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GENETIC AND MORPHOLOGICAL ANALYSES OF THE SOUTHERN BULL KELP *DURVILLAEA ANTARCTICA* (PHAEOPHYCEAE: DURVILLAEALES) IN NEW ZEALAND REVEAL CRYPTIC SPECIES[1]

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Many macroalgae exhibit considerable intraspecific morphological variation, but whether such variation reflects phenotypic plasticity or underlying genetic differences is often poorly understood. We quantified both morphological and genetic variation of 96 plants from seven field sites across eastern South Island, New Zealand, to assess genetic differences between morphotypes of the southern bull kelp *Durvillaea antarctica* (Cham.) Har. Consistent DNA sequence differentiation across mitochondrial, plastid, and nuclear loci was correlated with two broadly sympatric morphotypes: "cape" and "thonged." These ecologically, morphologically, and genetically distinct bull-kelp lineages were previously considered to be environmentally determined phenotypes with no underlying genetic basis. Interestingly, the sheltered "cape" lineage appears essentially genetically uniform across its South Island range, whereas the exposed "thonged" lineage exhibits marked phylogeographic structure across its range. Results suggest that *D. antarctica* in New Zealand comprises two reproductively isolated species.

Key index words: **18S; bull kelp; COI; cryptic species; *Durvillaea antarctica*; Phaeophyceae; *rbc*L**

Abbreviations: **bp, base pair; COI, cytochrome c oxidase I gene; dNTP, deoxyribonucleotide triphosphate; ML, maximum likelihood; mtDNA, mitochondrial DNA; nMDS, nonmetric multidimensional scaling; *rbc*L, RUBISCO LSU**

Morphological variation within species of macroalgae is well documented, particularly in association with physical gradients such as changes in wave exposure (see reviews by Dayton 1985, Hurd 2000). Whether this variation is primarily due to phenotypic plasticity or genetic differentiation is, in most cases, yet to be convincingly established, although its basis is clearly vital to our understanding of algal evolutionary mechanisms and systematics. Many studies of morphological variation in brown algae (Phaeophyceae) have included experiments such as transplantation of morphotypes among distinct habitats (e.g., for *Laminaria digitata:* Sundene 1964; and more recently, for *Eisenia arborea*: Roberson and Coyer 2004), and morphometric comparisons of populations in sites of varying exposure (e.g., South and Hay 1979, Roberson and Coyer 2004). Studies that also incorporate genetic data are increasingly being used to assess variation between environmentally correlated algal morphotypes, and some are revealing genetically isolated clades within what have previously been considered single species, for example, windward versus leeward forms of *Pelagophycus porra* (Miller et al. 2000) and low-flow versus high-flow forms of *Eisenia arboria* (Roberson and Coyer 2004). The evolutionary implications of such genetic differentiations are profound, as they may represent neo-nascent species, with divergence potentially being driven by small-scale environmental heterogeneities or past geographic isolation. Cladistic studies of the Phaeophyceae have effectively only been possible since the application of genetic techniques to the field in the early 1990s, as prior classifications relied largely on morphological or life-history characteristics that were often patchily known among different groups and whose evolutionary statuses (derived or ancestral) were often purely speculative (de Rousseau et al. 2007). With molecular techniques revolutionizing our approach to, and knowledge of, phaeophycean phylogenetics

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(see review in de Rousseau et al. 2007), more studies examining fine-scale genetic variation and local adaptation at high taxonomic resolutions are clearly warranted.

The buoyant southern bull kelp *Durvillaea antarctica* has an extensive geographic range in the Southern Hemisphere, including New Zealand, Chile, parts of Argentina, and most subantarctic islands (Hay 1979). This distribution is much wider than that of any congeneric solid-bladed taxa (e.g., *Durvillaea potatorum* in Australia and *Durvillaea willana* in southern New Zealand). The particularly wide range of *D. antarctica* seems likely to reflect its uniquely honeycombed, buoyant blades that permit it to drift long distances (Skottsberg 1941, Hay 1994). In New Zealand, *D. antarctica* is distributed from Three Kings Islands, at latitude 34°S, southward to subantarctic Campbell Island, at 52°S. In the north, the kelp is confined to the most wave-exposed rocky shores, while farther south, in addition to exposed shores, *D. antarctica* grows in relatively sheltered habitats. These include broad, flat reefs, where much wave energy is expended inshore of the kelp zone, and inside some harbors. South and Hay (1979) showed that, in New Zealand's South Island, the morphology of *D. antarctica* varies according to physical environment, with a narrow-bladed (''thonged'') morphotype observed in wave-exposed sites, and a wider-bladed (''cape'') form observed in comparatively sheltered locations (Fig. 1). These authors conducted a detailed morphological comparison of the two morphotypes throughout New Zealand and concluded that there was a trend for blades to become wider and less divided, and for holdfasts and stipes to become proportionally smaller, with diminishing wave action, but that the forms were probably phenotypic variants of the same species, *D. antarctica*. They noted that the wide-bladed (''cape'') form has a relatively limited geographic distribution (Fig. 2, inset), being apparently restricted to South Island and Stewart Island. We have also observed both forms growing together on the Auckland Islands, part of the New Zealand subantarctic, under differing degrees of wave exposure (C. Fraser, personal observation) (Fig. 1).

