INTRODUCTION

Earth’s climate fluctuated between glacial and interglacial periods throughout the Quaternary (Petit et al. 1999). With each major climate shift, many organisms were forced to change their distributional ranges, generally moving towards the equator as the planet entered an ice age, and towards the poles during interglacial periods (e.g., Hewitt 2000, Fraser et al. 2012). Where organisms have recolonised higher-latitude regions post-glacially, these more recently established populations generally show lower genetic diversity than at lower latitudes, where populations have been able to persist locally or in situ for longer periods (Hewitt 2000).

Several recent studies on Southern Hemisphere sub-polar and cool-temperate littoral ecosystems have found such latitudinal genetic diversity gradients, indicating that many of the sub-Antarctic islands have been recolonised post-glacially (approximately during the last 18 000 years) by highly-dispersive marine species that are unable to withstand ice scour (Fraser et al. 2009, Nikula et al. 2010). In contrast, sub-Antarctic marine species that are less adversely affected by sea ice do not appear to show strong genetic diversity gradients. These biological studies support the hypothesis that Antarctic sea ice extended to most of the higher-latitude regions post-glacially, presumably via rafting at sea in the path of the Antarctic Circumpolar Current. During glacial maxima, sub-Antarctic littoral communities would have been severely reduced, comprising mainly ice-scour hardy taxa such as small and/or seasonal macroalgae, and mobile molluscs.

Key Words: sub-Antarctic, ice scour, postglacial recolonisation, rafting, West Wind Drift, global warming.

SUB-ANTARCTIC LITTORAL ECOSYSTEMS TODAY

Many intertidal and shallow subtidal ecosystems of the sub-Antarctic islands north of the Antarctic Polar Front (APF) are dominated by Southern Bull-Kelp (*Durvillaea antarctica* (Chamisso) Hariot) communities (e.g., Klemm & Hallam 1988) (pl. 1). Southern Bull-Kelp can reach densities of more than 100 kg wet mass/m² (Haxen & Grindley 1985), and makes a large contribution to local marine (Kachel et al. 2000) and terrestrial (Dufour 2011) trophic webs. Kelp plays an important role in local community structure by facilitating settlement and growth of some macroalgal species over others (Taylor & Schiel 2005), and providing habitat and food for a diverse array of invertebrate taxa (Edgar & Burton 2000, Smith & Simpson 2002) including polychaetes, echinoderms, crustaceans and molluscs. Beach-cast bull-kelp (wrack) is consumed by a wide variety of insects and crustaceans (Dufour 2011) which in turn form the prey of many birds.

In deeper (>5m) subtidal sub-Antarctic waters, the giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh dominates, and, like *D. antarctica*, performs important ecosystem-structuring services by providing habitat and food for many organisms. Pugh & Davenport (1997) hypothesised that *M. pyrifera* might survive some degree of ice scour as its holdfasts attach to the substrate deeply enough to avoid the ice foot. Molecular data, however, indicate that this species has probably recolonised many sub-Antarctic islands post-glacially (Macaya & Zuccarello 2010b), suggesting it does not survive long periods of sustained ice scour. Indeed, *Macrocystis* is not presently recorded from any of the islands within the northern limit of sea ice. More than a century ago, Skottsberg (1904) noted the absence of *Macrocystis* from the South Orkney Islands and suggested it was unlikely to occur near any islands within the northern limit of drifting sea ice (which he defined as the “Antarctic” zone).

