Glacial oceanographic contrasts explain phylogeography of Australian bull kelp

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Abstract
The evolutionary effects of Southern Hemisphere Pleistocene oceanographic conditions — marked by fluctuations in sea levels and water temperatures, and redirected currents — are poorly understood. The southeastern tip of Australia presents an intriguing model system for studying the biological impacts of palaeoceanography. In particular, contrasting oceanographic conditions that existed on eastern vs. western sides of the Bassian Isthmus during Pleistocene glacial periods allow for natural comparisons between putative refugial vs. re-invading populations. Whereas many western Tasmanian marine taxa were likely eliminated by cold subantarctic water during the last glacial period, eastern Tasmanian populations would have persisted in relatively warm temperatures mediated by the ongoing influence of the East Australian Current (EAC). Here we test for the effects of contrasting palaeoceanographic conditions on endemic bull kelp, Durvillaea potatorum, using DNA sequence analysis (COI; rbcL) of more than 100 individuals from 14 localities in southeastern Australia. Phylogenetic reconstructions reveal a deep (maximum divergence 4.7%) genetic split within D. potatorum, corresponding to the ‘eastern’ and ‘western’ geographical regions delimited by the Bassian Isthmus, a vicariant barrier during low Pleistocene sea levels. Concordant with the western region’s cold glacial conditions, samples from western Tasmania and western Victoria are genetically monomorphic, suggesting postglacial expansion from a mainland refugium. Eastern samples, in contrast, comprise distinct regional haplogroups, suggesting the species persisted in eastern Tasmania throughout recent glacial periods. The deep east–west divergence seems consistent with earlier reports of morphological differences between ‘western’ and ‘eastern’ D. potatorum, and it seems likely that these forms represent reproductively isolated species.

Keywords: cytochrome c oxidase I, Durvillaea potatorum, palaeoceanography, phylogeography, RuBisCo

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Introduction
The evolutionary and biogeographical significance of glacial periods is well recognized, particularly for terrestrial systems affected by ice sheets (reviewed by Hewitt 1996, 2000; Provan & Bennett 2008). In the marine realm, fluctuation of sea levels, water temperatures and sea ice driven by glacial cycles are also likely to have had a strong influence on species distributions and genetic connectivity (Maggs et al. 2008). For instance, lowered sea levels during glacial maxima can lead to the emergence of land bridges which, while facilitating dispersal of terrestrial biota (e.g. Tiffney 1985; reviews by Wen 1999; Sanmartin et al. 2001), effectively divide marine populations. Scientists have speculated on such biotic effects for centuries; Darwin (1872), wrote ‘a narrow isthmus now separates two marine faunas; submerge it, or let it formerly have been submerged, and the two faunas will now blend ... or may formerly have blended.’ The Sunda and Sahul shelves, for example, separated many Pacific and Indian Ocean marine taxa at Pleistocene sea level lowstands, leading to vicariant
divergence (e.g. Chenoweth et al. 1998; Nelson et al. 2000; Reid et al. 2006), while similar marine biogeographical disjunctions have been noted on either side of the Baja California Peninsula (e.g. Bernardi et al. 2003). In Australia, the Bassian Isthmus — a land bridge that periodically connects Tasmania to the mainland as sea levels drop during glaciations (Lambeck & Chappell 2001) (Fig. 1) — has frequently been suggested as a potential vicariant barrier to gene flow among temperate marine taxa (Dartnall 1974). Indeed, recent phylogeographical analyses of several marine species (e.g. cirrhitoid fish: Burridge 2000; Patiriella sea stars: Waters et al. 2004; Catostylus jellyfish: Dawson 2005; Nerita gastropods: Waters et al. 2005; Spencer et al. 2007; Waters 2008; Catomerus barnacles: York et al. 2008) in southeastern Australia have revealed distinct geographical partitioning into eastern vs. western clades, generally consistent with the vicariant hypothesis of allopatric divergence during glacial periods.

