

Evolution of the Antarctic marine fauna: what can DNA and fossils tell us?

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Summary The opening of the Drake Passage, establishment of the Polar Front and the onset of cooling around the Eocene-Oligocene boundary have been recognised as the most significant events in shaping the recent Antarctic marine fauna. Orbitally-forced glacial cycles leading to loss of shelf habitat during glaciations may have been integral in determining extant biodiversity, including the establishment of regional isolation and diversification. Adaptive radiation of major clades, notably icefish, molluscs and crustaceans, occurred in isolation from the rest of the world. Cooler periods may have been associated with isolation and extinction of cold intolerant species but rapid evolution of groups that could adapt to extreme low temperatures. These cold-tolerant groups have radiated and there is evidence that some have invaded other parts of the world such as the deep seas. Modern techniques utilising DNA, fossil and biogeographical evidence can be used to give robust estimates to determine the dates of divergence and molecular rate. This sheds light onto the evolutionary history of the Antarctic marine fauna.

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Introduction

The Antarctic marine fauna comprises a significant part of the Earth's biodiversity. Many of these species are found nowhere else on the planet and endemism may reach over 90% for some groups of Antarctic organisms (Clarke and Johnston, 2003). This unique diversity is thought to have evolved because, unlike other large ecosystems, Antarctica is an island continent and is isolated from other parts of the Southern hemisphere by distance, air and water currents and extreme environmental conditions including low temperatures, the presence of ice and exceptional seasonality.

There is increasing evidence that extreme or marginal environments such as the Antarctic may encourage the evolution of novel taxa. This has occurred through habitat fragmentation (vicariance; Clarke and Crame, 1992) and strong selective pressure driving evolution and the origination of new taxa (e.g. Clarke and Johnston; 1996, Brandt et al 2007a,b) but possibly also by the elimination of competitors and predators failing to adapt to increasingly severe conditions in the Antarctic, and subsequent stimulation of speciation amongst survivors (niche saturation theory; Brown, 1995, Sepkoski, 1992). However, the relationship between speciation and extinction events is unclear. This is particularly important in the Antarctic, as entire groups of organisms common elsewhere in the world have been eliminated by extreme environmental changes (e.g. crabs and lobsters; Feldmann and Crame, 1998) whilst others have unexpectedly high numbers of species (e.g. sea spiders; Clark and Johnston, 2003). These extreme changes in the diversity of groups of animals, especially in the marine environment, over the last 40 million years mean that the Antarctic offers insights into macro-evolutionary processes, especially the relationship between speciation and extinction.

Globally, climate change is causing significant alterations in the environment (Solbrig et al., 1994). This transformation of natural habitats arising from climate change and other human impacts coincides with the loss of species giving rise to the possibility of the world's sixth major extinction event. In order to try to predict the long-term impacts of climate change on biodiversity in the future, we have to look back in time. This requires using accurate modelling of previous climate change events and understanding of how this has influenced biodiversity in the past. Antarctica, being at one extreme of the Earth's gradient in temperature and seasonality is a sensitive indicator of the effects of climate change (Convey, 2003). The organisms inhabiting the Antarctic environment are highly sensitive to even small changes in the environment (e.g. Peck et al., 2002, 2006). Studies of how the Antarctic biota has been influenced over geological timescales by past climate change events are possible using both molecular biological and palaeontological studies. Recent studies have shown how ranges of Antarctic marine animals have expanded and contracted with changes in climate and ice sheet extent (e.g. Jonkers, 2003). Such studies enable us to judge the significance of climate change on the biodiversity of the Antarctic and other parts of the world in the future. Understanding the past distribution of organisms also provides verification of models of past climate change events by validating reconstructions of ice sheets and landmasses.

The Antarctic biota provides an ideal test case with which to characterise the effect of climatic and tectonic change on molecular evolutionary processes. The climatic, tectonic and glacial history of Antarctica is particularly well defined (Clarke and Crame, 2003) and is understood to have been integral in shaping the Antarctic marine fauna. For example, events such as the opening of Drake passage, leading to thermal isolation of the continent, marked and sudden

temperature changes (such as the late Paleocene thermal maximum) and orbitally-forced glacial cycles have all been suggested to have been important in shaping the present day Antarctic marine biota (Clarke and Crame, 1989; 1992; Prothero and Berggren, 1992). Furthermore, the establishment of deep water connections between the Southern Ocean and the rest of the major ocean basins of the world, following the opening of the Drake Passage, has been suggested to have facilitated recolonisation of deep sea areas after extinction events due to deep ocean oxygen depletion (Jacobs and Lindberg, 1998; Rogers, 2000; Little and Vrijenhoek, 2003, Brandt et al 2007a, b).