Molecular studies of *D. antarctica* (Fraser et al. 2009), *M. pyrifera* (Macaya & Zuccarello 2010b), and some kelp-associated invertebrates (Nikula et al. 2010) indicate that most sub-Antarctic kelp communities have recolonised LGM sea-ice affected regions (fig. 1) post-glacially, presumably via rafting. Circumpolar dispersal would have been facilitated by the strong eastward-flowing Antarctic Circumpolar Current (ACC), also known as the West Wind Drift (Waters 2008). Tens of millions of detached *D. antarctica* are estimated to be drifting in the path of the ACC at any time (Smith 2002), and can carry associated invertebrate communities...
long distances among isolated oceanic landmasses (Fraser et al. 2011). Post-glacial recolonisation of the sub-Antarctic by rafting would therefore have been possible even for some otherwise sedentary or poorly motile organisms. Based on molecular patterns, recolonisation by *D. antarctica* is inferred to have occurred from a refugium in the New Zealand sub-Antarctic (Fraser et al. 2009, Fraser et al. 2010a).

Not all intertidal and shallow subtidal organisms are likely to have been driven locally extinct at sub-Antarctic islands within the range of sea ice at the LGM. Some taxa are ice-resistant, able to survive at depths below the reach of scouring ice, or in shelters such as rock cracks (Barnes 1999), and these might have survived Quaternary ice ages in situ on the islands (Fraser et al. 2012). Thus, sub-Antarctic nearshore ecosystems could have cycled, with glacial–interglacial changes, between ecosystems structured largely by the ice-scour susceptible kelps *D. antarctica* and *M. pyrifera*, and more ice-resilient communities.

**SUB-ANTARCTIC LITTORAL ECOSYSTEMS DURING GLACIAL MAXIMA**

During Quaternary glacial maxima, when Antarctic sea ice is hypothesised to have – at least occasionally – extended far enough north to have affected Marion, Macquarie, Crozet, Kerguelen and Heard islands (Fraser et al. 2009, Fraser et al. 2012) (fig. 1), sub-Antarctic intertidal and shallow subtidal ecosystems might have been comparable to those found today at islands still within the reach of Antarctic winter sea ice, such as the South Shetland or South Orkney islands (pl. 2). There, sparse and relatively small macroalgae with short or biphasic/seasonal life cycles dominate the shallow marine floral assemblages, and hardy, motile invertebrates such as limpets and amphipods can persist despite frequent scouring of the rocky shores by ice. Mercier & Hamel (2005, p. 87) described the littoral flora and fauna of the Scotia Arc islands:
The impacts of past climate change on sub-Antarctic nearshore ecosystems

Overall, the biota of the intertidal region is poor... the midlittoral zone ... is characterized by the presence of the Porphyra algae ... there are also algae in the tide pools and crevices. Limpets ... occur in crevices, whereas amphipods, nemertines, and flatworms are found clustered under stones and rocks. The tide pools of the midlittoral are home to many Antarctic species of algae such as Leptosomia, Iridaea, Adenocystis that can also extend their distribution to the infralittoral fringe area with Desmarestia, Curdica, Monostroma, and Plocamium. The infralittoral fringe is characterized by numerous algae, mainly of the genera Desmarestia and Ascosiera. The huge Phyllogigas grandifolius [now Himantothallus grandifolius] dominates this [subtidal] area ...

On South Georgia, some littoral regions are scoured by ice breaking away from the island’s glaciers, whereas other areas are rarely impacted by ice, providing an interesting system for studies of the impacts of ice scour. An ecological study on South Georgia by Pugh & Davenport (1997)

PLATE 1

*Durvillaea antarctica* is an important ecosystem-structuring species in the sub-Antarctic. These photographs, from Marion Island in April 2007, show: (A) *D. antarctica* growing densely in the intertidal, as well as detached and cast up on the beach (Fur and Elephant seals indicate scale), and (B) *D. antarctica* and other macroalge covering almost all available rocky substrate in the intertidal (scale represents approximately 20 cm) (Photos: Ceridwen Fraser).

