

Chapter 5

Change in Southern Hemisphere Intertidal Communities Through Climate Cycles: The Role of Dispersing Algae

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Abstract Macroalgae are fundamental components of most marine ecosystems, creating habitat and food sources for a wide range of other organisms. Macroalgal distributions are strongly linked to water temperature, and global environmental change is therefore likely to drive major shifts both in the distributions and compositions of marine communities. Phylogeographic research on macroalgae and associated organisms can reveal ecological changes that have occurred with global warming since the Last Glacial Maximum (LGM), which can help us to predict what might happen under future climate change scenarios. Such research shows that many macroalgae have changed their distributions, broadly shifting poleward or into deeper waters. Importantly, for organisms to change their distributions in response to climate change, they must be able to disperse, sometimes long distances. Some buoyant, robust macroalgae are extremely good long-distance travellers, and others have apparently been able to disperse across oceans indirectly, such as via rafting. However, not all macroalgal species are capable of long-distance dispersal, and with global warming, ecosystems thus do not simply slide poleward in their entireties, but both move and change. Studies are already showing that contemporary climate change is affecting the distributions of macroalgal-dominated ecosystems. This chapter summarizes some of the ways in which Southern Hemisphere macroalgal distributions are inferred to have shifted with past climate change, and speculates on how they might change in the future. Processes underpinning these changes, such as climate drivers and dispersal capacity, are also discussed.

Keywords Drifting · Last Glacial Maximum (LGM) · Rafting · Sea surface temperature · Seaweed

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5.1 Introduction

Macroalgae are key components of almost all marine ecosystems; indeed, many macroalgal species create critical habitat for other organisms, and thus act as fundamental ecosystem engineers (Jones et al. 1997). The large brown (phaeophycean) algae, or kelps (Fraser 2012a), often play particularly important roles in the physical and biological structure of the local environment. For example, *Macrocystis* species form kelp ‘forests’ that can support extraordinarily diverse ecosystems (Graham 2004), pelagic clumps of *Sargassum* act as floating islands inhabited by a wide range of vertebrates and invertebrates (Fine 1970), and stands of bull kelp—*Durvillaea* (in the Southern Hemisphere) and *Nereocystis* (in the Northern Hemisphere)—support diverse assemblages of flora and fauna (Edgar and Burton 2000; Taylor and Schiel 2005; Springer et al. 2010). For many of the large kelps, particularly diverse communities of invertebrates inhabit the structurally complex holdfasts, which are discs or domes at the base of the stipe that attach the plant to the substrate (Smith 2000) (Fig. 5.1). Green (Chlorophyta) and red (Rhodophyta) macroalgae, even in apparently simple structural forms such as crusts, can also create important habitat for many other marine organisms (Marx and Herrnkind 1985; Sánchez-Moyano et al. 2001; Chenelot et al. 2011), and all divisions of macroalgae are primary producers, providing food sources for fauna.

The composition of most marine ecosystems—notably excluding deep-sea ecosystems that are inimical to photosynthesizing organisms—therefore hinges on which algal species are present, which in turn is largely determined by environmental conditions. The large kelps are rare in shallow tropical waters, due to high water temperatures and low nutrient availability (Bolton 2010), but are more common in tropical waters of 30–200 m depth (Graham et al. 2007), and are abundant in cool-temperate and sub-polar zones (Mann 1973). In Antarctic waters, large brown algae do occur but are mostly restricted to members of the order Desmarestiales (Moe and Silva 1977). In coral reef ecosystems, a complex competitive relationship exists between macroalgae and corals, with macroalgal growth generally suppressed on healthy reefs (McCook et al. 2001). The distributional ranges of marine macroalgae are largely related to water temperature (Adey and Steneck 2001), although they may also be influenced by available sunlight (e.g. Schwarz et al. 2003), nutrients (Burkepile and Hay 2006), and other factors such as wave exposure (Underwood and Jernakoff 1984) and the presence of herbivores (Underwood and Jernakoff 1984; McCook et al. 2001; Burkepile and Hay 2006). With environmental conditions driving biogeographic patterns in these important—and often keystone—macroalgae, large-scale environmental change is likely to drive major shifts both in the distributions and compositions of entire marine communities. Indeed, changes in macroalgal distributions, and hence those of associated organisms, have been inferred to have occurred with past climate change (Adey and Steneck 2001; Fraser et al. 2009; Nikula et al. 2010; Fraser 2012b). In the face of ongoing and accelerating (Cox et al. 2000) global warming, inferring