A less-explored aspect of climate change is the effect of altered oceanography (specifically currents) on the phylogeography of modern marine taxa. Pleistocene glacial periods were characterized by both substantially reduced water temperatures and redirected currents (Wells & Okada 1996; Herbert et al. 2001), but although some authors have suggested that ancient changes in major Northern Hemisphere current systems may partially explain modern phylogeographical structuring (e.g. Muss et al. 2001; Wares 2001; Marko 2004), few studies, particularly in the Southern Hemisphere, have directly assessed the impacts of such palaeoceanographic features. Around southeastern Australia, the subtropical convergence (STC), a boundary zone between temperate and subantarctic waters, is believed to have abutted southern Tasmania and extended along its western coast during recent glacial maxima, blocking the eastward flow of the warm Leeuwin/Zeehan current (Wells & Okada 1996; McGowran et al. 1997; Nürnberg et al. 2004) (Fig. 1). The absence of the Zeehan Current from southern Tasmania at glacial maxima would have strengthened east-west isolation by limiting dispersal, and the colder waters on the eastern coast may have driven temperate marine organisms to considerably higher latitudes; in contrast, the warm East Australian Current (EAC) is known to have extended its southward flow along eastern Tasmania during glacial periods (Nürnberg et al. 2004), potentially maintaining temperate marine conditions on the eastern, but not western, coasts of Tasmania.
Table 1  Morphological and ecological differences between ‘eastern’ and ‘western’ forms of *Durvillaea potatorum* in southeastern Australia, after Cheshire *et al*. (1995)

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Western</th>
<th>Eastern</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary stipe length</td>
<td>generally &lt; 0.5 m</td>
<td>generally &lt; 0.5 m or &lt; 1.0 m</td>
</tr>
<tr>
<td>Primary stipe distally branched</td>
<td>never</td>
<td>infrequently</td>
</tr>
<tr>
<td>Secondary stipes on primary stipe</td>
<td>never</td>
<td>infrequently</td>
</tr>
<tr>
<td>Habitat</td>
<td>always subtidal, &lt; 10 m</td>
<td>infrequently intertidal, or subtidal &lt; 10 m</td>
</tr>
</tbody>
</table>

Here we present the first direct assessment of the expected phylogeographical effects of these contrasting glacial oceanographic conditions.

Australian bull kelp, *Durvillaea potatorum* (Labillardière), forms a dense band in the upper subtidal and intertidal of exposed rocky reefs from Robe in South Australia (Huisman 2000) to Tathra on the east coast of New South Wales (Millar 2007) (Fig. 1), and along the western and eastern shores of Tasmania. It grows abundantly on King Island, on the western sill of Bass Strait, but is rare on the Furneaux Island Group of the eastern sill (Hay 1994). *Durvillaea potatorum* is considered endemic to Australia (Cheshire *et al*. 1995); additional historical records reporting *D. potatorum* from the subantarctic Auckland Islands (cited in Papenfuss 1964) and from Constución in Chile (cited in Ramirez & Santelices 1991) are extremely dubious and require confirmation. In western Bass Strait, detached, beach-cast *D. potatorum* wrack is so abundant that a flourishing kelp-wrack harvesting industry for alginates operates on King Island (Kirkman & Kendrick 1997). *Durvillaea potatorum* is an unusually large macro-alga, with individuals commonly reaching several metres in length (Cheshire & Hallam 1988) and weighing over 40 kg (Hay 1994); an early botanist described it as ‘a plant which, when fully grown, is measured, not by inches, but by fathoms’ (Harvey 1863). Cheshire & Hallam (1989) noted morphological differences in individuals from eastern vs. western populations: those from the east (eastern coasts of Tasmania and New South Wales) were found to have some — albeit variable — characteristics (such as stipe length, habitat and position of secondary stipes) that differed from western specimens (southern and western coasts of Victoria, and King Island in Bass Strait) (Table 1). Like other members of its genus, *D. potatorum* is dioecious, with both female and male individuals, producing eggs and sperm, respectively. Although these gametes are released into the water column, and could theoretically disperse with currents, unfertilized eggs are unlikely to survive in a viable condition for more than a few days at sea (M. Clayton, Monash University, Melbourne, personal communication) and fertilized eggs are rapidly — within minutes — surrounded by adhesive secretions that effectively attach zygotes to the substrate (Clayton & Ashburner 1994). Dispersal via gametes or zygotes seems therefore unlikely to be successful over long distances, particularly where populations are patchy or separated by stretches of sandy coast or open ocean (Hidas *et al*. 2007). As *D. potatorum* is a solid-bladed, nonbuoyant member of its genus (Hay 1994), adults are also unlikely to disperse far once detached. A kelp with such limited potential for dispersal would be expected to show strong phylogeographical differentiation and this feature, combined with the distribution of *D. potatorum* in Australia around Bass Strait, make it well suited for studies of the effects of Pleistocene vicariance and oceanography. Here we examine phylogeographical structure in Australian bull kelp to test the hypotheses that: (i) Pleistocene emergence of the Bassian Isthmus separated this species into distinct eastern and western lineages, and (ii) altered oceanography of Tasmania during recent glacial periods, with subantarctic water impacting the western (but not eastern) coasts, will be reflected in contrasting phylogeographical patterns consistent with elimination of the western and persistence of the eastern populations.

