

Research Article

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The phylogeographic history of amphitropical *Callophyllis variegata* (Florideophyceae, Rhodophyta) in the Pacific Ocean

Trevor T. Bringloe^{1,*}, Erasmo C. Macaya^{2,3,4} and Gary W. Saunders¹

¹Centre for Environmental and Molecular Algal Research (CEMAR), Biology Department, University of New Brunswick, P.O. Box 4400, Fredericton, New Brunswick E3B 5A3, Canada

²Laboratorio de Estudios Algales (ALGALAB), Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile

³Millennium Nucleus Ecology and Sustainable Management of Oceanic Islands (ESMOI)

⁴Centro FONDAF de Investigaciones en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Independencia 631, Valdivia, Chile

Chilean species of marine macroalgae with amphitropical distributions oftentimes result from introductions out of the Northern Hemisphere. This possibility was investigated using haplotype data in an amphitropical red macroalgae present in Chile, *Callophyllis variegata*. Published sequence records from Canada and the United States were supplemented with new collections from Chile (April 2014–November 2015). Specimens of *C. variegata* were amplified for the 5' end of the cytochrome *c* oxidase subunit I gene (COI-5P) and the full length nuclear internal transcribed spacer region. Haplotype networks and biogeographic distributions were used to infer whether *C. variegata* was introduced between hemispheres, and several population parameters were estimated using IMA2 analyses. *C. variegata* displayed a natural amphitropical distribution, with an isolation time of approximately 938 ka between hemispheres. It is hypothesized that contemporary populations of *C. variegata* were established from a refugial population during the late Pleistocene, and may have crossed the tropics via rafting on buoyant species of kelp or along deep-water refugia coincident with global cooling, representing a rare case of a non-human mediated amphitropical distribution.

Key Words: amphitropical; Chile; IMA2; non-native; red algae

Abbreviations: ITS, internal transcribed spacer; ka, thousand years; Ma, millions of years

INTRODUCTION

Studies on the phylogeographic history of seaweeds is a burgeoning field (Hu et al. 2016). As genetic data become increasingly available, phycologists are exploring the phylogeographic history of macroalgal species in the context of glaciation events (Maggs et al. 2008, Li et al. 2016), long distance dispersal via rafting on buoyant species of kelp (Fraser et al. 2011, Saunders 2014, Ma-

caya et al. 2016, López et al. 2017) and human-mediated introductions (Thomsen et al. 2016). Such fundamental understanding regarding the origins of local flora serve as critical baseline data during a time of increasing human activities and climate change. Whether a species is considered native or introduced, in particular, has implications for how it is treated in ecological studies and



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*Corresponding Author

E-mail: Trevor.Bringloe@unb.ca

management efforts.

Several temperate species of macroalgae have disjunct populations occurring in both hemispheres (i.e., amphitropical), many of which are the result of introductions out of the North. For instance, most of the 14 macroalgal species reported as being introduced to Chilean waters by Villaseñor-Parada et al. (2018) have distributions in the Northern Hemisphere, 12 of which are considered of northern origin. Another example of a possible introduction into the Southern Hemisphere is *Ahnfeltia plicata* (Hudson) Fries, which has a broad distribution range extending across both sides of the North Atlantic but has several genetically verified records in Australia and Southernmost Chile (Milstein and Saunders 2012). *Mastocarpus* is a genus with species distributions previously restricted to the North Pacific before it was recorded in Chilean waters nearly four decades ago, and is thus considered an introduced species to the Southern Hemisphere (Lindstrom et al. 2011, Macaya et al. 2013). Though this non-native species was initially identified as *Mastocarpus papillatus* (C. Agardh) Kützinger (Castilla et al. 2005), Lindstrom et al. (2011) identified this species as *Mastocarpus latissimus* (Harvey) S. C. Lindstrom, Hughey & Martone based on an internal transcribed spacer (ITS) sequence from a Chilean specimen, collected at “La Desembocadura” Biobío region. In contrast to the above examples, *Asparagopsis armata* Harvey has been widely introduced from Australia and New Zealand to northern temperate waters (Ní Chualáin et al. 2004).