Durvillaea shows remarkable morphological variation both within and among species, and this has, in the past, created problems for taxonomists; the genus has a history of multiple synonymizations and splits, and it is only with the advent of molecular techniques that the basis of these could be assessed by anything other than morphological or life-history traits. As long ago as 1854, Areschoug (1854) suggested that several ''species'' of *Durvillaea* were actually different forms reflecting local differences in habitat and wave action. In New Zealand, the two main morphotypes of *Durvillaea antarctica* have been recognized for centuries; indigenous Maori traditionally cultivated and used hollowed-out ''cape'' form plants as cooking and food-storage vessels, while the ''thonged'' form was used more rarely and for entirely different purposes (N. G. Metzger, personal communication). It was not until South and Hay's (1979) study, however, that an attempt was made to assess the status of these morphotypes. *D. antarctica* does not readily lend itself to

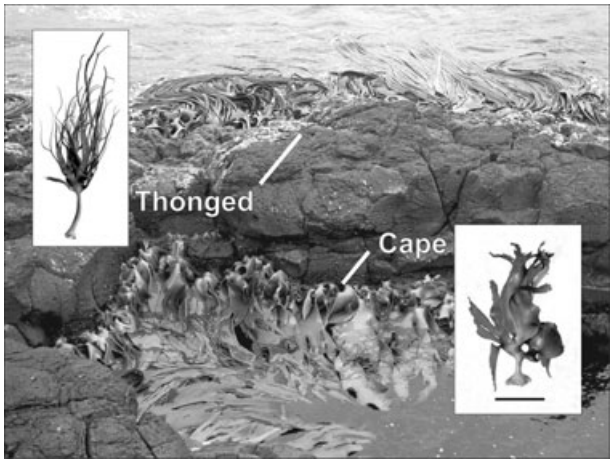

FIG. 1. Distinct *Durvillaea antarctica* morphotypes growing in close proximity on a rock platform at Enderby Island (Auckland Islands), January 2007, with ''cape'' form on the sheltered side and ''thonged' form on the exposed side. Inset: representative extreme morphotypes of *Durvillaea antarctica* from Second Beach, St. Clair, New Zealand; scale bar of inset images, 0.5 m.

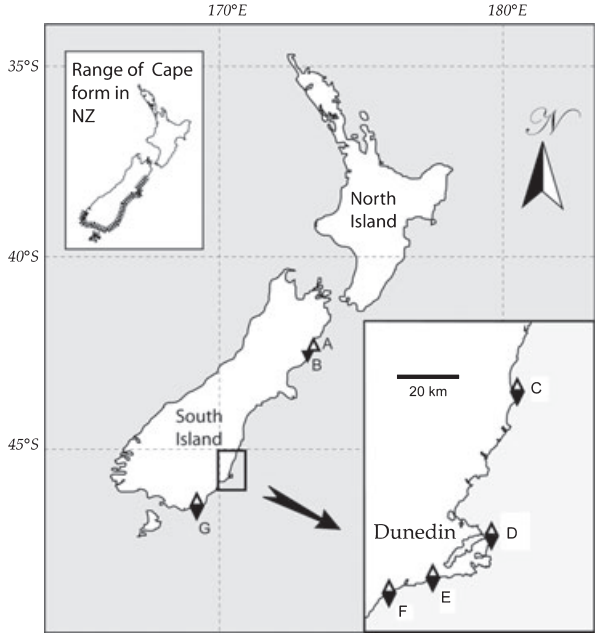

FIG. 2. Location of sites sampled in New Zealand: A, Raramai Tunnels; B, Oaro; C, Moeraki; D, Taiaroa Heads; E, Second Beach; F, Brighton; G, Tautuku Peninsula. Hollow triangles indicate the presence of sampled ''cape'' form, whereas filled triangles indicate ''thonged'' *Durvillaea antarctica*. The known New Zealand range of ''cape'' form (South and Hay 1979) is inset.