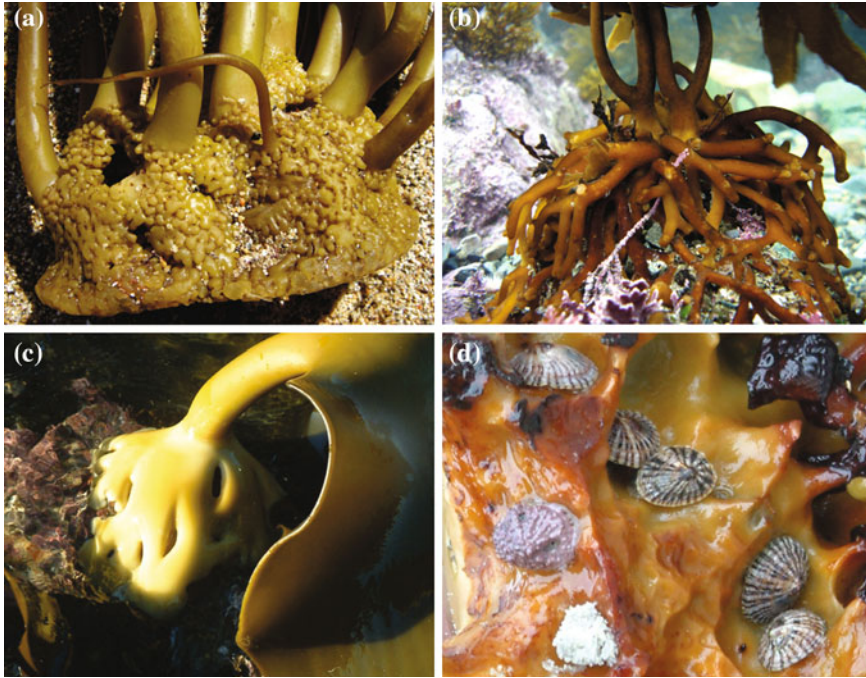


Fig. 5.1 Kelp holdfasts are often structurally complex and can form habitat for diverse organisms such as small invertebrates and algae, including during oceanic dispersal of the kelp (rafting). Pictured are holdfasts of **a** *Lessonia spicata* in Chile (E. Macaya, 2007); **b** *Macrocystis pyrifera* in New Zealand (E. Macaya, 2009); **c** and **d** *Durvillaea antarctica*, New Zealand (C. Fraser, 2006) (underside of detached holdfast, with resident gastropods, pictured in **d**)

past environmentally driven changes to marine ecosystems could help us to predict what might happen under future scenarios.

5.2 Pleistocene Glacial—Interglacial Cycles

During the Pleistocene (from approximately 2.5 Ma until the Holocene, which started 11.7 ka), the Earth underwent several glacial–interglacial cycles. The most recent glacial period peaked between 0.026 and 0.019 Ma, and is referred to as the Last Glacial Maximum (LGM) (Clark et al. 2009). Biological studies indicate that many species shifted their distributions as the planet warmed during interglacial periods, for example, with terrestrial trees generally moving to higher latitudes or higher elevations (Davis and Shaw 2001). Studies of modern taxa indicate that these trends hold true for a wide range of species under contemporary global warming (Parmesan and Yohe 2003; Chen et al. 2011), including marine species (Perry et al. 2005). For example, some Antarctic benthic taxa are inferred to have

retreated into deeper waters during glacial periods, and recolonized the continental shelf postglacially (Brey et al. 1996), and some marine species have shifted their distributions towards the poles with recent warming (Perry et al. 2005). When organisms are unable to move to suitable habitat as the environment changes, they face local or total extinction; indeed, a large number of species are predicted to face extinction under future climate change scenarios (Thomas et al. 2004). Some species can survive unfavourable conditions, for example, within glaciated regions, by sheltering in microrefugia—small areas that remain inhabitable, such as localized warm patches formed by geothermal heat (Fraser et al. 2014) or valleys (Stewart and Lister 2001). Recolonization of surrounding regions from such refugia is typically marked by low genetic diversity in the recolonized populations (Provan and Bennett 2008), as only a subset of the original population moves out of each refugium. Likewise, poleward distributional shifts following glacial periods are often characterized by high genetic diversity in the lower latitudes versus low diversity in the higher, recolonized latitudes (Hewitt 2000). Phylogeographic approaches can therefore help us to understand how species responded to past ice ages and subsequent global warming, and which species were capable of dispersing to new areas to track suitable environmental conditions.

