Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum

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The end of the Last Glacial Maximum (LGM) dramatically reshaped temperate ecosystems, with many species moving poleward as temperatures rose and ice receded. Whereas reinvading terrestrial taxa tracked melting glaciers, marine biota recolonized ocean habitats freed by retreating sea ice. The extent of sea ice in the Southern Hemisphere during the LGM has, however, yet to be fully resolved, with most palaeogeographic studies suggesting only minimal or patchy ice cover in subantarctic waters. Here, through population genetic analyses of the widespread Southern Bull Kelp (*Durvillaea antarctica*), we present evidence for persistent ice scour affecting subantarctic islands during the LGM. Using mitochondrial and chloroplast genetic markers (COI; *rbc*L) to genetically characterize some 300 kelp samples from 45 Southern Ocean localities, we reveal a remarkable pattern of recent recolonization in the subantarctic. Specifically, in contrast to the marked phylogeographic structure observed across coastal New Zealand and Chile (10- to 100-km scales), subantarctic samples show striking genetic homogeneity over vast distances (10,000-km scales), with a single widespread haplotype observed for each marker. From these results, we suggest that sea ice expanded further and ice scour during the LGM impacted shallow-water subantarctic marine ecosystems more extensively than previously suggested.

Durvillaea antarctica | genetic | phylogeography | raft

Climate change is a major force driving population extinctions, particularly near the limits of a species' range (1). During glacial maxima, many taxa retreat from the cooling poles into lower-latitude refugia, and subsequent interglacial recolonization of high-latitude habitats can occur rapidly, especially in highly dispersive taxa, as indicated by the genetic homogeneity of reinvading populations (1–3). Although such evolutionary patterns have been established for a variety of Northern Hemisphere species (1–7), relatively little is known about the biotic effects of recent glaciations in the more oceanic Southern Hemisphere. Nevertheless, it seems likely that ice-sensitive marine biota of the subantarctic would have followed comparable extirpation–recolonization patterns as receding sea ice "unlocked" the Southern Ocean. Contemporary ice scouring, for example, is known to purge much of the shallow water benthos within current Antarctic sea ice range (8, 9), and any coastlines within Last Glacial Maximum (LGM) sea ice limits are likely to have been similarly affected.

Sea ice can strongly affect global systems, influencing ocean circulation patterns, levels of reflected radiation (10, 11), and rates of climate change (12). Our understanding of LGM ice conditions in the south, however, remains incomplete. The best current estimate of Southern Hemisphere LGM sea ice cover, by Gersonde *et al*. (13), is an amalgamation of data from numerous previous studies and highlights substantial information gaps in the subantartic region. To date, most LGM sea ice estimates have been derived from subfossil diatom data [reviewed by Gersonde *et al*. (13)]. The advent of modern molecular techniques, however, provides an alternative means of assessing organismal history, and thereby shedding light on historical climate conditions (1, 14). Here, in a genetic approach to assessing past sea ice conditions, we use phylogeographical analyses of an ice-sensitive subantarctic macroalga to infer the extent of winter sea ice (WSI) during the LGM.

Southern bull kelp (*Durvillaea antarctica*) is a keystone species of cool-temperate intertidal ecosystems across much of the Southern Hemisphere (15, 16). One of the world's largest kelps (17), it is found in the intertidal and upper subtidal of almost all subantarctic islands, as well as along the coasts of New Zealand (NZ), Chile, and the Falkland Islands (18). Importantly, however, this species' southern range limits correspond to the northern extent of sea ice (18); it is entirely absent from severely ice-affected areas, such as the shores of South Shetland, South Orkney, South Sandwich, and Bouvet Islands (18), and from glaciated regions of Heard Island (16) and South Georgia (19). Although some macroalgal species may survive in ice-scoured regions, *D. antarctica* is completely eliminated (20), and its presence or absence has even been suggested as an indicator of ice scour extent (20), making this taxon an ideal model organism for studies of LGM sea ice. In addition, *D. antarctica* is robust and buoyant, and hence has extremely high dispersal potential: once detached, it may be capable of rafting vast distances (18, 21–24). Here, by using DNA sequence analysis (mitochondrial COI; chloroplast *rbc*L) to assess circum-subantarctic phylogeographic patterns of *D. antarctica* (≈300 specimens, 45 localities), we test the hypotheses that: (*i*) bull kelp was eliminated from ice-affected subantarctic regions during the LGM, resulting in genetic homogeneity of reinvading populations, and (*ii*) rafting of the buoyant adult plants facilitated rapid recolonization.

