counterparts (Patnick 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 (Gaston 1996). 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 species of the 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 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 spiers, 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 shelves where important and characteristic 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 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 same geographic group in the 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 diversity 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 marine and terrestrial realms, Hillbrand (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 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 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 large geographic scales can latitudinal diversity patterns be adequately demonstrated. 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 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. 2009b). It is important to emphasise that this does not exclude extratropical taxa 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 clionodiid echinoderms (Briggs 2003, Peckover & Stewart 2004). Not unexpectedly, all of 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).
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, Munididae, Stenetriidae and Paramunididae (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), foraminifers (Pawłowski 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) 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 1985). 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)! Schwagerellera strobil Poiz 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 1992). 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 there 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 (Sliujs 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, Sliujs et al. 2007). Global changes in the nature and distribution of Paleocene marine invertebrate faunas are currently under intense investigation.
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 assemblages, ophiuroids, crinoids 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 three bivalve clades comprising predominantly infaunal, siphanate bivalves. The globally most common euheterodont family, the Veneridae, is virtually absent today in the deep sea or in the past in the Palaeozoic era (Aronson et al. 2007, 2009). For much of the Pliocene and Pleistocene the Veneridae was very strongly linked to the presence of polynyas which in effect 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 of polynyas 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 the availability of food to higher trophic levels 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 fortunate 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). The centric phylogeography of planktonic foraminifera is currently being used to point to the existence of hitherto cryptic refugia where various temperate terrestrial faunas and flora clearly survived long glacial intervals (Stewart et al. 2010).
than the onset of enhanced global cooling at 34 Ma. There is evidence to suggest that both the mass extinctions at the K-Pg boundary (65 Ma) and the recent biotic crisis (1.8 Ma) reflect the global warming of the PETM (55 Ma), the global evolutionary stage, including both polar regions. Certain taxa have managed to survive cold periods and extinction events in the face of radiative forcing and environmental conditions (e.g., nototheniid fish, pentadactyl crustaceans, bicoenodont gastropods). The OTT model does not predict 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 (e.g., echinoderms, bivalves, molluscs) (Crame 1994) and the response to climatic factors of the distribution and abundance of ancient taxa in the Southern Ocean and Antarctica, demonstrated by the biogeography of Antarctic Cenozoic faunas (Brandt et al. 2010). The Southern Ocean, 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

I am grateful to many Antarctic colleagues who helped develop the ideas and discussions that underlie this review and who contributed financially to the BAS Polar Science for Planet Earth programme. I am grateful to many Antarctic colleagues who helped develop the ideas that underlie this review. The exploration of marine ecosystems is conducted both on land and in the cold sea, 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 postulate substantial thermal isolation of Antarctica and massive extension of continental ice sheets. It has 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 polynomial in particular over the last 15 million years has been crucial in helping the Antarctic marine fauna.

References


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) 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 both 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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