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Genetic connectivity between trans-oceanic populations of *Capreolia implexa* (Gelidiales, Rhodophyta) in cool temperate waters of Australasia and Chile

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ABSTRACT

Capreolia is a monospecific genus of gelidioid red algae and has been considered to be endemic to Australasia. This is the first report on the occurrence of *Capreolia implexa* outside of Australasian waters, based on investigations of fresh collections in southern Chile as well as Australia and New Zealand. Thalli are prostrate and form entangled turfs, growing on high intertidal rocks at three locations in Chile. Analyses of *rbc*L and *cox*1 revealed that *C. implexa* was of Australasian origin and also distinct from its relatives. Analyses of 1356 bp of *cox*1 revealed cryptic diversity, consisting of two genealogical groups within *C. implexa*; one present in Australia and New Zealand, and the other in Chile and Stewart Island, New Zealand. The extremely low genetic diversity found in *C. implexa* in Chile and the absence of shared haplotypes between Chile and Australasia suggest genetic bottleneck possibly as a result of colonization after dispersal by rafting from Stewart Island, New Zealand to Chile.

1. Introduction

Investigations of benthic marine algae distributed over trans-oceanic regions can offer insights into ecological and evolutionary processes. Genetic assessment using molecular markers is a suitable tool to decide whether the distribution of interoceanic populations has resulted from either recent introductions (e.g., dispersal by post glacial rafting or anthropogenic introductions/invasions) or historical processes, or some combination of both events (Boedeker et al., 2010; Fraser et al., 2013). Low genetic diversity is generally considered to be related to contemporary dispersal events or invasions, while evidence of high genetic diversity may reflect the effect of historical events (e.g., Boedeker et al., 2010; Fraser et al., 2011; Kim et al., 2010; Voisin et al., 2005).

Capreolia is monospecific and reported as endemic to cool temperate waters of Australasia, displaying a biphasic, rather than the triphasic life history typical of members of the Gelidiales (Guiry and Womersley, 1993). Guiry and Womersley (1993) erected the genus for a mat-forming species found in the mid-intertidal zone on both exposed and sheltered coasts in south-eastern Australia and New Zealand. In establishing this genus they recognized that specimens previously identified as *Gelidium pusillum* (Stackhouse) Le Jolis had been misidentified in Australasia. *Capreolia implexa* Guiry & Womersley is distributed from Wittelbee Point, Southern Australia to Broken Bay, New South Wales, around Tasmania, and is also widespread in New Zealand (Nelson, 2013; Womersley and Guiry, 1994).

Molecular analyses of *rbc*L as well as *cox*1 have confirmed the distinctiveness of *Capreolia* (Boo et al., 2013, 2014; Freshwater et al., 1995; Millar and Freshwater, 2005; Nelson et al., 2006). In an *rbc*L phylogeny, *C. implexa* formed a clade with *Gelidium caulacanthum* and *G. hommersandii* from Australasia, and *G. divaricatum* from northeast Asia (Freshwater et al., 1995; Millar and Freshwater, 2005; Nelson et al., 2006). However, additional taxon sampling revealed that *G. divaricatum* was distinct from *Capreolia*, and formed a separate clade (Boo et al., 2013, 2014).

The Chilean Gelidiales were extensively studied by Santelices and Montalva (1983), and only species of *Gelidium* and *Pterocladiella* have been reported to occur on the Chilean coast (Hoffmann and

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Santelices, 1997; Santelices and Stewart, 1985). During a survey of gelidioid red algae, we collected three specimens of *C. implexa* from Calbuco, Puerto Montt in southern Chile in January 2005, a region where the species had never been previously reported. The aims of the present study were to 1) confirm the presence of *C. implexa* in Chile by comparing morphology and *rbc*L sequence data from additional collections from Chile and Australasia, 2) compare the level of genetic diversity in Australasian and Chilean populations of *C. implexa* using *cox*1 sequence data for addressing questions about the relationships of these transoceanic populations, and 3) test whether there is evidence that the Chilean *C. implexa* populations were introduced after Last Glacial Period (LGM) or distributed by historical processes.