Though many amphitropical species are the result of introductions, haplotype data in some species indicate this distribution can occur naturally. *Polysiphonia morrowii* Harvey, for example, has private haplotypes occurring in the Northwest Pacific, Northeast Atlantic, and Southwest Atlantic, leading Geoffroy et al. (2016) to designate it as a cryptogenic species, though they note multiple introductions could be contributing to the haplotype pattern, a conclusion consistent with earlier reports for this species (Kim et al. 2004). The buoyant brown alga *Macrocystis pyrifera* (Linnaeus) C. Agardh likely originated in the North Pacific, with dispersal into the Southern Hemisphere sometime within the past 3 millions of years (Ma) (Coyer et al. 2001, Astorga et al. 2012). *Laminaria* is also hypothesized to have crossed the equator on two separate occasions in the Atlantic, giving rise to *Laminaria abyssalis* A. B. Joly & E. C. Oliveira and *Laminaria pallida* Greville (Rothman et al. 2017). *Callophyllis variegata* (Bory) Kützinger also exhibits a disjunct distribution spanning both hemispheres in the East Pacific, but its population history remains unresolved. *Callophyll-*

lis is considered a speciose genus spanning both hemispheres, however, considerable taxonomic confusion persists in this group (Saunders et al. 2017). The type locality for *C. variegata* occurs in Chile (Arakaki et al. 2011), yet this species groups with a well-supported cluster of *Callophyllis* sensu stricto species occurring in the Northeast Pacific (Saunders et al. 2017), suggesting it speciated in the North Pacific and subsequently moved south. Though this species was first described in the South Pacific, the disjunct distribution and its phylogenetic relationship with North Pacific species open the possibility that *C. variegata* may be non-native to Chile.

This study sought to investigate haplotype patterns in amphitropical populations of the red algae *C. variegata*. This species is among the economically important seaweeds of Chile, which are harvested for carrageenan and human consumption (Buschmann et al. 2001, Castilla and Neill 2010, Mansilla et al. 2012). Utilizing population level data, the objectives of this study were to (1) determine if *C. variegata* was introduced between hemispheres; and (2) if *C. variegata* has been introduced, determine what hemisphere it was introduced out of, or, alternatively, if *C. variegata* has a naturally occurring amphitropical distribution, what is the nature of its population history (e.g., isolation time, effective populations sizes, migration rates).

MATERIALS AND METHODS

In order to study the phylogeographic distribution of *C. variegata*, records were amalgamated from several collection episodes spanning 1998-2010, and supplemented with sampling of Chilean specimens (i.e., new samples to this study; April 2014-November 2015) (Supplementary Table S1). During collection, specimens were preserved in silica gel and brought back to the University of New Brunswick for DNA extraction (Saunders and McDevit 2012) and amplification of the 5' end of the cytochrome *c* oxidase subunit I gene (COI-5P) using M13LF3 and M13Rx forward and reverse primers (Saunders and Moore 2013). The full length nuclear ITS was amplified using P1 and G4 forward and reverse primers (Saunders and Moore 2013). Polymerase chain reaction products were sent to Genome Quebec for forward and reverse sequencing using the sequencing primers M13F and M13R for COI-5P, and P1 and G4 for ITS. All genetic data were edited in Geneious ver. 10.2.3 (Kearse et al. 2012). The lengths of the sequenced amplicons were 664 and 683 base pairs for COI-5P and ITS, respectively. See Supple-