Results

Mitochondrial and chloroplast markers (COI; *rbc*L) both revealed substantial genetic diversity within *D. antarctica* (uncorrected distances up to 5.4% for COI), with well-supported clades (or divergent haplotypes) corresponding to northern NZ, southern NZ, Chile, and the subantarctic region [Fig. 1, COI; and supporting information (SI) Fig. S1, *rbc*L]. Although the clustering of samples into these 4 major geographic clades was essentially identical across both data sets (posterior probabilities 0.97–1.00 for COI; Fig. 1), deeper nodes had weaker phylogenetic support, particularly for the less-informative *rbc*L marker, and tree topologies differed. The morphologically and genetically distinct "cape" *D. antarctica* lineage, recently identified from southern NZ, the Snares, and the Auckland Islands (indicated by asterisks in Fig. 1 and Fig. S1) (25), was clearly

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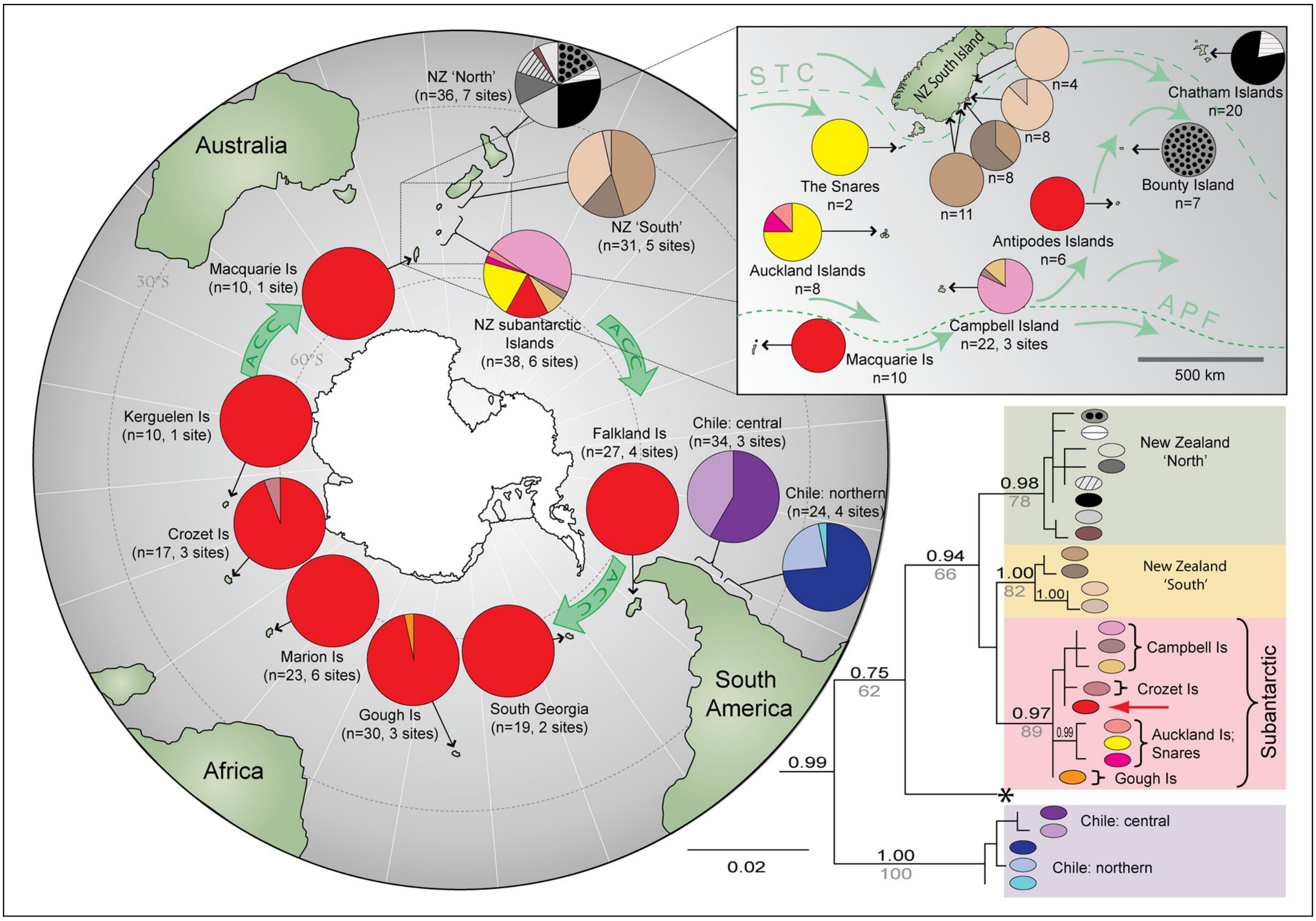