2. Materials and methods

2.1. Sample collection and morphological examination

Samples of *C. implexa* were collected from Chile, Australia and New Zealand. In Chile, sampling was conducted at three locations: (1) the collection site (Caicaen) in January 2005 and October 2013 and a nearby additional site (Port of Calbuco) in Calbuco, Puerto Montt, (2) Bahia Mansa, Osorno, and (3) Chaihuin, Valdivia in October 2013. Australian samples were collected in four locations in February 2014, and New Zealand samples were collected in seven locations from the northern North Island through to Stewart Island in1996, 1997, 1998, and 2014. Specimens from New Zealand previously used for *rbc*L analysis (Nelson et al., 2006) were also analyzed for *cox*1 sequences. Information on all specimens used in this study is given in Table S1. Specimens collected in the present study were pressed onto herbarium sheets and subsamples were dehydrated in silica gel for molecular work. For anatomical observations, thalli were sectioned using a freezing microtome (FX-801, Yamato Kohki Industrial Co., Ltd., Japan) and were stained with 1% aqueous aniline blue. Photographs were taken with a DP-71 camera (Olympus, Tokyo, Japan) mounted on a BX-51 microscope (Olympus, Tokyo, Japan). Voucher specimens are housed at Department of Biology, Chungnam National University (CNUK), Daejeon, Korea, and the Museum of New Zealand Te Papa Tongarewa (WELT) (Thiers, 2014).

Supplementary Table 1 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.aquabot.2014.08.004.

2.2. Molecular analyses

DNA extraction, PCR amplification, and sequencing were performed as described in Boo et al. (2013). The primers used for amplifying and sequencing were F7, F645, R753, and RrbcS start for *rbc*L (Freshwater and Rueness, 1994; Gavio and Fredericq, 2002; Lin et al., 2001), and COXI43F and COXI1549R for *cox*1 (Geraldino et al., 2006).

Phylogenies of *rbc*L and *cox*1 datasets were reconstructed using maximum likelihood (ML), including species in the Gelidiaceae and *Pterocladiella* species as outgroups (Boo et al., 2013, 2014). ML analyses were performed with RAxML v.7.2.8 (Stamatakis, 2006) using the GTRGAMMAI model. We used 300 independent tree inferences, applying options of automatically optimized subtree pruning regrafting (SPR) rearrangement and 25 distinct rate categories in the program to identify the best tree. Statistical support for each branch was obtained from 1000 bootstrap replications with the same substitution model.

Bayesian inference (BI) was performed for individual datasets with MrBayes v.3.2.1 (Ronquist et al., 2012) using the Metropolis-coupled Markov Chain Monte Carlo (MC3) with the GTR+G+I model. For each matrix, two million generations of two independent runs were performed with four chains and sampling trees every 100 generations. The burn-in period was identified graphically by tracking the likelihoods at each generation to determine whether they reached a plateau. The 36,002 trees sampled at the stationary state were used to infer Bayesian posterior probabilities (BPP).

To understand relationships and geographical distribution of mitochondrial *cox*1 haplotypes, we calculated haplotype diversities (*H*d) and nucleotide diversities (π), and reconstructed minimum spanning network using Arlequin v.3.5.1.2 (Excoffier and Lischer, 2010).

3. Results

Our collections from Chile (24 specimens) matched the morphological features of *C. implexa* from Australia and New Zealand. Thalli purple-red, formed compact, entangled mats on upper intertidal rocks about 10 mm high and usually spreading up to 10 cm across (Fig. 1A and B). Stolons were prostrate or slightly erect but without distinct erect axes, irregularly branched, tapered gradually to a protruding apical cell (Fig. 1B). Cortices were composed of round cells, and the medulla composed of a network of elongate cells (Fig. 1C and D). Rhizoidal filaments were few in the outer medulla (Fig. 1C). Stichidia were formed on terminal or lateral branches, compressed, stipitate, with rounded tips. Tetrasporangia were in regular, acropetally developed rows, ovoid, and decussately or cruciately divided (Fig. 1E and F).