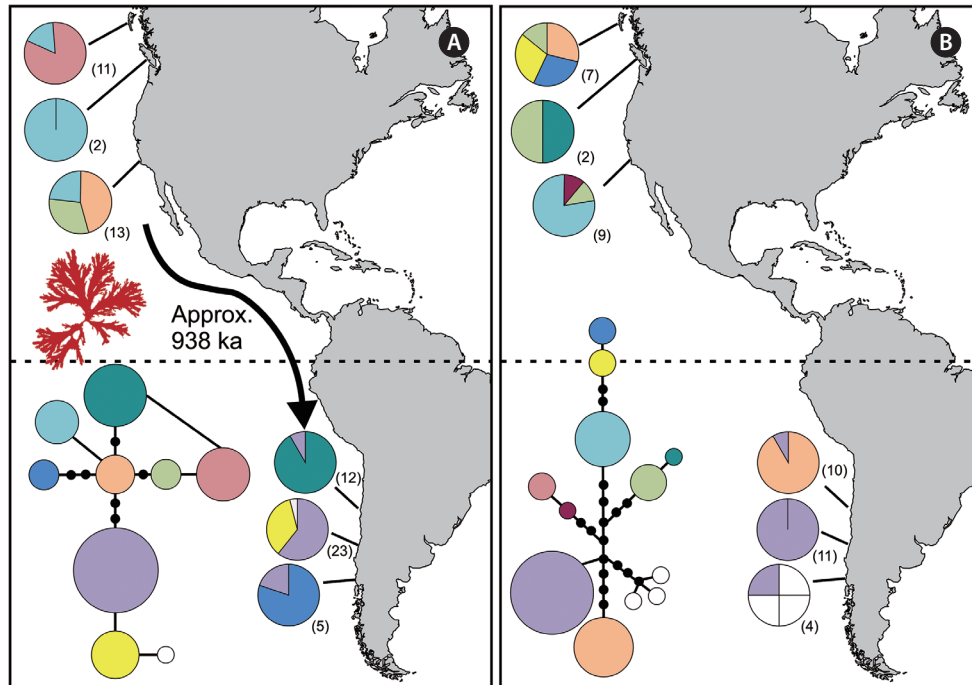


Fig. 1. *Callophyllis variegata* haplotype networks and biogeographic distributions in the Pacific Ocean for mitochondrial COI-5P (A) and nuclear internal transcribed spacer (ITS) (B) genes. The dashed line represents the equator. Numbers in parentheses refer to sample sizes from given sites. Black circles indicate hypothesized substitutions between clades. The size of the circles is proportional to sampling frequency. In the COI-5P map, the arrow refers to the putative migration event that established populations in the Southern Hemisphere, including the estimated isolation time estimate (ka).

mentary Table S1 for GenBank accession numbers. Insertions and / or deletions were removed from these networks, as were heterozygous individuals (Supplementary Table S1).

IMa2 analyses were used to test various population scenarios in *C. variegata* and to estimate the timing of divergence between North and South populations. A two-population model (North and South) with migration was tested using a previously calibrated COI-5P clock of $0.007 \text{ substitutions site}^{-1} \text{ Ma}^{-1}$ (Bringloe and Saunders 2018). The mutation rate for ITS was scaled during IMA2 analyses (IMa2 flag: -y1.1826256). Sequences with ambiguities (i.e., sharing signatures of multiple populations, as in, putatively recombinant haplotypes) were removed from the IMA2 analyses. Once run parameters (priors, heating terms) were optimized, five independent two million length chains were run using an HKY substitution model, and geometric heating ($hn = 10$), with sampling every 100 steps, for a total of 20,000 genealogies saved run^{-1} . The results from the five runs were combined using L mode, sampling 20,000 saved genealogies, and log-likelihood ratios were used to determine if the full model tested could be rejected in favour of a given nested model

(Supplementary Table S2). Values for isolation time and historical effective population sizes are presented in demographic units; the values for effective population size assume a generation time of 1 year.

RESULTS

In total, COI-5P data were obtained for 28 North Pacific and 40 South Pacific specimens of *Callophyllis variegata*, while ITS data were also obtained for 23 and 32 North and South Pacific specimens, respectively (Supplementary Table S1). Within the ITS data, 6 specimens shared genetic signatures with multiple populations (i.e., additivity at a given site), though none shared signatures between the two hemispheres (Supplementary Table S1). In addition, no haplotypes were shared between North and South hemispheres for *C. variegata* in both the COI-5P and ITS data. North and South populations were reciprocally monophyletic for the ITS data, but this was not the case for COI-5P (Fig. 1). IMA2 analyses converged on similar values for historical effective population sizes for *C. variegata* in the North and South Pacific, while the

posterior probability for the ancestral population size was largely flat, showing a modest peak at smaller values (Table 1, Fig. 2). Posterior probabilities on migration between North and South populations peaked at 0 (Table 1, Fig. 2). The posterior probability for isolation time between North and South populations peaked at 938 ka, with a flat posterior at higher values (Table 1, Fig. 2).