**Materials and methods**

**Site selection and sample collection**

Tissue samples were collected by hand, at low tide, from the distal ends of fronds of attached *Durvillaea potatorum* growing in the intertidal or shallow subtidal at 14 sites across the species’ range (Table 2). In some cases, where attached individuals were not obtainable due to extreme conditions, samples were taken from fresh beach-cast wrack (listed in Table 2). At one site — King George III Reef — all samples were taken from attached plants in the subtidal, using SCUBA, at between 10 and 12 m depths. Sites were categorized on the basis of geography as either eastern or western, and either mainland or Tasmania (Table 2).

**DNA extraction, sequencing and phylogenetic analyses**

Tissue preservation, DNA extractions and polymerase chain reactions were carried out as described in Fraser *et al*. (2009a), with a 629-bp portion of the mitochondrial gene cytochrome c oxidase I (COI) amplified using primers...
GazF1 and GazRI (Saunders 2005), and a 886-bp region of the chloroplast gene RuBiCO (rbcL) amplified using primers KL2 and KL8 (Lane et al. 2006). Phylogenies for each data set were built by maximum likelihood (ML) and Bayesian analyses, and included outgroup sequences from *Durvillaea willana* (South Island, New Zealand; GenBank accessions: COI: EU918569; rbcL: EU918578) and *Durvillaea antarctica* (Falkland Islands; GenBank accessions: COI: FJ550107; rbcL: FJ550124). ML analyses were performed with a HKY + G model for both COI (base frequencies A = 0.2182, C = 0.1726, G = 0.1895, T = 0.4197; Tratio = 3.7086; gamma shape parameter = 0.0144) and rbcL (base frequencies A = 0.2922, C = 0.1667, G = 0.2168, T = 0.3243; Tratio = 2.9827; gamma shape parameter = 0.0081), that was selected using the hLRT of ModelTest 3.06 (Posada & Crandall 1998). The robustness of the ML topology was estimated by bootstrapping (Felsenstein 1985), with heuristic analysis of 1000 replicate data sets (Figs 2 and 3). Bayesian posterior probability (PP) values, also indicated on the ML phylogenies (Figs 2 and 3), were calculated using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Markov chain Monte Carlo (MCMC) searches, each with four chains of 5 000 000 generations and trees sampled each 100 generations, were carried out. The first 10 000 trees sampled were discarded as ‘burn-in’, based on the stationarity of ln L as assessed using Tracer version 1.4 (Rambaut & Drummond 2007); a consensus topology and posterior probability values were calculated with the remaining trees. An unrooted statistical parsimony network was reconstructed using tcs 1.21 (Clement et al. 2000) in order to examine relationships among ‘eastern’ haplotypes for COI — these analyses were not performed on rbcL data due to limited diversity (only two haplotypes in each major clade). Analysis of the precise expansion time of the ‘western’ clade was not possible, as robust mutation rate estimates have not yet been developed for the Phaeophyceae (Hoarau et al. 2007). All unique DNA sequences obtained during this study were deposited with GenBank (Accession nos FJ872919–FJ873102).