In southern Chile, thalli were usually epilithic or epizoic on mollusk shells or on jetty poles in intertidal zones, and sometimes were abundant compared to other intertidal algae on shaded rock or artificial constructions of rocks. Thalli often formed entangled clumps with *Caulacanthus ustulatus* (Mertens ex Turner) Kützing. Tetrasporangial thalli were found in both January 2005 and October 2013, but neither cystocarpic nor spermatangial plants were observed in all 27 specimens collected from three locations in Chile. *C. implexa* thalli were commonly found in Chaihuin, a very exposed location with strong waves, and in Bahia Mansa and Calbuco (see Table S1 for latitude and longitude), small fishery harbors where fishery transportations as well as floating objects occur with frequency.

We generated seven *rbc*L (1389 bp) and 66 *cox*1 (1356 bp) sequences in the present study (Table S1). Specimens of *C. implexa* from two locations in southern Chile were identical in *rbc*L. Pairwise divergences between specimens from Chile and Australia/New Zealand ranged between 0.0 and 0.3%. The *rbc*L tree revealed the monophyly of *C. implexa* from Chile, Australia and New Zealand (Fig. 2). *C. implexa* formed a clade with *G. hommersandii* and *G. caulacantheum*.

Comparisons of the 67 *cox*1 (1356 bp) sequences including one published sequence from Spirits Bay, New Zealand, revealed 180 polymorphic sites (13.3%), defining 17 haplotypes. Thirteen haplotypes (76%) were 'private' (unique to a single location). All specimens of *C. implexa* from Chile (except one in Calbuco) were identical in *cox*1 (Fig. S1). Pairwise divergence within Chilean populations was up to 0.2% (a difference of 2 bp). However, the pairwise divergences were up to 2.2% (a difference of 30 bp) between Chile and Australia, and 2.9% (a difference of 33 bp) between Chile and New Zealand. The Australian populations differed by 2.1% (29 bp) from those of New Zealand. Haplotype and nucleotide diversities of *cox*1 were high (*H*d, 0.781; π, 0.0114) in the New Zealand populations, while both indices were very low (*H*d, 0.077; π, 0.0001) in Chile (Table 1). Both of these diversity measures were lower in Australian populations than in the New Zealand populations that were sampled (Table 1).

Supplementary Fig. 1 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.aquabot.2014.08.004.