PLATE 2

At the peak of the last Ice Age, many sub-Antarctic littoral ecosystems probably resembled those of Antarctic islands currently within the reach of sea ice, such as the South Shetland Islands. These photographs, taken during intertidal surveys in the South Shetland Islands (King George Island) in February 2008, show ice-scoured rocky shores lacking the diverse macroalgal cover of sub-Antarctic islands. Some algae (see arrow in panel B) and motile fauna such as limpets can persist by sheltering in rock cracks and crevices. Scale in panel B represents approximately 40 cm (Photos: A: Carlos Olavarria; B: Emma Newcombe).
documented differences in these shallow marine ecosystems, and demonstrated that some macroalgae, such as Porphyra and Urospora species, survive in rock crevices in the ice scoured areas. Many of the intertidal/shallow subtidal algae (e.g., Desmarestia ligulata (Stackhouse) J.V.Lamouroux, Adenocystis utricularis (Bory de Saint-Vincent) Skottsberg, Bostrychia intricata (Bory de Saint-Vincent) Montagne, several Porphyra species) of islands presently within Antarctic sea ice extent also occur on sub-Antarctic islands further north. Preliminary molecular data from A. utricularis and B. intricata – circumpolar macroalgae that occur throughout the sub-Antarctic, including on some currently ice-affected islands – indicate that these taxa do not show classic genetic signatures of post-glacial recolonisation of LGM ice-affected islands (Fraser, unpublished data). These species may therefore have persisted in situ throughout recent glacial maxima. Similarly, limpets of the genus Nacella show considerable phylogeographic diversity in the sub-Antarctic (González-Wevar et al. 2010), indicating that congeners have likely been scattered throughout the sub-Antarctic since well before the LGM. Sub-Antarctic littoral ecosystems during glacial periods therefore probably comprised a depauperate subset of modern-day sub-Antarctic taxa.

CONCLUSIONS AND IMPLICATIONS

Some of the dominant macroalgal species – and associated invertebrate communities – of the littoral ecosystems of many sub-Antarctic islands today were apparently extirpated from the islands during the last Ice Age (and presumably at previous Quaternary glacial maxima). When sea ice extended far enough north to scour sub-Antarctic shores, littoral ecosystems would have been drastically different, with diversity reduced to those species capable of surviving in ice-affected regions. Dispersal by rafting would have allowed recolonisation of the islands by ice-sensitive taxa during warmer interglacial periods.

Sub-Antarctic littoral ecosystems thus appear to have been able to recover from some of the impacts to biodiversity of Quaternary climate change cycles, but predicting the impacts of, and biological response to, future climate change in the region is not straightforward. Global average temperatures in coming decades are predicted to exceed any experienced during the Quaternary (I.P.C.C. 2007), and using pre-Quaternary warm periods as analogues of future climate change is complicated by uncertainties related to factors such as changes in oceanography, topography and continental positions (Haywood et al. 2011). Global warming is expected to lead to poleward range shifts for many taxa (Fickling et al. 2006), but southward dispersal of sub-Antarctic taxa would require traversal of oceanic barriers such as the Antarctic Polar Front (Fraser et al. 2012).

Fortunately, the sub-Antarctic is expected to experience slower rates of global warming than at similar latitudes in the Northern Hemisphere (Sandel et al. 2011), perhaps largely due to oceanic climate buffering. D. antarctica cannot tolerate high water temperatures (greater than about 17°C), and its northern limit is currently approximately in line with the limit of sub-Antarctic waters (although relatively sparse northern populations occur up to about 30–35°S in the cool-temperate waters of New Zealand and Chile) (Fraser et al. 2010b). The now monospecific genus Macrocyctis has a slightly broader distribution in the Southern Hemisphere, ranging from the sub-Antarctic to cool-temperate latitudes (e.g., the southern coast of South Africa, southeastern Australia, and along the path of the Humboldt Current in South America) (Macaya & Zuccarello 2010a). If either species is extirpated from sub-Antarctic islands by warming ocean temperatures, significant changes to littoral (and, indirectly, terrestrial) ecosystems in the region are sure to result, but these changes will be unlike any the region has experienced during the past 2–3 million years.

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