Results

DNA sequencing of 107 *Durvillaea potatorum* specimens yielded eight distinct haplotypes for COI, whereas 77 rbcL sequences yielded a total of four haplotypes. Thirty variable sites were found over the 629-bp fragment amplified for COI (4.8% of sites), with approximately one-third of the inferred changes being transversions. For rbcL, seven variable sites were found across the 886-bp fragment (0.8%), with all but two sites showing transitional mutations. In both markers, variable sites occurred at the third codon position, with the exception of one inferred transitional mutation in COI.

ML and Bayesian phylogenetic analyses yielded trees with consistent topologies for each genetic data set. Specifically, both COI (Fig. 2), and rbcL (Fig. 3) analyses revealed a deep and strongly supported genetic split within *D. potatorum* (uncorrected distances up to 4.7% for COI and up to 0.9% for rbcL; Bayesian PP values of 1.00), largely corresponding to ‘eastern’ and ‘western’ geographical regions (Figs 2 and 3). Although both ‘eastern’ and ‘western’ haplotypes were found along the east coast of Tasmania, the presence of all ‘eastern’ haplotypes at only eastern geographical locations,

<table>
<thead>
<tr>
<th>Site name</th>
<th>Site locality</th>
<th>Sample</th>
<th>No. of samples sequenced</th>
<th>Haplotype/s COI</th>
<th>Haplotype/s rbcL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Port Fairy</td>
<td>Western-mainland</td>
<td>a</td>
<td>5</td>
<td>C-I</td>
<td>R-I</td>
</tr>
<tr>
<td>Warrnambool</td>
<td>Western-mainland</td>
<td>a</td>
<td>7</td>
<td>C-I</td>
<td>R-I</td>
</tr>
<tr>
<td>Peterborough</td>
<td>Western-mainland</td>
<td>a</td>
<td>6</td>
<td>C-I</td>
<td>R-I</td>
</tr>
<tr>
<td>Phillip Island</td>
<td>Western-mainland</td>
<td>a</td>
<td>9</td>
<td>C-I</td>
<td>R-I</td>
</tr>
<tr>
<td>Green Point</td>
<td>Western-Tasmania</td>
<td>w</td>
<td>9</td>
<td>C-I</td>
<td>R-I</td>
</tr>
<tr>
<td>Couta Rocks</td>
<td>Western-Tasmania</td>
<td>w</td>
<td>10</td>
<td>C-I</td>
<td>R-I</td>
</tr>
<tr>
<td>KGIII Reef</td>
<td>Eastern-Tasmania</td>
<td>a</td>
<td>7</td>
<td>C-IV, C-V</td>
<td>R-III</td>
</tr>
<tr>
<td>Bruny Island</td>
<td>Eastern-Tasmania</td>
<td>w, a</td>
<td>10</td>
<td>C-I, C-IV</td>
<td>R-I, R-III</td>
</tr>
<tr>
<td>Pirates Bay</td>
<td>Eastern-Tasmania</td>
<td>a</td>
<td>10</td>
<td>C-II, C-III</td>
<td>R-II, R-III</td>
</tr>
<tr>
<td>Bicheno</td>
<td>Eastern-Tasmania</td>
<td>w</td>
<td>5</td>
<td>C-II, C-III</td>
<td>R-II, R-III</td>
</tr>
<tr>
<td>Binalong Bay</td>
<td>Eastern-Tasmania</td>
<td>a</td>
<td>8</td>
<td>C-II, C-III</td>
<td>R-II, R-III</td>
</tr>
<tr>
<td>The Gardens</td>
<td>Eastern-Tasmania</td>
<td>a</td>
<td>7</td>
<td>C-II, C-III</td>
<td>R-II, R-III</td>
</tr>
<tr>
<td>Gabo Island</td>
<td>Eastern-Mainland</td>
<td>a</td>
<td>6</td>
<td>C-VI, C-VII, C-VIII</td>
<td>R-IV</td>
</tr>
<tr>
<td>Tathra</td>
<td>Eastern-Mainland</td>
<td>a</td>
<td>8</td>
<td>C-VI, C-VIII</td>
<td>R-IV</td>
</tr>
<tr>
<td><strong>TOTAL sequenced</strong></td>
<td></td>
<td></td>
<td><strong>107</strong></td>
<td></td>
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<tr>
<td><strong>TOTAL sequenced</strong></td>
<td></td>
<td></td>
<td><strong>77</strong></td>
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<td></td>
</tr>
</tbody>
</table>
and the broad geographical range of ‘western’ haplotypes across western coasts, indicates a general east–west split despite some geographical overlap. The more informative COI data set also revealed considerable diversity and phylogeographical structuring within the ‘eastern’ clade, which comprised a total of six haplotypes (uncorrected distances 0.2–0.8%). Three were restricted to the east coast of Tasmania (haplotypes C-III–C-V), and three were found only at eastern mainland sites (haplotypes C-VI–C-VIII) (Fig. 2). Although rbcL data showed relatively little overall diversity, the genetic division between eastern mainland and eastern Tasmania was still apparent, with a single ‘eastern’ haplotype (R-III) across Tasmanian sites, and another (R-IV) shared by Tathra and Gabo Island samples (Fig. 3). Strong phylogenetic concordance was found between mitochondrial and chloroplast markers, with all specimens allocated to the equivalent clade (‘eastern’ or ‘western’) for each marker.