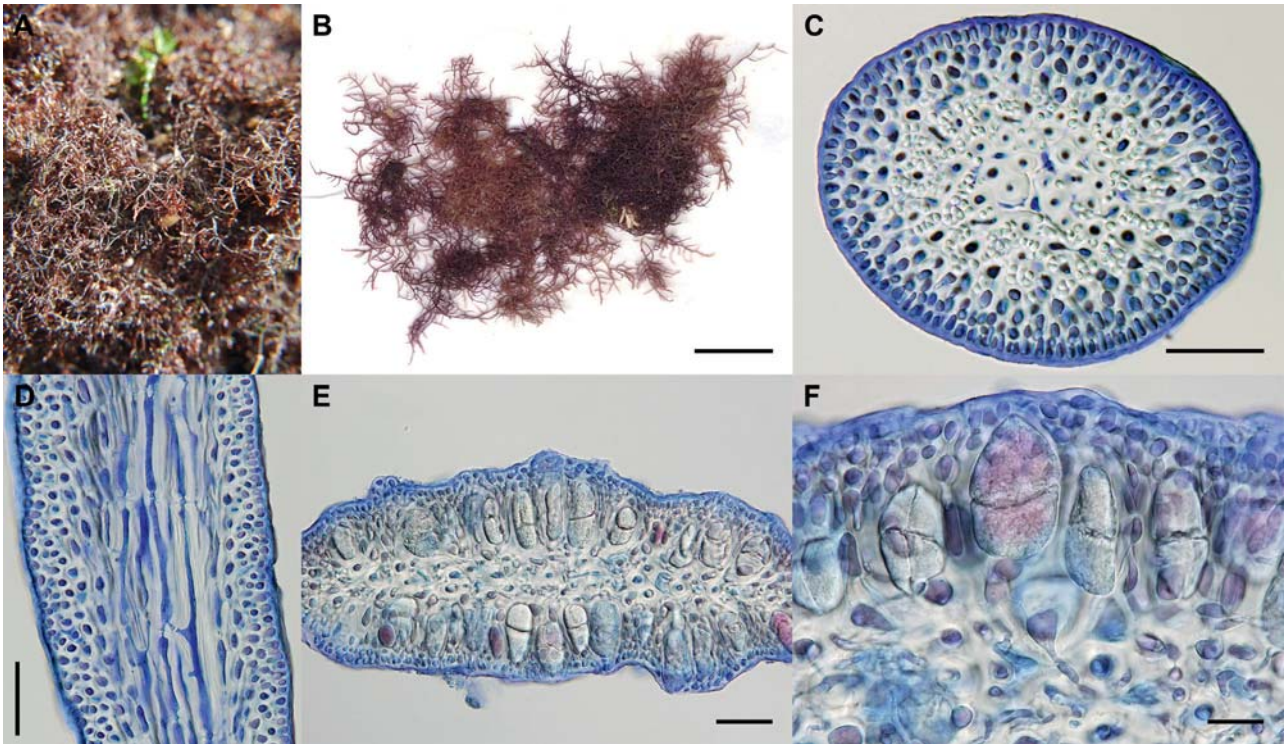

Fig. 1. Morphology of *Capreolia implexa* from Chile. (A) Habit of thalli growing on a rock in the intertidal zone in Calbuco, Chile (2 August 2014). (B) Habitat of the thallus. (C) Transverse section of axis. (D) Longitudinal section of axis. (E) Transverse section of tetrasporangial sorus with tetrasporangia. (F) Cruciately divided tetrasporangia. Scale bar = 1 cm (B); 50 μm (C, D, E); 20 μm (F).

The haplotype network of *cox*1 revealed two groups connected with 24 missing haplotypes, suggesting restricted genetic flow between northern and southern populations in New Zealand (Figs. 3 and 4).

4. Discussion

Our analyses of mitochondrial *cox*1 and plastid *rbc*L sequences combined with an examination of morphological features, clearly demonstrate that our collections from Chile belong to *C. implexa*, a genus and species previously not recorded from South America. The occurrence of *C. implexa* at Chaihuin in Valdivia, Bahia Mansa in Osorno, and Calbuco in Puerto Montt is confirmed in the present study. These three locations are separated by at least 200 km, distributed from 39°56′ to 41°45′ S in Chile. Although many factors may influence the distribution of this intertidal alga, the occurrence of reproductive structures (tetrasporangia) in Chilean specimens from this study suggests that this species may already be well-established in its new range and capable of further range-extension. For example, given the influence of the West Wind Drift and Humboldt Current to the north, and the Cape Horn Current to the south, the potential range of this species may extend north of Valparaiso (33°01.33′ S, 71°02.34′ W) in central Chile to Golo de Penas in the south (Hinojosa et al., 2011). The annual seawater temperature range (13.1–17.9 °C; http://www.seatemperature.org/south-america/chile/valparaiso.htm) in Valparaiso is similar to that of Wellington in central New Zealand (12.6–17.1 °C; http://www.seatemperature.org/autralia-pacific/new-zealand/wellington), where *C. implexa* commonly occurs. The seawater temperature (8–10 °C) of Colpo de Penas (46°50.50′ S, 77°38.32′ W) is also close to that of Stewart Island in New Zealand (8–15 °C; http://www.surf-forecast.com/breaks/Saber-Reef-Stewart-Island/seatemp) in Stewart Island, as shown above. This latitudinal range (33–46° S) in Chile roughly corresponds with the distributional range (33–47° S) of *C. implexa* in Australia and New Zealand (Guiry and Womersley, 1993). Further studies should sample this potential broad geographical range and quantify the presence, abundance and reproductive potential of *C. implexa* in Chile.