5.3 Phylogeographic Evidence for Changes in Intertidal Communities Through Climate Cycles

One of the major environmental changes that occurs as the planet warms is a rise in sea levels, effected through the melting of glaciers and sea ice, and through thermal expansion of ocean water (Rahmstorf 2007). Since the LGM, sea levels have risen about 135 m (Yokoyama et al. 2000), although with some variation according to geographic location (Lambeck and Chappell 2001). This large sea level rise has obscured most LGM shores, impeding direct (e.g. fossil) analysis of LGM shallow-water communities. Molecular research can, however, shed light on ecological changes that have occurred since the LGM, through phylogeographic studies that assess geographic patterns of genetic diversity in representative marine organisms.

5.3.1 *Polar and Sub-polar Latitudes*

Among the subantarctic islands, south-western South America, and New Zealand, intertidal ecosystems are largely dominated by *Durvillaea antarctica* communities (Klemm and Hallam 1988), with other large brown algae, such as *Lessonia*, co-dominant at some locations (Huovinen and Gomez 2012). This large kelp has a strong influence on community structure, for example, by affecting which other

macroalgal species are able to settle and grow (Taylor and Schiel 2005), and by supporting a wide range of invertebrate species (Edgar and Burton 2000; Smith and Simpson 2002). In the shallow subtidal of this region, the giant kelp *Macrocystis pyrifera*, which is also an important ecosystem engineer, is more dominant. Both *D. antarctica* and *M. pyrifera* are removed by ice scour, and thus do not occur in regions with much glacial or sea ice (see Fraser 2012b). Both species have also been inferred, based on phylogeographic research that demonstrates higher northern versus lower southern molecular diversity, to have recolonized the higher latitudes postglacially (Fraser et al. 2009, 2010; Macaya and Zuccarello 2010) (Fig. 5.2). Studies of some of the kelp-associated invertebrates support the hypothesis that these communities were absent from higher latitudes at the LGM (Nikula et al. 2010; Cumming et al. 2014). There are few studies of postglacial recolonization patterns for smaller macroalgal species in the high latitudes of the Southern Hemisphere, but recolonization of ice-affected areas of Chile has been inferred for *Mazzaella laminarioides* (Montecinos et al. 2012). Despite the absence of the large kelps and their associated communities from the high latitudes during glacial maxima, these shores are unlikely to have been entirely denuded of life. Some taxa can persist in areas where ice scour is common, for example, by living below the reach of the ice or sheltering in crevices (Barnes 1999). During glacial maxima, subantarctic nearshore ecosystems might therefore have resembled those found today in ice-scoured Antarctic waters, comprising mainly small macroalgae with short or biphasic/seasonal life cycles, and motile invertebrates such as limpets, amphipods, and worms (Fraser 2012b). In the Scotia Arc islands, for example, intertidal algae include *Porphyra*, *Leptosomia*, *Iridaea*, and *Adenocystis*, while genera in the shallow subtidal include *Desmarestia*, *Curdiea*, *Monostroma*, *Plocamium*, *Phyllogigas*, and *Ascosiera* (Mercier and Hamel 2005). Many of these species are also found on subantarctic islands today. A phylogeographic study of *Adenocystis utricularis* and *Bostrychia intricata* indicates that these species may have survived the LGM in situ in the subantarctic, whereas the larger kelps did not (Fraser et al. 2013). Many *Nacella* limpets also show relatively high genetic diversity at subantarctic latitudes, suggesting they are not postglacial recolonists of the region (González-Wevar et al. 2010), although they appear to have been absent from higher latitude, Antarctic shores at the LGM (González-Wevar et al. 2013).

