

ANTARCTIC ECOSYSTEMS

An Extreme Environment in a Changing World

Edited by
Alex D. Rogers
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ANTARCTIC ECOSYSTEMS

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Introduction

Antarctic Ecology in A Changing World

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1 Introduction

Antarctica offers an unrivalled natural laboratory for fundamental research on the evolutionary processes that shape biological diversity on both local and regional scales. Physiologists and ecologists have long been attracted to environments that lie at the limits of the physical conditions capable of supporting life. This is because the polar regions, the deep-sea, hot springs or hydrothermal vents demand striking adaptations at the molecular, cellular or whole-organism level to allow organisms living there to survive, grow and reproduce. Early work on these systems tended to concentrate on specific adaptations, such as membrane function in high-temperature microbes, or antifreeze proteins in polar fish. These specific adaptations are aspects of environmental adaptation in general (Clarke, 1983, 1991; Hochachka & Somero, 2002), and hence the comparative approach has contributed to our overall understanding of evolutionary adaptation at the molecular level. In addition

the recent revolution in molecular techniques, particularly those in transcriptomics and proteomics over the past decade, has allowed us to link the genome to the environment in entirely new ways (Feder & Mitchell-Olds, 2003; Chen *et al.*, 2008). For example it is now possible to couple data on protein structure and gene expression to ecosystem-level processes, and thereby to the evolution of entire communities (Whitham *et al.*, 2006). This brings with it the implicit recognition that these links operate over a range of scales of both time and space.

The isolation of the Antarctic continent following the break-up of Gondwana and the subsequent establishment of the Antarctic Circumpolar Current (ACC) and its associated oceanographic regime in the Early Cenozoic have meant that the recent evolution of both the marine and terrestrial biotas has taken place relatively undiluted by biotic exchange. The dramatic climatic changes that characterize the period since the Late Mesozoic have caused major shifts in the composition of both the marine and terrestrial biotas (Clarke & Crame, 1989. 1992. 2010; Chown & Convey, this volume; Rogers, this volume), and the present extreme environmental conditions provide powerful insights into how physiology affects ecology. Finally, the rapid recent regional climate change along the Antarctic Peninsula is already having a strong effect on the physical environment, with biological signals apparent both in land and in the sea (Chown & Convey, this volume; Clarke *et al.*, 2007; Wall this volume; Schofield *et al.*, 2010). This is superimposed on ecosystem-level changes that have already been caused by man through overexploitation of marine biotic resources (e.g., Ainley & Blight, 2009) and, in the sub-Antarctic in particular, the introduction of non-native species (Frenot *et al.*, 2005; Convey *et al.*, 2010).

All of these topics have received detailed attention over the past decade or more, but it is only now that the impacts

of molecular genomics and new approaches in the study of Antarctic ecosystems at large scales are significantly influencing our understanding of Antarctic ecology and evolution (Clark *et al.*, 2004; Peck *et al.*, 2005). It is therefore timely to synthesize current knowledge by collating invited contributions from key workers in many of the important areas of Antarctic evolution, ecology and ecosystem management. Two unifying background themes provide a framework for this synthesis. The first is climate change, and the second is the importance of spatial, temporal and organizational scale in ecology. The various chapters cover a diverse range of organisms, from microorganisms through marine and terrestrial invertebrates to fish and higher predators, and also a wide array of habitats including deep and continental shelf marine benthos, open-ocean pelagic and terrestrial. Key areas of Antarctica (the western Antarctic Peninsula, East Antarctica, Scotia Sea and Ross Sea) are treated in detail, and topics include physiological adaptation, evolution, biological diversity, trophic interactions and the spatial and temporal structure and operation of ecosystems. Considerable importance has been placed on the historical context and how this influences modern day diversity and biogeography, and also the influence of the latter on management decisions for fisheries and conservation.

2 Climate Change

The Antarctic Peninsula is one of the three areas of the globe that are currently experiencing rapid regional climate change (King, 1994; Vaughan *et al.*, 2003; Ferrigno *et al.*, 2009), the other two being north western North America and an area centred on central Siberia. These are all at high latitude areas and each has experienced a mean annual

temperature rise of more than 1.5 K since 1950, compared with a global mean increase of ca 0.6 K.