Fig. 1. Phylogeographic relationships within *D. antarctica* based on COI data. The phylogenetic tree (lower right corner) indicates haplotype relationships, with Bayesian PP values above branches and ML bootstraps below. Outgroup taxa have been removed for clarity. ''NZ subantarctic'' refers to the Snares, Auckland, Campbell, and Antipodes Islands. The morphologically and genetically distinct ''cape'' form of *D. antarctica*, recently identified by Fraser *et al*. (25) from southeastern NZ, is indicated by an asterisk. The global projection shows haplotype distributions and proportions at each locality. Diversity in the southern New Zealand region is illustrated at higher magnification (*Inset*, upper right). Green arrows show major surface currents.

distinguishable from all 4 of these geographic clades. This undescribed lineage was not detected at any sites outside the NZ region and is not considered subsequently in this paper. Phylogenetic analyses revealed dramatic geographic contrasts in levels of genetic differentiation among populations. At temperate latitudes (NZ and Chile), strong geographic partitioning of genetic variation was observed across small spatial scales (tens to hundreds of kilometers apart), whereas samples from high latitudes (red haplotype; Figs. 1 and 2) showed genetic homogeneity across vast geographic distances.

Levels of population differentiation were particularly high around the coasts of mainland NZ, with geographically proximate samples exhibiting clear genetic divergence (Fig. 1 and Fig. S1). Similarly, Chilean samples were distinguished by considerable genetic diversity among sites and by a north–south phylogeographic break between 36°36′S and 39°49′S for COI (Fig. 1). In contrast, southern subantarctic samples exhibited remarkable genetic homogeneity across both molecular datasets. Of the 174 subantarctic samples sequenced for COI, 140 yielded a single widespread haplotype (red haplotype in Fig. 1). Of the 8 additional subantarctic COI haplotypes, 6 were restricted to the NZ subantarctic region. Similar results were obtained for chloroplast DNA (*rbc*L), although this less-informative marker exhibited lower overall diversity and weaker deep-node phylogenetic support than COI.

Haplotype networks constructed for subantarctic COI and *rbc*L datasets (Fig. 2) show strong congruence, each characterized by a widespread (red) haplotype common to South Georgia, Marion, Kerguelen, Crozet, Macquarie, and the Falkland Islands. In each case, a "Gough Island" haplotype was one mutation step away and was intermediate to an Auckland Islands/Snares cluster. Interestingly, although the Antipodes Island samples yielded the widespread COI haplotype, the same samples gave a distinct haplotype for *rbc*L (also shared with Gough Island samples; Fig. 2 and Fig. S1).