transplantation experiments, making it difficult to study the basis of environmentally correlated morphological variation by purely experimental methods in this species. It does not produce a free-living gametophyte that is easily seeded onto ropes or other artificial substrata. Although *D. antarctica* zygotes can be induced to colonize artificial substrates, such as tiles, it is difficult to fix such items to the rock in the low intertidal zone where the impact of waves is very strong, and to exclude grazers until the plants are large enough for morphological comparisons. In 1973, G. R. South and C. H. Hay successfully transplanted 50 juvenile *D. antarctica* collected from an exposed location on Kaikoura Peninsula to the semisheltered Oaro Reef by removing portions of the limestone rock with the holdfast and then cementing the plants to concrete slabs; while the plants initially survived this treatment, within weeks all were eaten by fish (C. H. Hay, personal observation).

In the present study, we used a combination of genetic techniques (analysis of DNA sequences from mitochondrial COI, plastid *rbc*L, and nuclear 18S markers) and field measurements to determine whether environmentally correlated morphotypes of *D. antarctica* in New Zealand differ genetically, or merely phenotypically. As the morphotypes are largely sympatric in the South Island, consistent genetic differences between the two forms over a range of locations would suggest some level of reproductive isolation, indicating a species-level difference.

MATERIALS AND METHODS

Site selection and sample collection. Samples were collected at low tide from rocky shores at seven sites throughout New Zealand (Table 1 and Fig. 2). Sites A and B (northern South Island) represent proximate populations dominated by ''cape'' and ''thonged'' forms, respectively. At site A (Raramai Tunnels), only ''thonged'' forms were collected, whereas only ''cape'' plants were sampled from site B (Oaro). At each of three southern South Island sites (C, E, and F), both tissue samples and basic morphometric measurements were taken along a transect of rock platform from relatively sheltered to relatively exposed regions (Fig. 3). The degree of wave exposure was determined qualitatively by simple observations. Sampling and measurements of stipe length, stipe circumference, and holdfast circumference were carried out in situ along transects of 30 to 50 m, with every 10th individual *D. antarctica* sampled. Although our research measured fewer morphological characteristics than many other studies of macroalgal plasticity (such as Miller et al. 2000, Duggins et al. 2003, Stewart 2006), the ''thonged'' and ''cape'' morphotypes considered here have been comprehensively described previously (''cape'' and ''thonged'' morphotypes of South and Hay 1979). These authors considered a range of characters including overall length, total weight, stipe length, stipe weight, stipe diameter, degree of blade division, and degree of honeycombing, several of which exhibited significant differences between extreme morphotypes. Stipe length was the major indicator of morphotype, but significant differences in other characteristics were also observed, with ''thonged'' plants having significantly greater overall length and more blade divisions than ''cape''

TABLE 1. Number of samples of each morphotype collected from each site.

Site	Site name	No. thonged	No. cape
A	Raramai Tunnels	10	0
B	Oaro	0	10
C	Moeraki	4	11
D	Taiaroa Heads	8	5
E	Second Beach	8	7
F	Brighton	7	13
G	Tautuku Peninsula	7	6