The ‘western’ clade in both COI and rbcL data sets each yielded just two haplotypes, one of which was particularly geographically widespread, extending from Port Fairy on Australia’s mainland to Bruny Island in southern Tasmania (C-I, Fig. 2 and R-I, Fig. 3). For rbcL, the widespread haplotype R-I (which differs from R-II by merely one transversion) also occurred at Bicheno in a single sample, although the same individual yielded the less common ‘western’ haplotype for COI (C-II). Notably, *D. potatorum* populations along the western coasts of both the mainland and Tasmania were completely homogeneous for both markers, showing no evidence of genetic division across Bass Strait. The ‘western’ clade also extended into the eastern coast of Tasmania, with haplotypes C-II and R-II found from Pirates Bay northward to The Gardens (Figs 2 and 3).

Analysis of the relationships of COI haplotypes resulted in two networks — corresponding to the ‘eastern’ and the ‘western’ clades — that could not be parsimoniously connected at the 95% confidence limit. The ‘western’ network contained only two COI haplotypes, separated by one mutational step, and was therefore largely uninformative. The ‘eastern’ network (Fig. 4) showed two potentially ancestral, central haplotypes, one from the mainland (C-VI) haplogroup and one from Tasmania (C-IV). The four remaining haplotypes radiated from an ancestral
haplotype via a single mutational step. The ‘ancestral’ haplotypes — and the mainland vs. Tasmania groups — were themselves separated by two mutational steps, linked by a hypothetical undetected haplotype.

**Discussion**

**Ancient vicariant influences**

The substantial phylogenetic split between ‘eastern’ and ‘western’ clades of *Durvillaea potatorum* (Figs 2 and 3) supports the hypothesis that past emergence of the Bassian Isthmus has promoted vicariant divergence in this poorly dispersive shallow-water marine macro-alga (hypothesis i). Although contemporary longitudinal variation in water temperature, salinity and wave action might also be suggested as contributing causes, the presence of both clades across a wide geographical area and latitudinal range, as well as their co-occurrence along the east coast of Tasmania, would appear to refute a causal role for such abiotic factors in generating the deep phylogeographical structuring observed for *D. potatorum*. This study therefore emphasizes the important role of vicariance in driving diversification of Australia’s marine temperate biota (e.g., Dartnall 1974; Burridge 2000; Waters et al. 2005; York et al. 2008). Indeed, Waters (2008) proposed that the Bassian Isthmus had likely driven cladogenesis — with cryptic eastern and western lineages — in many components of southern Australia’s littoral and shallow sublittoral communities.