C. implexa is often confused with *C. ustulatus* because both species form entangled clumps together in the field. However, the latter species has more slender branches with pointed and divergent tips (Nelson, 2013). The occurrence of *C. implexa* has gone unnoticed in this range of South America, until now, probably due to its growth in clumps with *C. ustulatus*, which is common in Chile (Hoffmann and Santelices, 1997).

Phylogenetic analysis of *rbc*L sequences resulted in recognition of the *Capreolia* clade containing *G. caulacanthum* and *G. hommersandii*, consistent with that in Boo et al. (2013, 2014). Interestingly, the *Capreolia* clade does not include any other species in the Gelidiaceae from Chile and/or Peru. Considering the endemic occurrence of *G. caulacanthum* in New Zealand and *G. hommersandii* in southeast Australia and New Zealand (Millar and Freshwater, 2005; Nelson, 2013), it seems highly probable that the common ancestor of *C. implexa* with either *G. caulacanthum* or *G. hommersandii* would have been in Australasian waters. The close relationship of Chilean populations with those in Stewart Island in both phylogeny and haplotype network of *cox*1 suggests that Chilean populations may be dispersed from the Stewart Island populations, as discussed below.

Although the *cox*1 and *rbc*L trees highlighted a single evolutionary origin for *C. implexa*, the analysis of the *cox*1 sequences revealed genealogical partitioning (Groups I and II), which differed from one another by up to 33 bp (2.4%). This degree of pairwise divergence is lower or similar to that (up to 2.7%) within *Gelidium crinale* (Boo et al., 2014). The distributions of these two groups were geographically separated into Australia/New Zealand and Chile/Stewart Island, the southern tip of New Zealand.