The unimodal mismatch distribution for subantarctic COI haplotypes was consistent with the expectations of a sudden population expansion model (26), with no significant deviation from the expected distribution ($P > 0.05$). The Fu neutrality test (27) also supported the subantarctic population expansion, with stasis rejected ($F_S = -5.63$, P sim $F_S \leq$ obs $F_S = 0.01$).

Discussion

Our circum-subantarctic analyses of DNA variation in *D. antarctica* support the hypothesis that this kelp species only recently recolonized the subantarctic region; the species exhibits a striking degree of genetic homogeneity in these regions compared with lower-latitude putative glacial refugia, a pattern typical of rapidly expanding, reinvading populations (1–3). Recolonization is likely to have involved a series of long-distance rafting events

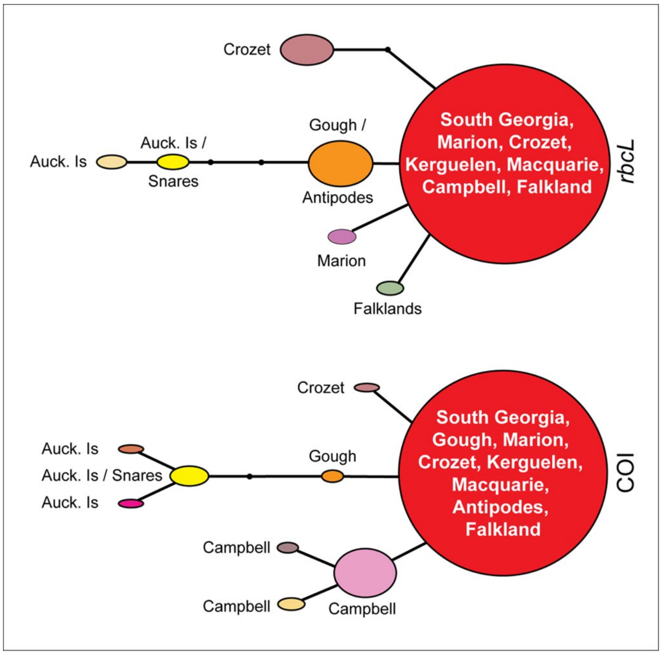

Fig. 2. Haplotype network diagrams for the ''subantarctic'' clade of *D. antarctica* for both mtDNA (COI) and chloroplast (*rbc*L) datasets. Circle size is scaled according to haplotype frequency. Black dots represent hypothetical haplotypes not detected in the current study.