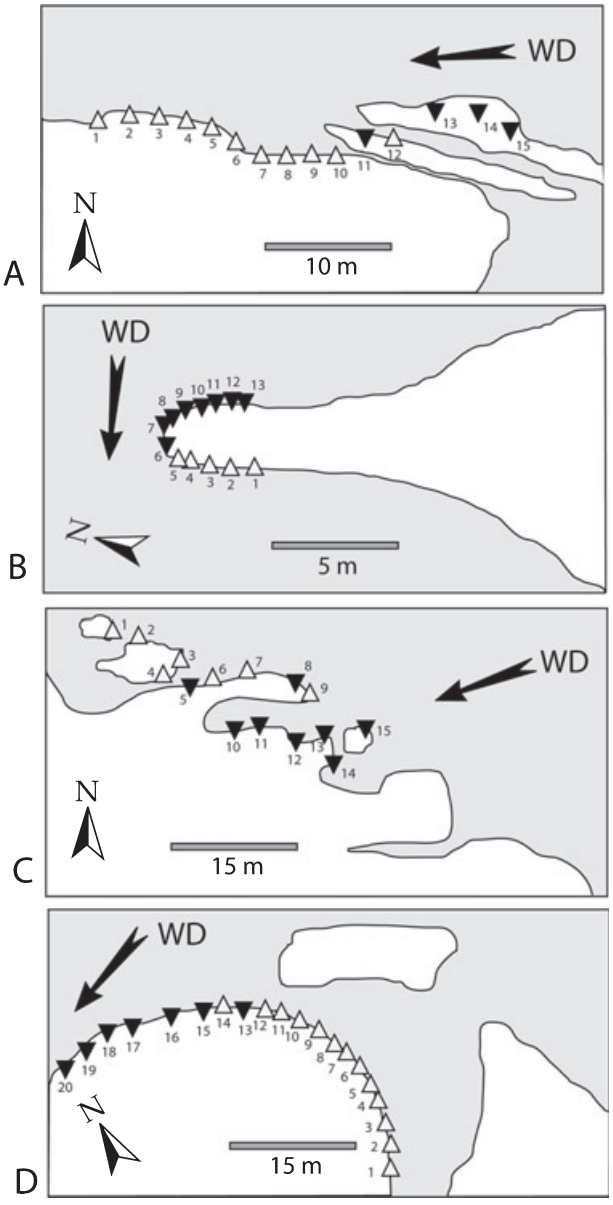

FIG. 3. Site diagrams showing locations of sampled ''cape'' (hollow triangles) and ''thonged'' (filled triangles) *Durvillaea antarctica* plants at Otago sampling sites: C, Moeraki; D, Taiaroa Head; E, Second Beach, St. Clair; and F, Brighton Beach. Symbols correspond to mtDNA clades (Fig. 5); prevalent wave directions for each site are indicated by WD.

plants. Although overall length and blade characteristics can be important indicators of morphotype, our current study focused primarily on stipe dimensions, as blades are often battered and highly variable in extremely wave-exposed sites (South and Hay 1979). At site D, a narrow (<2 m wide) rocky outcrop at the entrance to Otago Harbour, genetic samples were randomly collected from eight plants on the more exposed side and five plants on the more sheltered side (Fig. 3D); no morphological measurements were taken of these plants, to test the discriminatory power of genetics alone. Site G (a rock platform at Tautuku Peninsula) was determined by South and Hay (1979) to primarily comprise ''thonged'' plants, which these authors attributed to high wave exposure; however, wave force was observed to dissipate across the platform such that ''cape'' form plants high on the rock platform were subjected to relatively low-energy waves. Additionally, Hay (1977) noted significant differentiation of kelp stipe lengths between the upper zone (n = 37, mean = 22.5, SE = 1.3) and lower zone (n = 53, mean = 31.2, SE = 1.2) of this rock platform, and that the stipes of the uppermost plants often divided distally into several thick ''boughs,'' each supporting a major division of the blade. In the current study, we randomly sampled six ''cape'' plants from the upper zone and six ''thonged'' plants from the lower zone at site G. At sites A, B, and G, sampled plants were categorized as ''cape'' or ''thonged'' based on visual qualitative appreciation of the morphology (see Fig. 1).

DNA extraction and sequencing. Frond tissue from each plant was dehydrated in 95% ethanol for 2 d and allowed to air-dry for 15 min prior to DNA extraction. A small (<1 mm^2) piece of cortical tissue was removed and extraction performed using standard Chelex® procedure (Walsh et al. 1991). Although some algal DNA extraction methods involve freezing samples in liquid nitrogen and grinding with mortar and pestle (Lane et al. 2006), this procedure was unnecessary for freshly preserved samples of *D. antarctica*. Extracted DNA was diluted 100-fold, and PCR amplification carried out in 20 μL volumes containing 1.0 μL DNA, 0.5 μM of each primer, 1× buffer, 0.8 mM dNTP, 1.5 mM $MgCl_2$, and 1 U Taq polymerase (Bioline 'BIOTAQ,' London, UK). PCR primers for COI were taken from Saunders (2005): forward primer GazF1 5′ TCAACAAATCATAAAGATATTGG 3′ and reverse GazR1 5′ ACTTCTGGATGTCCAAAAAAYCA 3′. PCR primers for *rbc*L were from Lane et al. (2006): forward primer KL2 5′GATGCTGATTATAACGTTAAAG 3′ and reverse KL8 5′ GTTGGTGCATTTGACCACA 3′. PCR primers for 18S were from Whiting et al. (1997): forward primer 18Sai 5′CCTGAGAAACGGCTACCACATC 3′ and reverse 18Sbi 5′ GAGTCTCGTTCGTTATCGGA 3′. Amplification was performed in an Eppendorf Mastercycler® (epgradient S, Hamburg, Germany) using the following profile: 94°C for 2 min; 40 cycles of 15 s at 94°C, 30 s at 45°C, 1 min at 72°C, followed by a final 4 min extension at 72°C. PCR products were purified using an Invitrogen Purelink PCR purification kit (Invitrogen, Carlsbad, CA, USA) and sequenced by the Allan Wilson Centre Genome Service (Palmerston North, New Zealand).