Here we present a review of current molecular phylogenetic studies on Antarctic marine biota and set them into the geological and biogeographical context. Comparisons within and across marine taxa like fish, molluscs and crustaceans will indicate if the species radiations occurred at similar times and where set off by the same geological and climate events.

Antarctic biodiversity

The opening of the Drake Passage, establishment of the Polar Front and the onset of cooling around the Eocene-Oligocene boundary (33.7 Ma) have been recognised as the most significant events in shaping the recent Antarctic marine fauna (Clarke and Crame 1992). Just before or during this period many groups of marine organisms are thought to have become extinct whilst the initial radiation of major Antarctic clades occurred in isolation from the rest of the world (e.g. Clarke and Johnston, 1996). However, the view that the Antarctic marine fauna comprises a number of relict lineages that have evolved in isolation is an over-simplification. Knox and Lowry (1977) suggested that the Southern Ocean fauna comprises of 3 additional elements: (i) a fauna derived from adjacent deep-water basins, (ii) a fauna dispersing from South America along the Scotia Arc, (iii) a fauna that has spread in the opposite direction from the Antarctic, northwards along the Scotia Arc.

The relative importance of these processes in the formation the Southern Ocean fauna is not well understood. Firstly, the fossil record of the Antarctic marine fauna is poor as a result of the lack of well-preserved post-Eocene rock exposures. Secondly, data on Antarctic marine biodiversity are far from complete. Compared to the continental shelf, the deeper waters around the Antarctic include some of the least explored parts of the oceans, and we know little about the benthic fauna that inhabits them (Brandt et al., 2004, 2007a, b). Exploratory and commercial fishing activities around the Antarctic in deep water have captured rays and anomuran crabs not found in shallower waters of the continental shelf (Thatje and Arntz, 2004). Results from recent expeditions sampling the deep Scotia and Weddell Seas also indicate a higher diversity than expected (Brandt et al, 2007b). Our current perception of the Antarctic fauna is distorted by emphasis on shallow habitats that may have suffered recent losses in biodiversity as a result of severe disturbance from recent glaciations. The lack of a detailed fossil record in the Antarctic has led to an increasing emphasis on studies of molecular phylogenetic relationships amongst extant taxa. Whilst these studies are sparse they have already suggested that at least some Antarctic groups show speciation continuing subsequent to the isolation of the Antarctic, especially over the last 20 MY and some as recently as the last 10 MY (Bargelloni et al., 2000a,b; Page and Linse, 2002, Lörz and Held, 2004). This may have coincided with the ending of a warm period of climate (early Miocene; Clarke and Crame, 1992) and strengthening of the Polar Front and associated temperature gradient. These examples suggest that pulses of invasions into Antarctic waters from both shallow and deep waters may have occurred during warmer phases of climate over the last 40 MY, with subsequent isolation of taxa and speciation in the extreme Antarctic environment occurring with climatic cooling. The Antarctic may act as a “speciation pump” with evolutionary novelty arising from strong selection in a periodically isolated fauna.

Another striking feature of the diversity of the Antarctic marine fauna is that it is not evenly distributed amongst higher taxa. Several groups of marine invertebrates show high species diversity including bryozoans, amphipods and pycnogonids (Clarke and Johnston, 2003, Barnes and Griffiths, in press). Bivalve and gastropod molluscs have a very low diversity compared to elsewhere, with described species making up less than 5.5% and 1% of world species respectively (Clarke and Johnston, 2003, Linse et al., 2006). Recent molecular studies in groups with low general diversity in the Antarctic have suggested that many of them have undergone recent radiations (Held, 2000, 2001a; Lörz, 2003). The contrast in species richness between different phyla in the Antarctic suggests that speciation and extinction rates have varied markedly between groups in response to tectonic and climate change events.