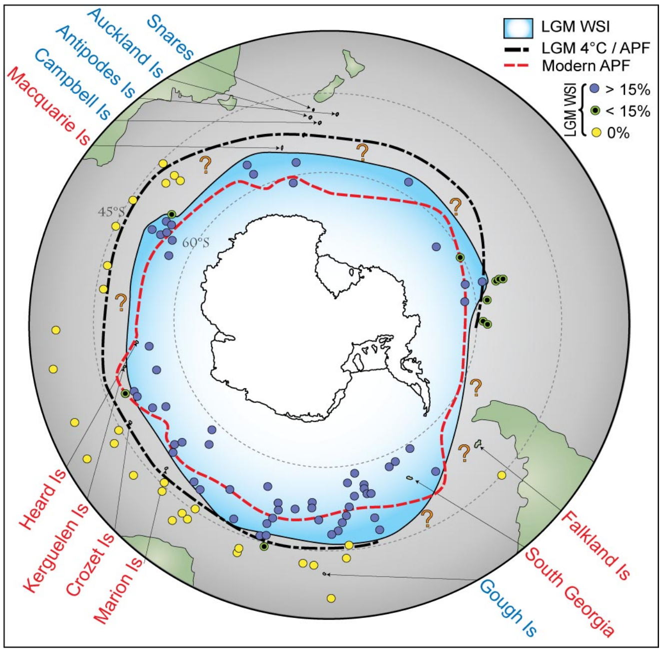

Fig. 3. Positions of the subantarctic islands in relation to present-day conditions and reconstructed LGM oceanographic features, including LGM WSI extent, modified from Gersonde *et al.* (13). Dot points indicate sediment core sites used to reconstruct LGM sea ice cover (after ref. 13): yellow dots contained no evidence of sea ice-associated diatoms, green dots indicate (minimal) evidence, and blue dots indicate high proportions of ice-indicator diatoms. Regions demarcated by question marks lack core data (13). Based on *D. antarctica* genetic data, red labels indicate ''recolonized'' islands putatively affected by LGM ice scour, whereas blue labels indicate putative ''refugial'' islands. The LGM 4 °C isotherm has been identified as a feature roughly equivalent, in terms of water properties and gradients, to the modern APF (13).

of the buoyant kelp from remote source populations (21, 24). Our findings strongly suggest that subantarctic kelp populations were eliminated during the LGM, most plausibly via ice scour. Although this interpretation conflicts with recent oceanographic reconstructions, which suggest LGM sea ice did not reach many subantarctic islands (Fig. 3) (13), it should be noted that fine-scale LGM data are still lacking for many Southern Ocean regions (Fig. 3) (13). On the basis of our analysis, therefore, we suggest that LGM subantarctic sea ice extended substantially further north than is currently recognized. More broadly, our study emphasizes the utility of phylogeographic analysis for studying the evolutionary effects of climate change and for potentially elucidating paleoenvironmental history (28).

Recent Recolonization of Bull Kelp in the Subantarctic. Although the widespread *D. antarctica* is a genetically diverse species, the vast majority of this variation is restricted to temperate latitudes. Within NZ and Chile, for example, substantial genetic differentiation was detected between populations separated by relatively small geographic distances (e.g., tens of kilometers). In high subantarctic latitudes, by contrast, genetic homogeneity was detected over vast geographic distances. For instance, South Georgia, Marion, Crozet, Kerguelen, Macquarie, and the Falkland Island samples were essentially indistinguishable at both COI and *rbc*L. This striking latitudinal contrast in diversity strongly suggests recent colonization of the southern islands from more northern refugial population(s), mirroring postglacial recolonization patterns observed in numerous Northern Hemisphere taxa (1–7). Although we are unable to accurately estimate the timing of recolonization because of a lack of robust mutation rate estimates (7), circumpolar genetic homogeneity certainly seems consistent with postglacial origins. Latitudinal variation in phylogenetic diversity was also detected within the subantarctic region itself, with northern ''refugial'' islands (e.g., Auckland Islands and the Snares) represented by distinct genetic assemblages (Figs. 1 and 2) relative to the homogeneous ''recolonized'' southern subantarctic populations.

Although a number of factors could potentially explain the apparent LGM extinction of bull kelp in the subantarctic, sea ice scouring remains the most plausible. Low temperatures alone cannot account for its LGM extinction in the subantarctic. Although *D. antarctica* thrives in the comparatively warm waters of Gough Island (≈12 °C), northern NZ (up to 22 °C), and Chile (up to about 16 °C), the species also currently flourishes in remarkably cold waters, persisting in ice-free areas of partially glaciated Heard Island (16) and South Georgia (20), where water temperatures are near freezing (<2 °C). Additionally, although it might be suggested that the lowered LGM coastlines in some sandy regions (e.g., the Falkland Islands) lacked suitable rocky shore habitat for *D. antarctica*, this explanation cannot apply to steep volcanic (e.g., Marion, Crozet) and tectonic (Macquarie) islands, which must have offered abundant rocky habitat during glacial periods. Finally, although a few subantarctic islands (South Georgia, Kerguelen) were extensively glaciated during the LGM, most (Macquarie, Falkland, Gough, Crozet, Campbell) had relatively scant terrestrial ice cover (29, 30). In contrast to the above explanations, ice scour has been observed to eliminate intertidal and shallow water benthos in the Southern Ocean (8, 9, 20), and the presence/absence of *D. antarctica* has even been suggested as an indicator of contemporary ice scour (20).