Analyses. Morphological characteristics between ''thonged'' and ''cape'' haplotypes at sites C, E, and F were compared by multivariate analysis using PRIMER version 5 (Clarke and Gorley 2001). Data were first transformed logarithmically to minimize the effects of outliers. Nonmetric multidimensional scaling (nMDS) ordinations and analysis of similarities (ANOSIM), using Euclidean distance, were performed to determine significant differences between groups, and similarity percentage (SIMPER) analyzed factors responsible for such differences.

Maximum-likelihood (ML) phylogenetic analyses of COI and *rbc*L incorporated published sequences from the phaeophyte genus *Fucus* (GenBank accessions AY494079, *Fucus vesiculosus* for COI; AF195515, *Fucus gardneri* for *rbc*L), along with sequences from *Durvillaea willana* (Brighton and Kaikoura, South Island, New Zealand) as outgroups. Analyses were carried out using the exhaustive search option of PAUP*4.0b10 (Swofford 1998). ML analyses were performed with an HKY + G model for COI (base frequencies A = 0.2183, C = 0.1653, G = 0.1951, T = 0.4213) and a TrN + G model for *rbc*L (base frequencies A = 0.2962, C = 0.1525, G = 0.2199, T = 0.3314; rate matrix: A-C = 1.0000, A-G = 3.3099, A-T = 1.0000, C-G = 1.0000, C-T = 8.1611, G-T = 1.0000), as selected by Modeltest 3.06 (Posada and Crandall 1998). Relative phylogenetic support for each node was assessed by bootstrapping (Felsenstein 1985) with heuristic analysis of 1,000 replicate data sets. Uncorrected sequence divergence values among haplotypes were calculated using PAUP.

RESULTS

''Cape'' and ''thonged'' clades (as defined by genetic data; see below) were significantly different morphologically, based on measurements of stipe length, stipe circumference, and holdfast circumference (ANOSIM Global R = 0.60, P = 0.001) (Fig. 4). SIMPER analysis indicated that most (58.19%) of this difference was due to stipe length, with significantly longer stipes in ''thonged'' (mean = 39.4 cm) versus ''cape'' (mean = 13.1 cm) plants. Randomly sampled individuals from site G showed significant differences in stipe length, with longer stipes in the lower, more wave-exposed region (lower/more exposed: n = 6, mean = 56 cm, SE = 0.96; upper/more sheltered: n = 6, mean = 17.5 cm, SE = 0.98; $F_{1,10}$ = 58.5, P < 0.0005). All six plants sampled from the exposed area of site G had ''thonged'' haplotypes, and all six from the sheltered region had ''cape'' haplotypes, for both COI and *rbc*L.

Molecular analyses revealed considerable genetic variation within *D. antarctica* in New Zealand. Each unique DNA sequence obtained in this study is available from GenBank (accession numbers: EU918563–EU918578; EU919398). Of the 96 samples analyzed, nine failed to amplify for COI, and two for *rbc*L, but in each case, sequences were obtained for the alternate gene. Although only 41%

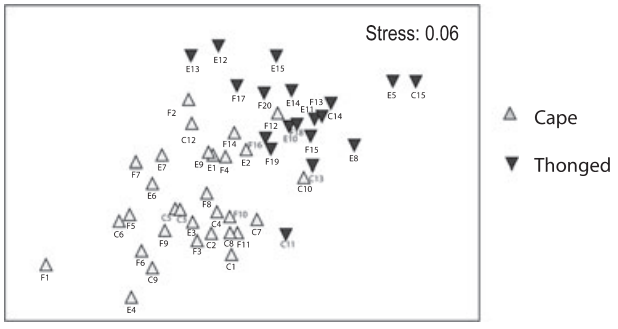

FIG. 4. Nonmetric multidimensional scaling (nMDS) plot of *Durvillaea antarctica* morphology (holdfast circumference, stipe circumference, and stipe length) at sites C, E, and F (transect sites), with ''thonged'' and ''cape'' mtDNA clades (see Fig. 5) indicated by filled and open triangles, respectively.