5.3.2 *Tropical and Temperate Latitudes*

Whereas the marine biogeography of polar and sub-polar regions appears to have been strongly affected by the extent of glacial and sea ice, postglacial climate change impacts in lower-latitude regions have been linked to water temperature, and/or to changes in sea level (and thus changes in shorelines). For example, in south-east Asia, low genetic diversity of the ecologically important brown macroalga *Sargassum polycystum* has been inferred to be a result of the postglacial flooding of the Sunda Shelf (Chan et al. 2013). In New Zealand, postglacial water

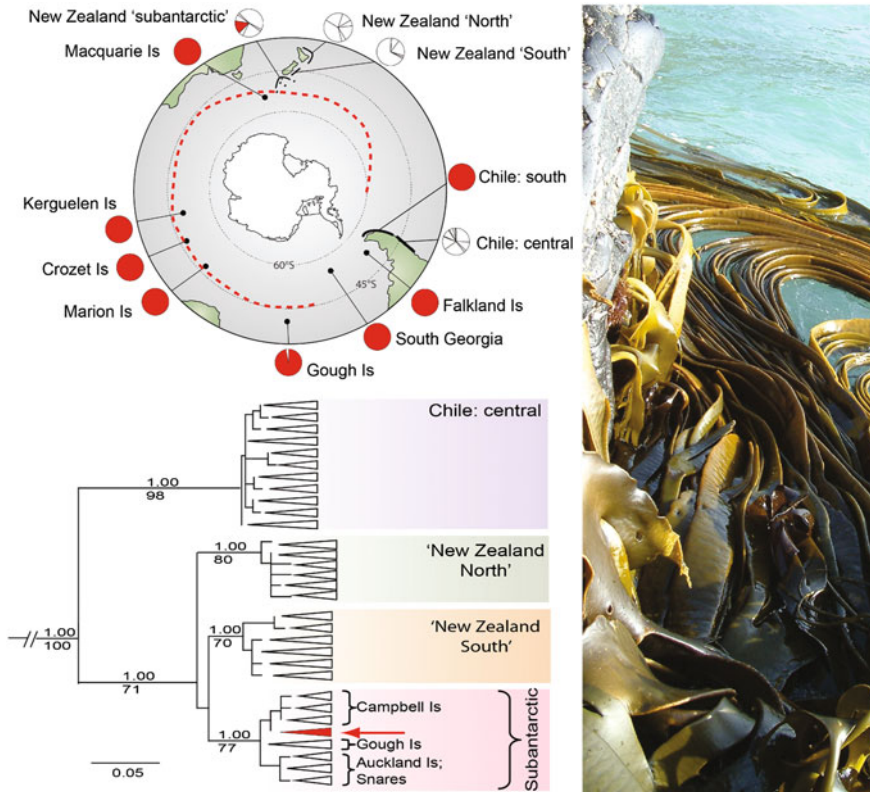


Fig. 5.2 Phylogeography of southern bull kelp, *Durvillaea antarctica* (pictured: right), based on mtDNA (COI) data. The phylogenetic tree (lower left) shows haplotype relationships, with Bayesian PP values above branches, and ML bootstraps below. The map (upper left) shows haplotype proportions at each locality. A single, widespread haplotype (see arrow) was detected at many sites throughout the subantarctic and along LGM-glaciated parts of the Chilean coast, whereas more northern regions showed relatively high genetic diversity. Genetically homogeneous regions with the common 'subantarctic' haplotype were generally within the range of the LGM 4 °C isotherm (dashed line), which may represent a proxy for the extent of sea ice at the LGM (Fraser et al. 2009). These patterns have been inferred to indicate postglacial recolonization of high latitudes by the buoyant kelp, which would have been removed from these regions by ice scour at the LGM (Fraser et al. 2009, 2010). Similar patterns have been observed for giant kelp, *Macrocystis pyrifera* (Macaya and Zuccarello 2010)

temperature and sea level rise have been invoked to explain patterns of genetic diversity in *Carpophyllum maschalocarpum* (Buchanan and Zuccarello 2012) and in cryptic species within *B. intricata* (Muangmai et al. 2015). In the Southern Californian Bight, in North America, palaeogeographic modelling indicates that a larger area of rocky substrate (a consequence of sea level fall during the glacial period) and increased upwelling supported large, rich, kelp-dominated ecosystems similar to those that are found further north today (Graham et al. 2003).