The suggestion that southern Australia’s major marine biogeographical break occurs specifically in the vicinity of Wilsons Promontory in southern Victoria (e.g. Dawson 2005; Waters 2008) is not rejected by our findings, with the Phillip Island site immediately to the west of this feature fixed for the common ‘western’ haplotype. Clearly, however, finer-scale research is required to confirm the precise location of the phylogeographical disjunction, although the patchiness of *D. potatorum* would limit the possibility of geographically intensive sampling. Wilsons Promontory (Fig. 1) lies at the final point of contact between Tasmania and mainland Australia during submerging of the Bassian Isthmus; it represents the site of reunion of western and eastern mainland geminate taxa as sea levels rose and is therefore a natural biogeographical break. A long stretch of uninhabitable sandy coast to the immediate east of Wilsons
Promontory (Ninety Mile Beach, Fig. 1) presumably inhibits genetic exchange (or dispersal) across this region (Hidas et al. 2007; York et al. 2008; Ayre et al. 2009), enhancing isolation of eastern vs. western mainland populations. An equivalent point cannot be identified in Tasmania, as *D. potatorum* does not grow along the relatively sheltered northern coast.

**Ancient oceanographic influences**

The broad genetic homogeneity of the ‘western’ *D. potatorum*, with one particularly widespread haplotype ranging from Port Fairy (the westernmost site sampled) to Bruny Island in southeastern Tasmania (Figs 2 and 3), contrasts with the relatively high diversity found in the ‘eastern’ clade for COI. The genetic homogeneity observed across western populations is unlikely to be due to anthropogenic translocation (e.g. Voisin et al. 2005), as the range of *D. potatorum* has apparently changed little since early records (see Harvey 1863). Patterns of low-latitude genetic diversity vs. high-latitude homogeneity are frequently interpreted as evidence of postglacial recolonization in the Northern Hemisphere, with rapid range expansion by leading-edge migrants (Hewitt 1996, 2000; Maggs et al. 2008; Provan & Bennett 2008). Similarly, extensive sea ice during the last glacial maximum (LGM) has been linked to patterns of high-latitude homogeneity in *Durvillaea antarctica* in the Southern Hemisphere (Fraser et al. 2009b). The monomorphism observed here in western *D. potatorum* most probably reflects recent recolonization following postglacial retraction of the subtropical convergence and cold waters that affected western Tasmania during the last glacial period (Fig. 1; Wells & Okada 1996; McGowan et al. 1997; Nürnberg et al. 2004) (hypothesis ii). This postglacial expansion might have been facilitated by the strong Zeehan Current (a continuation of the Leeuwin Current; Ridgway & Condie 2004) that flows east from the southern coast of mainland Australia to southern Tasmania during interglacial periods (Fig. 1). In contrast, the southern extension of the warm EAC during glaciations (Nürnberg et al. 2004) presumably allowed temperate marine biota — such as *D. potatorum* — to persist along the eastern coasts of Tasmania.

If the genetic homogeneity of western *D. potatorum* does indeed reflect severe glacial population decline and subsequent postglacial range expansion, the divergence observed between mainland and Tasmanian representatives of the ‘eastern’ clade almost certainly predates the LGM. This pre-LGM time frame of molecular divergence is also supported by the findings of Fraser et al. (2009b), who reported distinct *D. antarctica* haplotypes from ‘refugial’ islands in the New Zealand subantarctic. Despite the absence of reliable mutation rate estimates for brown algae (Hoarau et al. 2007) precluding precise dating of the time of *D. potatorum* recolonization, the near-absolute genetic homogeneity of the ‘western’ samples certainly seems consistent with a post-LGM timeframe. For the ‘eastern’ clade, by contrast, the presence of two apparently ‘ancestral’ haplotypes (Fig. 4), one on the mainland (found at both Tathra and Gabo Island) and one in southern Tasmania, suggests persistence of multiple eastern populations through the last glacial period, consistent with the warming influence of the EAC (hypothesis ii).