of specimens amplified successfully for 18S, these comprised roughly equal numbers of ''cape'' and ''thonged'' plants (Table 2). The ML phylogeny of *Durvillaea* mtDNA (COI: 633 base pairs, 24 variable sites within *D. antarctica*) supported the monophyly of *D. antarctica* (89% bootstrap support, Fig. 5). In addition, the analysis revealed two divergent groups within *D. antarctica* (Fig. 5), corresponding to ''thonged'' and ''cape'' morphotypes. No haplotypes were shared between these morphotypes. Only two ''cape'' haplotypes were detected for COI (divergence 0.3%, with all but one sample sharing an identical haplotype), whereas five distinct COI haplotypes (divergences 0.1%–0.9%) were observed in the ''thonged'' clade. This clade exhibited strong phylogeographic partitioning, with distinct far northern (site A: Raramai Tunnels), northern (sites C and D: Moeraki and Taiaroa Head), and southern (sites E, F, and G: Second Beach, Brighton, and Tautuku Peninsula) lineages. ''Cape'' and ''thonged'' haplotypes were 3.0%–3.8% divergent for COI. The phylogeny generated using chloroplast DNA (plastid: *rbc*L: 1,004 base pairs, 10 variable sites within *D. antarctica*) also demonstrated a split between ''thonged'' and ''cape'' plants concordant with COI data. Although the monophyly of ''thonged'' haplotypes was not supported, the distinction between ''thonged'' and ''cape'' was nonetheless consistent (Fig. 6), and analysis of concatenated COI and *rbc*L sequences supported the reciprocal monophyly of ''thonged'' versus ''cape'' clades (bootstrap values indicated in Fig. 5). In addition, *rbc*L haplotypes of ''thonged'' *D. antarctica* exhibited comparable phylogeographic structure relative to the COI data (above). ''Cape'' and ''thonged'' haplotypes were 0.8%–1.0% divergent for *rbc*L. The 18S sequences revealed only four variable sites and three sequence types (Table 2) across a 1,000 bp region, and hence yielded minimal phylogenetic information. Nevertheless, the partitioning of the three distinct sequences detected was consistent with morphology: two of the sequences were restricted to ''thonged'' form plants, whereas the third was detected only in ''cape'' form plants (Table 2).

Overall, morphometric analysis of stipe length, stipe circumference, and holdfast circumference at sites C, E, and F yielded morphological groupings concordant with genetic data (Fig. 4), with two distinct subclades within *D. antarctica* corresponding to ''cape'' and ''thonged'' morphotypes. High phylogenetic concordance was detected between mitochondrial, plastid, and nuclear data sets: each individual with a ''cape'' mitochondrial haplotype also had a ''cape'' haplotype for the plastid and nuclear markers, and complete association between the three markers was also found in the ''thonged'' group.

TABLE 2. Variable sites and sequence frequencies for nuclear 18S.

				18S nucleotide position			
Site/s	Morphotype	Sequence	*n*	195	198	206	215
B, C, D, E, F	Cape	18S-C-1	18	C	–	C	–
A	Thonged	18S-T-1	8	C	T	T	G
C, D, E, F	Thonged	18S-T-2	13	T	–	C	–

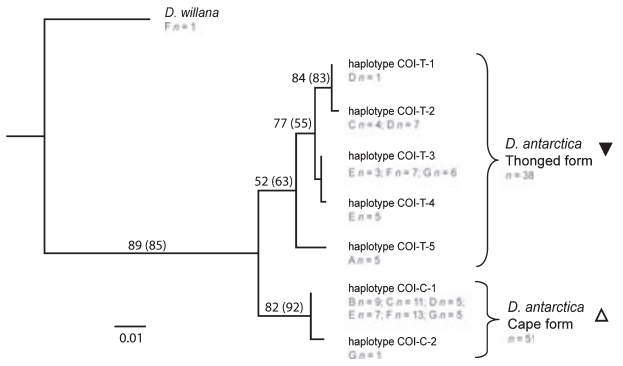

FIG. 5. Maximum-likelihood tree of *Durvillaea antarctica* mtDNA (COI), showing reciprocal monophyly of ''cape'' and ''thonged'' plants. Bootstrap values are based on 1,000 replicate analyses, with values for a combined analysis of COI and *rbc*L given in parentheses. The outgroup *Fucus vesiculosus* has been removed from this diagram to better illustrate relationships within *Durvillaea*.