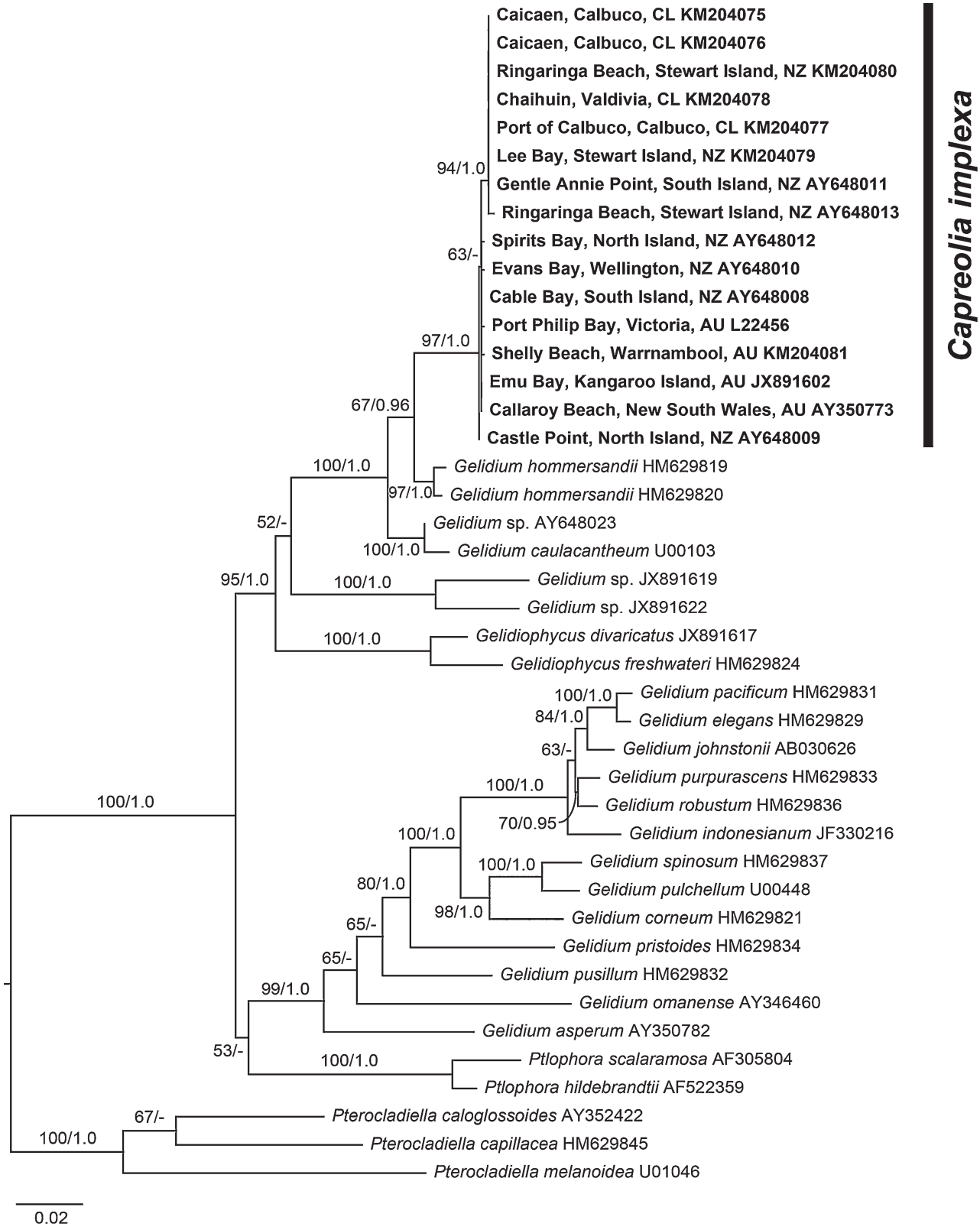

Fig. 2. Maximum likelihood tree of *Capreolia implexa* inferred from the phylogenetic analysis of *rbc*L sequences. Values shown near branches are bootstrap values (1000 iterations) and Bayesian posterior probabilities. Only bootstrap values >50% and Bayesian posterior probabilities >0.95 are shown.

Identical *rbc*L and *cox*1 sequences (except one *cox*1 in Calbuco) in *C. implexa* from Chile suggest genetic homogeneity of the three Chilean populations. However, these locations are very different environments; Chaihuin is very exposed with strong waves, Bahia Mansa is intermediate in wave exposure, and Calbuco is an extremely sheltered small port. Conversely, genetic diversity of *C. implexa* in *cox*1 is much higher (*Hd* 0.781 ± 0.102; π 0.0114 ± 0.0061) in Australia/New Zealand than

(*Hd* 0.077 ± 0.070; π 0.0001 ± 0.0002) in Chile. It is therefore concluded that the genetic homogeneity of *C. implexa* in Chile results from a trans-oceanic long distance dispersal by rafting likely after LGM from Stewart Island, New Zealand.

C. implexa grows on barnacles and small mussels and could easily form a bio-fouling community and move with these invertebrates on the hulls of vessels, both commercial and recreational (Thomsen et al., 2009) or along with commercial transportation of aquaculture species. Similarly, it is theoretically possible that planktonic propagules of *C. implexa* were introduced to Chilean harbors via ballast-waters exchange (Hewitt and Campbell, 2007), but given the typically short periods of viability of propagules of perennial algae (Santelices, 1990) it seems unlikely they would survive the voyage from New Zealand.

Table 1
Diversity measures of *cox*1 in *Capreolia implexa*.

	*cox*1				
	n	*h*	*S*	*Hd* ± SD	π ± SD
Chile	26	2	2	0.077 ± 0.070	0.0001 ± 0.0002
Australia	26	8	9	0.754 ± 0.073	0.0015 ± 0.0010
New Zealand	15	7	41	0.781 ± 0.102	0.0114 ± 0.0061

n, number of individuals; *h*, number of haplotypes; *S*, number of polymorphic sites; *Hd*, haplotype diversity; π, nucleotide diversity; SD, standard deviation.