To date, few marine phylogeographical studies have directly assessed the importance of palaeoceanographic features (but see Benzie 1999; Wares 2001). Although some previous studies have hinted at their role (e.g. Muss et al. 2001; Marko 2004), the current analysis represents, to our knowledge, one of the first studies to provide compelling evidence for lasting biological effects of Pleistocene oceanographic conditions.

**Ecology and biology of *D. potatorum***

Although this study assesses only genetic variation, a previous phylogenetic analysis of morphological and ecological data (Cheshire & Hallam 1989; Cheshire et al. 1995) has suggested a similar east–west split within *D. potatorum* based on morphological and ecological characteristics. The character states distinguishing these morphotypes were,
however, somewhat variable (Table 1). Nonetheless, when combined with our phylogeographical results, the differentiation between ‘eastern’ and ‘western’ clades seems likely to have a morphological, as well as genetic, basis. Interestingly, several of the character states listed by Cheshire et al. (1995) as ‘infrequent’ in eastern populations, compared to entirely absent in western populations (Table 1), were indeed observed in our ‘eastern’ samples, such as secondary stipes emerging from the primary stipe (Fig. 5) and stipes longer than 0.5 m. Perhaps the apparent variability of these characteristics reflects the simultaneous presence of both ‘eastern’ and ‘western’ genetic clades along the east coast of Tasmania. If these clades correspond to biologically distinct taxa, Cheshire & Hallam (1989) are likely to have measured both sympatric forms in eastern Tasmania. Further morphological and physiological work, combined with genetic identification, is clearly required to determine whether these two clades represent separate species, although their apparent morphological distinctness, and their cohabitation along eastern Tasmania, certainly suggests that they form separate taxonomic entities. Although both clades are clearly sympatric in eastern Tasmania, it is possible that their ecological characteristic may differ somewhat, as noted for cryptic Durvillaea taxa in New Zealand (Fraser et al., 2009a). Cheshire & Hallam (1989) claimed that the ‘western’ form of D. potatorum is never intertidal, compared to the ‘eastern’ form which is occasionally intertidal. In contrast, we observed some ‘western’ populations in northwestern Tasmania growing intertidally (J.M. Waters, personal observation), as well as intertidal plants at Tathra (‘eastern’ clade, C.I. Fraser, personal observation). Nonetheless, the dominance of ‘western’ individuals in our eastern Tasmanian collections, combined with the absence of any ‘western’ haplotypes from the subtidally collected samples at King George III Reef (southern Tasmania), suggests that the ‘eastern’ clade may grow lower in the littoral and sublittoral zones. Future studies will assess the genetic, morphological, ecological, and taxonomical characteristics of D. potatorum to rigorously test the hypothesis that it comprises two biologically distinct taxa. Ideally, future genetic analyses should also include a suite of variable markers (e.g. microsatellite loci) to further assess levels of gene flow among D. potatorum populations.

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References


C.F. is a postgraduate student at the University of Otago. Her interests include the ecology and phylogeography of Southern Ocean marine biota, with current research focusing on southern bull kelps (Durvillaea). She is particularly interested in applying molecular techniques to broad-scale questions of dispersal and climate change. H.S. is Professor of Zoology at the University of Otago and a Principal Investigator with the Allan Wilson Centre for Molecular Ecology & Evolution. His research covers aspects of evolutionary biology, from theoretical population genetics and phenotypic plasticity to the phylogenetics of birds and the biogeography of molluscs, as well as the history of genetics. J.W. is an Associate Professor of Zoology at the University of Otago. His research focuses on the phylogeography and evolution of Southern Hemisphere marine and freshwater biota. Current projects are centered on the use of freshwater vicariant events to calibrate molecular clocks, and the importance of macroalgae as facilitators for oceanic rafting.