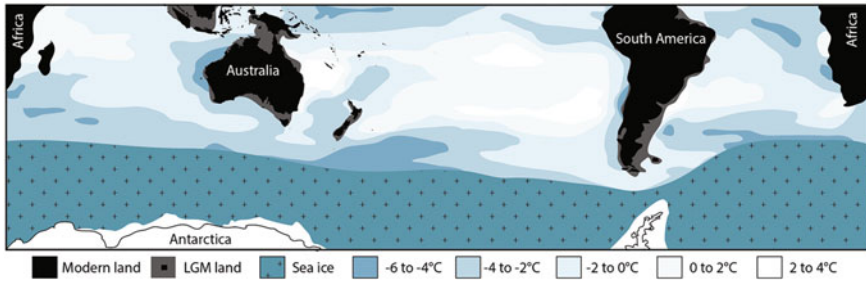


Fig. 5.3 Change in winter sea surface temperatures in the Southern Hemisphere at the Last Glacial Maximum (adapted from Fig. 5A in CLIMAP 1981). Water temperatures along much of the western coasts of major southern landmasses (Africa, Australia, South America and New Zealand) are estimated to have been considerably (up to 6 °C) cooler than today. Such changes will have had profound impacts on macroalgal communities and associated ecosystems in these regions

Estimates of sea surface temperatures (SST) at the LGM indicate that many of the coastal temperate regions in the Southern Hemisphere experienced less extreme cooling than at comparable latitudes in the Northern Hemisphere (CLIMAP 1981; Trend-Staid and Prell 2002). Some areas may even have had slightly warmer waters than today, such as the sub-tropical latitudes of the eastern coasts of Africa, South America, and Australia (Fig. 5.3). These areas might have been too warm for the large habitat-forming kelps, and may instead have supported more ‘tropical’ ecosystems of corals and smaller macroalgae. Regions that experienced little change in SST through glacial cycles may have had relatively stable macroalgal populations for up to several millions of years, and may therefore comprise distinctive biogeographic assemblages (Adey and Steneck 2001). The sub-tropical and tropical western coasts of the Southern Hemisphere continents, in contrast, are thought to have been cooler than now during glacial periods, from about 2 °C (Trend-Staid and Prell 2002) to 6 °C (CLIMAP 1981; Fig. 5.3) cooler at the LGM. Under such conditions, large kelps and their associated communities could have occurred considerably farther north than they do today.

5.4 Effects of Dispersal Ability on Community Structure

For organisms to achieve large-scale distributional shifts, they must be able to disperse, and in some cases to disperse hundreds or thousands of kilometres (Gillespie et al. 2012). Long-distance oceanic dispersal capacity is particularly important in the Southern Hemisphere, where landmasses are not as continuous across latitudes as they are in the more continental Northern Hemisphere. For example, coastal macroalgae that are restricted to southern Australia would need to disperse across thousands of kilometres of open ocean to colonise new shores if

their distributions continue to shift southward; those that are unable to achieve such long-distance dispersal face extinction (Wernberg et al. 2011).

Some of the key habitat-forming macroalgae are physiologically adapted to be extremely good long-distance travellers, particularly at lower temperatures and when solar radiation is not high (Rothäusler et al. 2011; Graiff et al. 2013; Tala et al. 2013). Both *D. antarctica* and *M. pyrifer*, for example, are robust and buoyant, and are commonly found drifting at sea in the mid- to high latitudes, forming large ‘rafts’ that are inhabited by a wide range of floral and faunal passengers (Smith 2002; Rothäusler et al. 2012). Other buoyant, raft-forming taxa in the Southern Hemisphere include *Sargassum*, *Carpophyllum*, *Phyllospora* and *Cystophora* (Rothäusler et al. 2012). Direct observations of kelp rafts, combined with phylogeographic data, have shown that these plants can travel across ocean basins, and can carry diverse epifaunal and epiphyte communities with them. *Durvillaea antarctica* plants have been found washed up on New Zealand shores that molecular data show are hundreds of kilometres from their source populations in the subantarctic (Collins et al. 2010; Fraser et al. 2011; Bussolini and Waters 2015), in some cases with a wide range of living invertebrate passengers (Fraser et al. 2011).