Although the rapid regional warming of the Antarctic Peninsula has attracted considerable attention (e.g., Turner *et al.*, 2005), it is important to emphasize that for continental Antarctica, significant trends in meteorological temperatures were identified later (Steig *et al.*, 2009). This is because most of the weather stations recording temperatures were from coastal locations around Antarctica and records from West Antarctica were few and discontinuous (Steig *et al.*, 2009). It is only with the development of climate-field-reconstruction techniques that a 50-year spatially complete estimate of temperature anomalies across Antarctica has been achieved (Steig *et al.*, 2009).

The causes of the marked regional warming along the Antarctic Peninsula are not completely understood, although the latest generation of coupled ocean/ice/atmosphere climate models used in the IPCC (Intergovernmental Panel on Climate Change) Fourth Assessment AR4 are able to reproduce the recent warming qualitatively, although with only about half the observed magnitude (Connolley & Bracegirdle, 2007). Recent data have shown a strong correlation between regional atmospheric circulation and air temperature in the Antarctic Peninsula, and it seems likely that an important factor has been a shift towards a more cyclonic atmospheric circulation (Turner *et al.*, 2005). Significant changes have also been observed in sea-ice to the west of the Antarctic Peninsula, where there has been a 40% reduction in annual sea-ice extent over a 26-year period, driven mainly by a reduction in the duration of winter sea-ice (Stammerjohn *et al.*, 2008).

The warming of the atmosphere of the Antarctic Peninsula has had a profound influence on the terrestrial environment. The length of the summer melt period has increased

(Vaughan, 2006) and most of the glaciers have retreated during the past 50 years, with the average rate of retreat accelerating (Cook *et al.*, 2005). Glacial retreat in the Peninsula region has been linked to the loss of ice shelves with seven ice sheets having broken up in the past 50 years (Vaughan & Doake, 1996; Ferrigno *et al.*, 2009), including the Wordie Ice Shelf in the 1980s (Doake & Vaughan, 1991) and the middle section of the Larsen Ice Shelf in 2002. Recent studies of aerial photographs and satellite images have confirmed that the retreat of ice shelves over this period along both the western and eastern Antarctic Peninsula is widespread (Ferrigno *et al.*, 2009). While these ice shelf collapses are undoubtedly spectacular, and hence have attracted widespread scientific and public attention, the rapid warming has also led to a significant loss of snow and ice banks, with a consequent increase in the area of open ground.

The rapid regional climatic warming of the Antarctic Peninsula has also been detected in the oceanic system to the west. Meredith and King (2005) have demonstrated a profound warming of the summer ocean surface in the Bellingshausen Sea during the second half of the 20th century (more than 1 K since the 1950s), and a small but significant warming has been detected in the waters of the ACC (Levitus *et al.*, 2000, 2005; Gille, 2002; Barnett *et al.*, 2005). The precise role of the ocean in the regional climate change of the Antarctic Peninsula is unclear, though there is strong evidence for linkage between oceanic processes, sea ice and atmospheric circulation (Yuan & Martinson, 2001; Harangozo, 2006; Ducklow *et al.*, 2007. this volume).

3 The Historical Context

Evidence for the recent rapid regional climate change of the Antarctic Peninsula is based on a relatively short duration of

the satellite and instrumental records in Antarctica. In order to place this into perspective a longer historical view is required.