DISCUSSION

Amphitropical species in the Southeast Pacific, particularly along the Chilean coastline, are typically reported as potential introductions from the Northern Hemisphere (Castilla et al. 2005). *Callophyllis variegata* occurs in the North and South Pacific, but its phylogeographic history remained unresolved. Here, it was determined that *C. variegata* exhibits a naturally occurring distribution between hemispheres, as in, its distribution does not appear to have been mediated by recent human activity. This was first evidenced by the lack of shared haplotypes between North and South populations (Fig. 1). Interestingly, the COI-5P data exhibited signs of incomplete lineage sorting, in contrast to the ITS results (Fig. 1). The northern and center portions of the Chilean coastline are characterized by patchy populations and strong genetic drift in algal populations, facilitated in part by recurrent bottlenecks due to El Niño events and tectonic activity (Guillemin et al. 2016). These factors, combined with the constrained effective population size of the mitochondrial genome, likely result in mutations becoming rapidly fixed in Chilean sub-populations. If the ancestral Chilean COI-5P haplotype has since diverged in several directions with little gene flow between populations, this in turn would hamper the sorting of Southern lineages from Northern populations. The ITS data, in contrast, demonstrated that Southern lineages have sorted completely from Northern counterparts (Fig. 1B), further corroborating our conclusion that *C. variegata* has a natural amphitropical distribution.

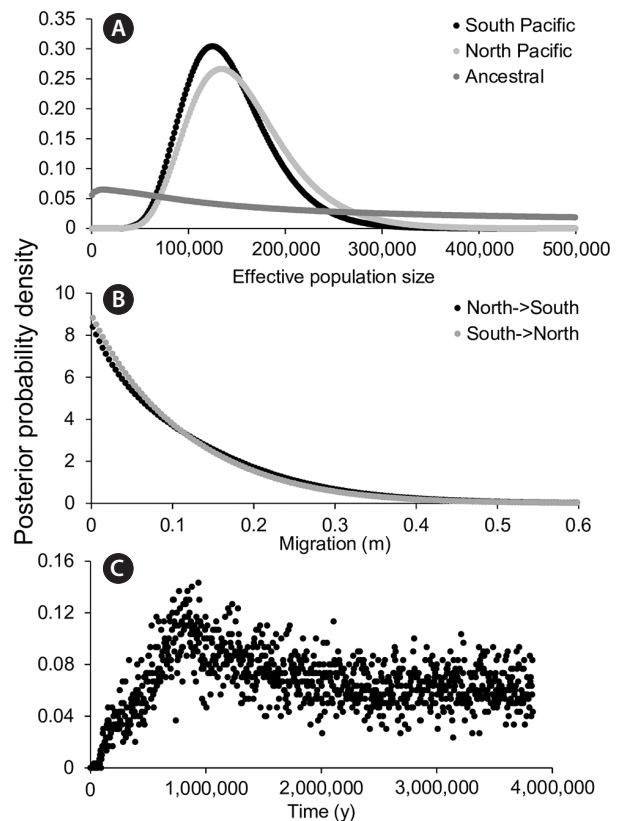


Fig. 2. Posterior probabilities for effective population sizes (A), migration rates (B), and isolation time (years) (C) based on 100,000 sampled COI-5P and internal transcribed spacer genealogies in *Callophyllis variegata*.

North and South populations of *C. variegata* likely stemmed from a refugial northern population during the Pleistocene. In particular, *C. variegata* is phylogenetically embedded in a well-supported clade of North Pacific species (Saunders et al. 2017), suggesting the species originated in the Northern hemisphere. Given the alternative scenario (speciating in the Southern Hemisphere) requires *C. variegata* to have migrated across the tropics twice, it can be speculated that speciation in the Northern Hemisphere is the most plausible history.