DISCUSSION

Species status. Our results reveal that New Zealand *D. antarctica* comprises two widespread lineages that are distinguishable both morphologically and genetically. This finding contradicts South and Hay's (1979) suggestion that the ''cape'' and

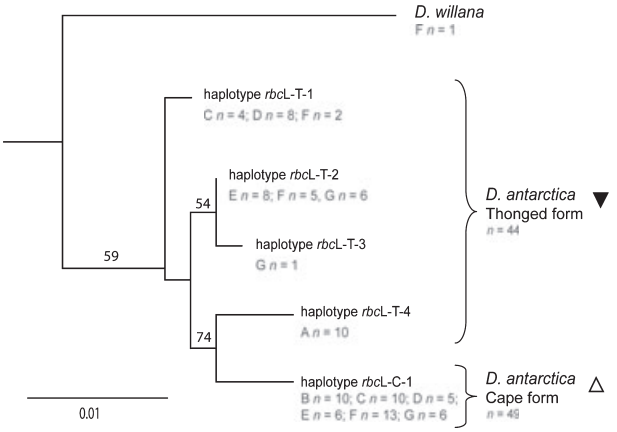

FIG. 6. Maximum-likelihood tree of *Durvillaea antarctica* chloroplast DNA (*rbc*L) showing consistent genetic divergence between ''cape'' and ''thonged'' plants across a range of geographic sites. Bootstrap values are based on 1,000 replicate analyses. The outgroup *Fucus gardneri* has been removed from this diagram to better illustrate relationships within *Durvillaea*.

''thonged'' forms of bull kelp are merely ecologically labile phenotypes. Rather, the concordant genetic differentiation of ''cape'' and ''thonged'' plants at both cytoplasmic (COI, *rbc*L) and nuclear (18S) loci, in sympatric populations and across a range of sites, indicates that these distinct ''morphotypes'' represent reproductively isolated species. Cross-fertilization experiments are required to help clarify whether reproductive isolation is pre- or postzygotic.

The level of COI divergence observed between ''thonged'' and ''cape'' haplotypes of New Zealand *D. antarctica* (3.0%–3.8%), considerably greater than values detected within clades (0.1%–0.9%), is comparable to interspecific COI variation (2.2%–4.7%) detected within the brown algal genus *Alaria* (e.g., *A. esculenta* vs. *A. marginata* species complex; Lane et al. 2007), and between some species pairs of red macroalgae (>4.5%; Saunders 2005). Our study detected reciprocal monophyly of ''cape'' and ''thonged'' haplotypes for mtDNA (COI) but not for chloroplast (*rbc*L) and nuclear (18S) markers. Nevertheless, all three markers indicated consistent genetic differentiation between ''cape'' and ''thonged'' kelp morphotypes, suggesting reproductive isolation. The separate species status of ''cape'' versus ''thonged'' *D. antarctica* can thus be supported under a phylogenetic species concept (reciprocal monophyly: Cracraft 1983), under a biological species concept (reproductive isolation: Mayr 1942), and under a simple COI barcoding approach to species delineation (Hebert et al. 2004). However, describing and naming new species of *Durvillaea* is not within the scope of this paper, although future work will address this matter. Determining which, if either, species is the ''true'' *D. antarctica* will require comparison with the holotype and/or specimens from the type locality (Cape Horn, Chile) and will necessarily form part of a larger biogeographical study of the genus. In addition, this study does not provide adequate diagnostic characterizations for clear separation of the two forms based on morphology alone, as evidenced by the degree of overlap of the genetic groupings in the nMDS plot (Fig. 4), and future taxonomic work should aim to identify any visible features that are consistently unique to each species.

The ''cape'' and ''thonged'' *D. antarctica* lineages were resolved as reciprocally monophyletic for mtDNA, but not for plastid and nuclear markers. Although algal mtDNA may have a fast evolutionary rate relative to plastid and nuclear loci (e.g., Evans et al. 2007), under neutrality, the rate of coalescence is determined by effective population size (Hudson and Turelli 2003) rather than mutation rate, and it therefore seems unlikely that variable evolutionary rates can fully explain the absence of reciprocal monophyly at *rbc*L and 18S. Relatively rapid evolution of reciprocal monophyly is expected for maternally inherited loci (e.g., mtDNA) due to their comparatively small effective population size (Kingman 1982, Palumbi et al. 2001). The absence of reciprocal monophyly observed here for chloroplast DNA (as well as nuclear DNA) might therefore suggest biparental inheritance of this genome. Although both mitochondria and chloroplasts are typically thought to be maternally inherited in brown algae (e.g., *Laminaria*: Motomura 1990, *Fucus*: Coyer et al. 2002), chloroplasts do exhibit biparental inheritance in *Scytosiphon* (Kato et al. 2006). At present, no information exists on chloroplast inheritance in *Durvillaea*, but future studies should assess the possibility that chloroplast inheritance is biparental. Alternative explanations for variable coalescence times among loci might simply involve ''inherent stochasticity of the … coalescent process'', or perhaps nonneutral evolution (e.g., selective sweeps) at a particular locus (Hudson and Turelli 2003, p. 182).