Ice Scour in the Subantarctic During the LGM. Credible, data-rich estimates of the extent of sea ice in the Southern Hemisphere during the LGM have existed for only a few decades [reviewed by Armand and Leventer (10) and Gersonde *et al.* (13)] and are largely based on ice-indicator diatoms from dated sediment cores (13, 32–34). These analyses typically differ in their estimates of LGM winter sea ice, often by several degrees of latitude. Gersonde *et al.* (13)

synthesized these datasets to generate new estimates of LGM sea ice (Fig. 3) but acknowledged that the analyses lacked data for several large areas of the Southern Ocean. In particular, the edge of the LGM sea ice zone (region of 15% ice cover) is poorly constrained for many regions. In the Indian Ocean sector, for example, a single data point (indicating 2.6% ice concentration) constrains the estimated LGM ice edge to the south of Crozet and Marion Islands. Similarly, the Macquarie Island and Falkland Island regions lack adequate data coverage (Fig. 3). On the basis of our genetic data for *D. antarctica*, we suggest it is premature to discount significant LGM sea ice at such subantarctic localities.

Southern Ocean marine ecosystems are heavily influenced by the Antarctic Polar Front (APF), a circumpolar oceanographic and biogeographic boundary that separates biologically diverse cool-temperate communities from species-poor, cold-water communities (35). Today, the winter sea ice edge roughly coincides with the APF (36). Although there is some debate as to whether the APF itself, which is strongly linked to bathymetric features, shifted northward during the LGM, there is little doubt that the surface isotherm separating cold polar water from warmer, saltier, "subantarctic" water lay considerably further north than at present (36), probably on or about the estimated LGM 4 °C isotherm (13); indeed, Gersonde *et al*. (13) mark this line as the "LGM APF" (Fig. 3). The 4° isotherm was situated north of most of the "recolonized" (genetically homogeneous) subantarctic kelp populations, whereas the genetically divergent "refugial" subantarctic populations (e.g., Campbell, Auckland, Snares) were all located to the north of this isotherm (Fig. 3). Based on this observation, we suggest that the 4° isotherm (putatively the LGM equivalent of the modern APF) may represent a proxy for the extent of LGM sea ice scour.

Drifting on Shifting Seas: Kelp Dispersal via Rafting. Rafting of buoyant kelp is likely to be an important ecological phenomenon, facilitating dispersal both of the kelp itself and of associated invertebrate fauna (22, 23, 37–40). Some robust species of brown (phaeophycean) kelp can potentially remain alive and reproductively viable for long periods adrift at sea (e.g., *Macrocystis*: refs. 41 and 42; *Hormosira*: ref. 43). The Antarctic Circumpolar Current (ACC; Fig. 1), a surface current driven by strong westerly winds circling Antarctica, is thought to facilitate dispersal of many Southern Ocean marine taxa (24). The sheer numbers of detached *D. antarctica* rafts in the Southern Ocean, estimated to be in the region of 70 million at any time (21), make effective eastward dispersal via rafting in the ACC a very real possibility for this species (24). In addition, bull kelp in the subantarctic appears to have an extended period of fertility: although *D. antarctica* in NZ is known to release gametes for 3 to 5 months per year (44, 45), plants on Macquarie Island remain fertile for more than 7 months of the year (16), and similarly long reproductive phases appear to occur on Marion Island, Gough Island, the Antipodes Islands, and South Georgia (45). *D. antarctica* reproduces in winter months, when water temperatures are coldest, and it is possible that the species' extended period of fertility in the subantarctic is simply due to lower overall water temperatures, permitting longer optimal reproductive conditions; such a characteristic might well increase the chances of successful gamete production in rafting plants, and thereby enhance colonization ability, at high latitudes.