Thus whilst it is possible that *C. implexa* was introduced to Chile via anthropogenic means, transportation has been uncommon between Stewart Island in New Zealand and Chile, and we do not have any data of deliberate movement of live species for

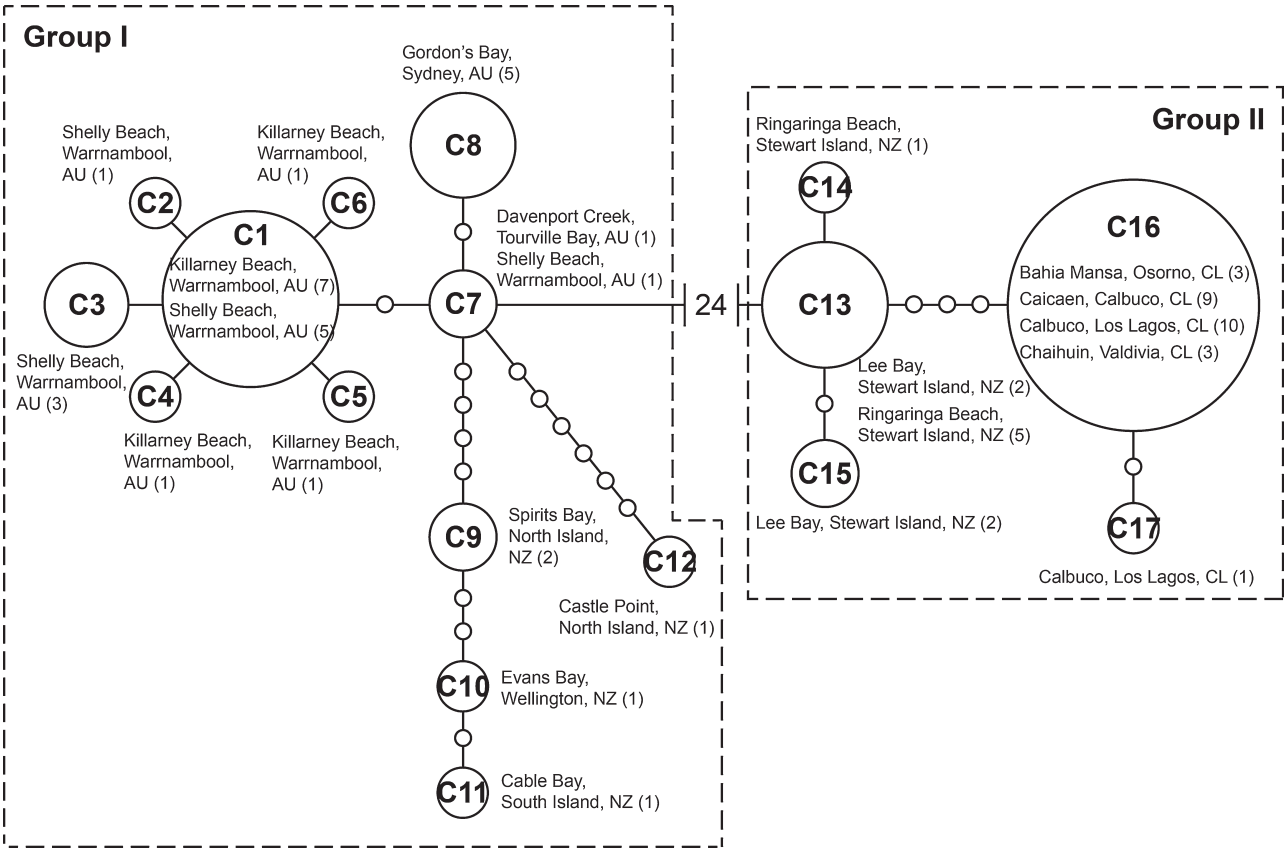

Fig. 3. Minimum-spanning tree of *Capreolia implexa* based on *cox*1 haplotypes. Circle sizes reflect haplotype abundances. Lines represent single mutational steps; small circles are inferred haplotypes not found in any sample. Numeral 24 indicates 24 mutation steps.