Evolution, biogeography and ecology. Despite their geographic overlap, the ''cape'' form of *D. antarctica* has a more restricted distribution within the New Zealand region than the ''thonged'' form (South and Hay 1979), suggesting that the former may be a local endemic species derived from the latter, more widespread taxon. However, a more comprehensive study of *D. antarctica* across its range is required to shed light on the evolutionary history of the genus. It is possible that these taxa speciated allopatrically (e.g., through vicariance; Lindstrom 2001), with subsequent range expansion facilitating their secondary contact. Alternatively, speciation can potentially occur in sympatry (see Barluenga et al. 2006) when plasticity enables a species to occupy distinct habitats, with subsequent divergence due to restricted gene flow (Agrawal 2001). Although the most obvious physical gradient in the habitat of ''cape'' and ''thonged'' *D. antarctica* is wave exposure, the underlying causes and physiological mechanisms of both the morphological and genetic variation observed in *Durvillaea* clearly warrant further investigation. It should be noted that *D. antarctica* is highly buoyant and, once detached, may be capable of drifting long distances (Edgar and Burton 2000, Smith 2002). While this study examined only ''cape'' and ''thonged'' *D. antarctica* in New Zealand, both forms possess the buoyant honeycombed internal structure, and it is possible that both are widely present throughout the Southern Ocean; indeed, Skottsberg (1907, 1921) described what he surmised were phenotypic forms of *Durvillaea* growing in South America and the Falkland Islands.

Many macroalgae exhibit morphological variation along gradients of wave exposure, with a general trend toward larger stipes in more exposed locations (*D. antarctica*: South and Hay 1979; *Agarum* and *Costaria*: Duggins et al. 2003; *Ecklonia radiata*: Fowler-Walker et al. 2005; *Turbinaria*: Stewart 2006). The benefits of larger stipes in high-energy environments

could include strength and resistance to herbivory (Duggins et al. 2003), whereas stipe flexibility is likely to be important in permitting streamlining and resistance to drag (Harder et al. 2006). Other morphological differences, such as degree of blade division (South and Hay 1979), may also be related to minimizing drag forces while maintaining sufficient photosynthetic surface area. The ''thonged'' form of *D. antarctica* has been shown to be better able to reconfigure into a drag-resistant morphology than the ''cape'' (Harder et al. 2004), making it more suited to sites of strong wave action. The ''cape'' form is, nonetheless, occasionally observed growing in close proximity to the ''thonged'' form even in extremely high-energy sites, suggesting that wave action may not be the sole factor responsible for spatial partitioning. Further research is clearly required to determine the relative influences of various environmental or other factors in the small-scale distributions of each form.

Bull kelp dominates many intertidal ecosystems in southern New Zealand, and the species diversity within what is currently known as *D. antarctica* in New Zealand may be relevant to researchers in a range of scientific disciplines. For example, several recent studies have used *D. antarctica* in New Zealand as a subject for investigations into algal responses to mechanical stress (e.g., Stevens et al. 2002, Harder et al. 2006). In such cases, consideration of morphotype is fundamental, as differences in morphology are likely to affect the way in which plants respond, as shown, for example, by Harder et al. (2004), who demonstrated that drag forces on *D. antarctica* were less for ''thonged'' than ''cape'' morphotypes. Additionally, future studies must necessarily compare the life history traits of the two species. Our data indicate strong phylogeographic structure of ''thonged'' haplotypes of *D. antarctica* across small geographic scales in southern New Zealand, with clear north-south differentiation, while the ''cape'' form shows no evidence of such geographic structure. Additional research is required to determine whether this phylogeographic contrast reflects differing dispersal abilities (e.g., rafting ability, dissimilar buoyancy of gametes, etc.) or some other ecological factor.

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