Although some macroalgal species owe their invasion success to anthropogenic translocation (46), *D. antarctica* has intrinsically high dispersal potential because of its rafting ability. Given this propensity to disperse, it seems intriguing that *D. antarctica* exhibits such strong phylogeographic structure along the temperate coasts of NZ and Chile. Disturbances have been shown to facilitate colonization by dispersive weed species (47), and we speculate that *D. antarctica* is effectively one such opportunistic "weed," whereby rafting plants permit rapid colonization of disturbed or vacant habitats but have little genetic impact on intact kelp assemblages. Specifically, we predict that in dense stands of *D. antarctica*, eggs from resident female plants may be almost immediately fertilized by spermatozoa from neighboring male plants, swamping the comparatively small number of immigrant gametes provided by any rafted individuals. The likely role of density blocking by leading-edge migrants of recolonizing populations has been well documented in Northern Hemisphere terrestrial taxa (1), and it could clearly apply to marine systems as well. Future research using microsatellite DNA markers will assess fine-scale genetic connectivity among *D. antarctica* populations.

Materials and Methods

Sites and Sample Collection. Tissue samples from fresh frond tips of *D. antarctica* were collected from 45 localities: 11 from the NZ mainland, 7 from the Chilean mainland, and the remainder from subantarctic islands (Table S1). Wherever possible, several sites were sampled per region (e.g., multiple localities across an island; Fig. 1 and Table S1). Samples were collected by hand from plants growing in the intertidal to subtidal, and an effort was made to sample plants from a range of morphologies and tidal depths at each site.

DNA Sequencing and Analyses. All DNA extractions and PCRs were carried out per Fraser *et al*. (25) by using the primers GazF1 and GazR1 (48) to amplify an ≈700-bp region of COI, and the primers KL2 and KL8 (49) for an ≈1,000-bp region of *rbc*L. Phylogenetic relationships were determined by maximum-likelihood (ML) and Bayesian analyses and included outgroup sequences from *Durvillaea willana* (Brighton, South Island, NZ) and *Durvillaea potatorum* (Tathra, Australia), as well as published sequences of *Fucus* (GenBank accession nos.: AY494079, *Fucus vesiculosus* for COI; and AF195515, *Fucus gardneri* for *rbc*L). ML analyses were performed with an HKY + I + G model for COI (base frequencies: $A = 0.2182$, $C = 0.1586$, $G = 0.1884$, and $T = 0.4348$; proportion of invariable sites = 0.6785) and a TrN + I + G model for *rbc*L (base frequencies: $A = 0.2974$, $C = 0.1592$, $G = 0.2140$, and $T = 0.3294$; rate matrix: A–C = 1.000, A–G = 4.0318, A–T = 1.000, C–G = 1.000, C–T = 10.5062, and G–T = 1.000; proportion of invariable sites = 0.7802) as selected by the AIC (COI) and the (h)LRT (*rbc*L) of Modeltest 3.06 (50). Relative levels of phylogenetic support for each node were assessed by bootstrapping (51), with heuristic analysis of 1,000 replicate datasets. Bayesian posterior probability (PP) values were calculated by using MRBAYES 3.1.2 (52) with separate substitution models for COI and *rbc*L determined by Modeltest. Markov Chain Monte Carlo searches were performed, each with 4 chains of 5 million generations, and trees were sampled every 100 generations. The first 10,000 trees sampled were discarded as ''burn-in,'' as determined by stationarity of lnL and other parameters assessed by using Tracer v1.4 (53), and the remaining trees were used to calculate a consensus topology and posterior probability values. Network analysis was performed by using TCS 1.21 (54) to explore relationships among closely related subantarctic haplotypes. Historic population expansions were assessed in the subantarctic clade by the Fu neutrality test (27) and mismatch distribution analysis (26) using Arlequin version 2.0 (55). The fit of the observed to the expected distribution under the sudden expansion model was tested by using bootstrapping. We are presently unable to accurately estimate the time since population expansion because of the lack of robust mutation rate estimates for marine heterokont algal mtDNA and cpDNA (7). Although some ancient calibration points exist for diatom taxa (see references in ref. 7), time-dependency issues preclude extrapolation of these calibrations to recent (e.g., Holocene or late Pleistocene) biological events (56, 57).

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