Several non-buoyant and more fragile macroalgae have apparently been able to disperse long, transoceanic distances (such as between New Zealand and South America), presumably via rafting on more robust, buoyant kelps or driftwood. Examples include the red alga *B. intricata* (Fraser et al. 2013) and *Capreolia implexa* (Boo et al. 2014), the green alga *Wittrockiella lyallii* (Boedeker et al. 2010) and others (also see Chapter by Macaya et al. (2016) in this volume). Some otherwise poorly dispersive faunal taxa have also been able to utilise drifting macroalgae to traverse large oceanic distances, particularly kelp-associated marine invertebrates (Donald et al. 2005; Nikula et al. 2010; Haye et al. 2012; Nikula et al. 2013; Cumming et al. 2014). However, not all species are capable of rafting with buoyant kelp; indeed, there is a sharp decline in diversity of associated invertebrates once kelp detaches from the substrate and begins to drift at sea (Gutow et al. 2009), and some species do not attach to the kelp at all. Distributional shifts with climate change must, therefore, involve large-scale movement of some species, and little or no movement of others. With global warming, ecosystems thus do not simply slide poleward in their intireties, but both move and change.

5.5 Summary and Outlook

Phylogeographic evidence has shown that some of the major habitat-forming algae shifted distributions with past climate change, with important consequences for the structure and diversity of marine ecosystems. In general, we are only able to infer what changes might have occurred since the last glacial period, as signals of previous climate cycles are obscured by the most recent events. We are now facing warmer global average temperatures than have occurred for tens of thousands of

years. Nonetheless, the insights we can gain by looking at the impacts of the global warming that took place following the LGM can help us to understand the general patterns and processes of climate-induced ecological changes, and thus to predict what might happen in the future.

Studies are already showing some of the impacts of contemporary climate change on macroalgal-dominated ecosystems. A major habitat-forming kelp in Australia, *Ecklonia radiata*, currently faces considerable physiological challenges in the warmer latitudes of its distribution, as well as from lower water clarity, suggesting that its distribution will shift significantly with ongoing global warming (Staehr and Wernberg 2009). Indeed, in South Africa, *Ecklonia maxima* populations have already been documented to have shifted more than 70 km southward with warming waters (Bolton et al. 2012). Observations following extreme weather events (such as heatwaves) also indicate that climate change will lead to major changes to marine ecosystems, as a result of reduced cover and/or altered distributions of habitat-forming seaweeds such as *E. radiata* (Wernberg et al. 2013) and *Scytothalia dorycarpa* (Smale and Wernberg 2013).

Broadly, Southern Hemisphere macroalgal species that can disperse are likely to move southward with future climate change. For those incapable of long-distance dispersal, the extent of southward shifts will be limited by the southern edges of the landmasses, unless they are able to travel with more dispersive taxa (e.g. via rafting). In contrast to terrestrial species, which are predicted to continue moving both poleward and to higher elevations with global warming (Chen et al. 2011), some marine species may shift downhill to deeper, cooler waters. Already, some large kelp species are found in the deep waters of the tropics, where temperatures are cooler and where water clarity allows light to penetrate to tens or hundreds of metres below the surface (Graham et al. 2007). Indeed, water clarity exerts a major influence on macroalgal distributions (e.g. Nielsen et al. 2002; Eriksson and Bergström 2005; De'ath and Fabricius 2010), and changing climates will lead to regional changes in turbidity and water chemistry as well as in temperature (Jickells 1998; Harley et al. 2006; Whitehead et al. 2009). Both forecast temperature and turbidity profiles should therefore be considered when attempting to model future distributions of macroalgae, although there is currently only limited information on predicted changes to water quality.

Importantly, because macroalgae are fundamental parts of many marine ecosystems, shifts in macroalgal distributions with environmental change will drastically alter the structure of many marine ecosystems. Although buoyant macroalgae can carry epifaunal and epifloral passengers when they disperse, not all species are suited to raft with seaweeds, and thus not all community members will shift their distributions in the same ways. With changing algal distributions, therefore, we can expect broad scale changes to marine ecosystems.

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