On the geological time-scale, the Antarctic marine environment has cooled from the warm Late Cretaceous to the present polar conditions (Lear *et al.*, 2000; Zachos *et al.*, 2001). Although the overall trend has been one of steadily decreasing temperatures, this smooth trend has been interrupted by episodes of both warming and rapid cooling (Zachos *et al.*, 2001, 2003). On land, the changes in climate and associated glaciations have eradicated almost all the flora and fauna that characterized the Early Cenozoic of Antarctica, driving the evolution of the polar marine and terrestrial biota we observe today (Clarke & Crame, 1989, 1992). There are, however, isolated populations which have been shown by biogeographic and molecular analyses to have been present throughout the Cenozoic glaciations (Chown & Convey, this volume; Convey *et al.*, 2010; Rogers, this volume). The existence of these isolated populations provides an important biogeographic control on reconstructions of the ice sheet through history (Clarke, 2003a; Convey *et al.*, 2009; Convey *et al.*, 2010). Cenozoic climate change has also forced key evolutionary adaptations within species, including changes in morphology, physiology and at the molecular level (Rogers, this volume) allowing species to live at low temperatures. Some of these adaptations, such as the evolution of antifreeze glycoproteins in notothenioid fish, provide some of the clearest examples of environmentally driven macroevolution in the natural world (Chen *et al.*, 1997; Cheng, 1998; Cheng and Detrich, in press; Cheng & Detrich, 2007, this volume).

Oceanographic changes around Antarctica, that have been intimately associated with tectonic events associated with the fragmentation of Gondwana, have been critical to this long-term climate change (Clarke & Crame, 1989, 1992).

2010; Rogers, 2007, this volume). Of particular importance were the opening of the Drake Passage between the Antarctic Peninsula and South America, and the Tasman Seaway, which together enabled the onset of the ACC. The precise dating of these events is still a matter of debate, but new isotopic data are starting to constrain the timing (Scher & Martin, 2006). Such oceanographic changes have been critical in the evolution of the Antarctic marine biota and have played a significant role in establishing patterns of marine biodiversity globally (Clarke & Crame, 1989, 1992; Rogers, this volume).

Of more immediate relevance to understanding recent climate change have been the results from sediment cores taken from the Palmer Deep, which reveal variability in the silt-to-clay ratio and microfossil composition at frequencies of between 1800 and 50 years (Leventer *et al.*, 1996). This variability has been interpreted as indicating changes in production linked to the extent of glaciation and long-scale variability in the dynamics of the ACC, notably the extent of the flux of warmer water of the Upper Circumpolar Deep Water onto the continental shelf (Warner & Domack, 2002). Although these data come at present from a limited location, they are important in that they reveal a long history of variability over a range of time scales. They are also critical in that they demonstrate clearly the current rate of regional climate change is unprecedented in the recent geological record (Domack *et al.*, 2005).

4 The Importance of Scale

A central theme of the work presented here is the importance of organizational, spatial and temporal scale in Antarctic ecology, from the genome to whole ecosystems, micro-habitats to ocean basins, and seconds to centuries (Murphy *et al.*, 1988). Biological processes are integrated at

a range of scales of organization, from the genome to the ecosystem. Climate change has caused large-scale changes at the ecosystem level in Antarctica over geological time-scales (Clarke & Crame, 1989. 1992. 2010; Rogers, 2007, this volume). Recent climate change has also been linked to changes in the distribution, biodiversity and structure of biological communities (Atkinson *et al.*, 2004; Chown & Convey, 2007, this volume; Wall 2007, this volume). Harvesting has also driven changes in the Antarctic ecosystem over the last two centuries and this is discussed below.

The interaction of the environment with the genome of individuals within populations ultimately governs the impact of climate change on communities (Hoffman & Willi, 2008). For organisms unable to shift distribution, the ability to alter gene expression in response to environmental variation at scales from seconds to seasons, or to change the structure and function of proteins over longer time scales in response to climate change, partially dictates the success of species and the composition of biological communities (Feder & Mitchell-Olds, 2003). Such genetic responses to short-term environmental variation or longer-term climatic changes are modified by interspecies (intergenomic) interactions (Whitham *et al.*, 2006). Environmental forcing of evolution, at the extremes of the physical ambit of life, in regions like Antarctica, may constraint adaptation to current and future climate change. This may not only be in terms of tolerance to unfavourable physical conditions, but also in functional limitations on the ability of species to compete successfully or survive predation. For example, terrestrial Antarctic species live in a physical environment characterized by a large variation in physical parameters, and hence the increase in mean temperature associated with climate change may not pose a significant immediate physiological challenge. In contrast, Antarctic marine species have a