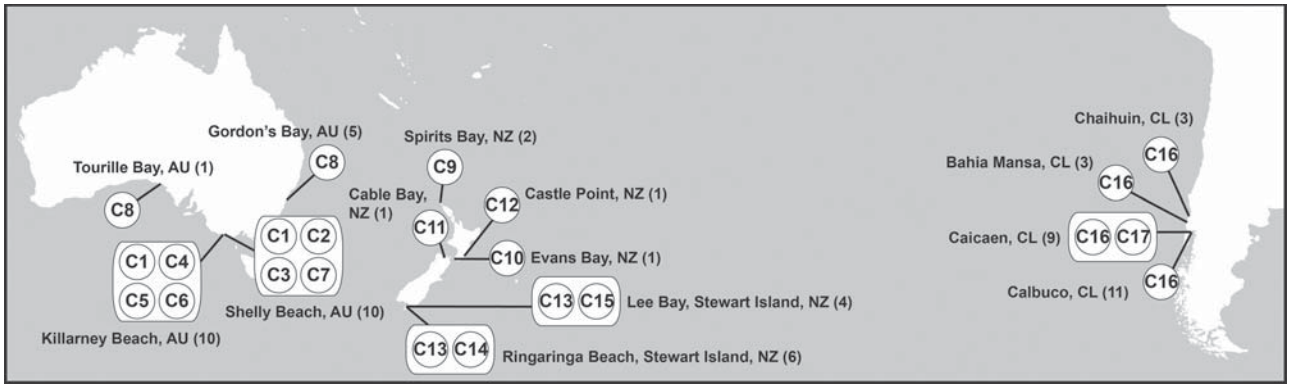

Fig. 4. Map of the *cox*1 haplotypes for *Capreolia implexa*. Parentheses indicate the number of specimens with same haplotype.

aquaculture, such as mussels, between these two countries. Indirect anthropogenic transport of *C. implexa* from Stewart Island to an intermediary location and then to southern Chile is also a possibility, but again we have no evidence to support this.

Of the possible vectors involved in the transport of *C. implexa* from Stewart Island directly to southern Chile, we consider rafting along the West Wind Drift at the end of last glacial maximum to be the most probable, as has been suggested for marine algae between Chile and New Zealand in previous studies (Boedeker et al., 2010; Fraser et al., 2011, 2013; Macaya and Zuccarello, 2010). Rafts are formed mainly by floating kelps and bull kelps, and invertebrates such as barnacles, decorator crabs, and mussels (Thiel and Gutow, 2005). Tree trunks or floating timber may also be vectors (Fraser et al., 2011; Hinojosa et al., 2011): *C. implexa* grows well on wooden surfaces as evidenced by its growth on jetty poles in Calbuco, Chile as well as on fallen logs and trees trunks in the high intertidal in New Zealand.

The dispersal of *C. implexa* within Chile may occur with floating objects along the Chilean coast (Hinojosa et al., 2011). However, because Calbuco is a key center for aquaculture of oysters in Chile (Buschmann et al., 2008), oyster transportation may be another pathway by which this species is spread as shown in many cases of invasive macroalgae elsewhere (Miller et al., 2011; Mineur et al., 2012). Because *C. implexa* was relatively abundant in the intertidal region of the Chilean locations in this study, the impact of this species to intertidal communities should be carefully tracked in the future. For example, *C. implexa* may rapidly reproduce, grow, and spread in the new distribution area with a high dispersal rate. It may also change the composition of seaweed grazers and other invertebrates, and affect biodiversity of the intertidal organisms.

In conclusion, our study presents the first record of the agarophyte, *C. implexa*, along the south Chilean coast and its possible origin from populations from Stewart Island, New Zealand. The introduction of *C. implexa* to the flora constitutes a substantial addition to the collective gene pool of the economic agar-producing algae in Chile. Future studies should aim to both clarify the extent of *C. implexa* in Chile and provide further evidence to discriminate between the hypotheses of anthropogenic transport versus rafting to explain the introduction of *C. implexa* from New Zealand demonstrated by our data. This will be an important contribution to our understanding of global patterns of species-reshuffling by ocean currents (Bates et al., 2014).

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