Our knowledge of the diversity of Antarctic marine biota has greatly increased recently with the availability of new databases, (e.g. SOMBASE Griffiths et al. 2003), syntheses (e.g. Clarke and Johnston, 2003; Allcock, 2005; Linse et al., 2006, Barnes and Griffith, in press) and the development and application of molecular sequencing techniques (e.g. Held, 2000; 2001; Page and Linse, 2002, Linse et al, 2007, Raupach et al., 2004, 2006). These studies confirm some unexpectedly high levels of taxonomic diversity and the presence of a number of species-rich clades (e.g. peracarid crustaceans, trematomid fish, pycnogonids). Evidence for dispersal from Antarctica into the deep sea has also been suggested for a number of taxa (e.g. isopods, Held, 2000; octopus, Strugnell, unpubl.) and pycnogonids, Kuznetsov and Turpaeva, 1997). Together these findings have focused attention on the timing, nature and potential causes of

diversification leading to these species-rich clades, and reinvigorated debate on whether polar regions should be regarded as evolutionary sources or sinks (Goldberg et al. 2005).

Rates of molecular evolution and diversification in Antarctica taxa

The rates of two molecular evolutionary processes of the Antarctic biota are likely to have been affected by climatic and tectonic change; 1) molecular rate, (i.e., the nucleotide substitution rate) and 2) diversification rate, (i.e., the rate of speciation and extinction). A number of studies have investigated hypothesised changes in molecular rate and diversification rate after major climatic and tectonic events, yet to date there has been very little focus on Antarctica.

The relatively few studies estimating molecular rates and divergence dates among Antarctic taxa have been analytically simple and have assumed a constant rate of nucleotide substitution among lineages (i.e., a strict molecular clock) (e.g. Held, 2001; Page and Linse, 2002) often applying a “universal” rate from other often distantly related taxa, to the taxa in question (e.g. Eastman and McCune 2000). However studies have shown that the assumption of a strict molecular clock is commonly violated with nucleotide substitution rates commonly varying even among closely related lineages. In an attempt to deal with this rate heterogeneity, relative rate tests have been employed to identify lineages that did not conform to rate uniformity, which are then removed so that a strict molecular clock can then be applied to the remaining data (e.g. Bargelloni et al., 2000; Lee et al., 2004). These methods have been shown to give unreliable estimates when evolutionary rate varies markedly between species groups. Furthermore, removing data that does not adhere to a molecular clock is an inefficient use of the data if many genes or species violate the clock. Many of these studies have ‘assigned’ fossil dates to nodes within phylogenies to calibrate the tree, however such fixed dates will tend to underestimate the true date of the divergence (and therefore overestimate molecular rates) as the incomplete nature of the fossil record means that it is unlikely that the very earliest specimens following a divergence will be preserved (Fortey et al., 2004). Few studies of Southern Ocean and Antarctic marine taxa have employed ‘tree-based’ likelihood methods of estimating divergence times which ‘relax’ the molecular clock and facilitate the estimation of divergence times despite the presence of significant rate heterogeneity. This method requires a single resolved tree topology to be specified, which is often problematic when parts of the tree may be unresolved and a number of plausible trees exist. Recent simulation studies investigating the accuracy of this method also show it to both overestimate and underestimate rates in many cases (Ho et al., 2005).

Although most of these studies estimating molecular rates and divergence dates have also commented on the diversification of taxa, none have used phylogenetic methods to infer relative rates of speciation and extinction and changes in these rates over time. A complete investigation of the factors determining biodiversity requires a more detailed investigation of the effects of speciation and extinction.

Summary

Major climatic and tectonic events in Antarctica’s history, such as the opening of the Drake Passage, establishment of the Polar Front and the onset of cooling around the Eocene-Oligocene boundary have been recognised as important events in shaping the recent Antarctic marine biodiversity. Such events are likely to have precipitated extinctions in Antarctic taxa, giving rise to vacant niches and providing opportunities for speciation. These events may have also facilitated the colonisation of other areas (e.g. deep sea) from a suggested centre of origin in Antarctica. Modern molecular techniques utilising DNA, fossil and biogeographical evidence can be used to give robust estimates to determine the dates of divergence and molecular rates of Antarctic marine taxa. This gives us insight into the evolutionary history of the Antarctic marine fauna.

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