Table 1. Values for population parameters for amphitropical *Callophyllis variegata*, estimated using IMA2

| Value | Isolation time (y) | q South | q North | q ancestral | m North to South | m South to North |
|--------------|--------------------|---------|---------|-------------|------------------|------------------|
| High point | 937,790 | 125,454 | 133,445 | 11,986 | 0.002 | 0.002 |
| 95% HPD low | 404,650 | 61,528 | 63,127 | 0 | 0 | 0 |
| 95% HPD high | 3,829,790 | 235,726 | 264,493 | 1,466,296 | 0.322 | 0.302 |

High point refers to the peak value in the posterior distribution.

q, effective population size (number of individuals, assuming a generation time of 1 year); m, migration scaled by the mutation rate per generation ($m = M/u$); HPD, highest posterior density.

Further supporting this hypothesis, the putative ancestral haplotype according to coalescent theory should be the central haplotype in the COI-5P network (depicted as orange) (Fig. 1A), which occurs in the Northern Hemisphere (Castelloe and Templeton 1994); the ancestral haplotype in ITS presumably has been lost or has yet to be sampled (Fig. 1B). The lack of detectable historical migration between hemispheres also suggests gene flow between North and South populations is exceedingly rare (Table 1, Fig. 2). Also noteworthy is that the historical effective population sizes of North and South populations were nearly the same (Table 1, Fig. 2), closely approaching significance in terms of being favorable compared to the full (free to vary) IMA2 model ($p = 0.945$) (Supplementary Table S2). This complicates interpretation of the location of origin for *C. variegata*; had one historical effective population size been significantly greater than the other, a longer population history could be inferred from a given hemisphere. The similar historical effective population sizes of North and South populations of *C. variegata* further suggests these populations were established from the same source at approximately the same time. It is possible these populations originated from a refugium that occurred south of Northern Hemisphere ice sheets during the Pleistocene, through considerably more sampling would be needed to establish a refugial location (see Dyke and Prest 1987 for Northern Hemisphere ice sheets during the Last Glacial Maximum). Indeed, IMA2 analyses estimated the isolation time between North and South populations to be approximately 938 ka, a time during which glaciation events were shifting towards 100 ka cycles (note the minimum Highest Posterior Density estimate of 404 ka and an unresolved maximum value) (Table 1, Fig. 2) (Lisiecki and Raymo 2005, Miller et al. 2010).

If contemporary populations of *C. variegata* were established in both hemispheres from a glacial refugial source, this may explain how the species was able to cross into the Southern hemisphere. Glaciation will have constricted temperate regimes towards the equator, pushing the ancestral population of *C. variegata* into southerly waters and likely creating a genetic bottleneck (Bennett and Provan 2008). Movement across the tropical barrier into the Southern Hemisphere may have been facilitated by buoyant species of kelp, which are known to raft other species of algae and invertebrates across large oceanic distances (Fraser et al. 2011, Saunders 2014, Macaya et al. 2016). Rafting of *C. variegata* along the Chilean coastline may have also occurred (López et al. 2017), though sampling from more sites is needed to

confirm this hypothesis. *M. pyrifera* is a candidate for having transported *C. variegata* across the equator, as populations in the Southern Hemisphere are thought to have been established from Northern populations during the Pleistocene (Coyer et al. 2001, Astorga et al. 2012). Indeed, several species of *Callophyllis* have been linked with transport on buoyant species of macroalgae, including *C. variegata* (Macaya et al. 2016). In an experimental study, Edgar (1987) recorded *Callophyllis rangiferina* (R. Brown ex Turner) Womersley growing on *M. pyrifera* after more than half a year at sea, which suggests *C. variegata* could have survived the long journey across the equator. Alternatively, if *C. variegata* persisted in deep water refugia (Graham et al. 2007), it may have crossed without the aid of rafting kelp by using these refugia as stepping stones. Though this hypothesis is rather speculative, recent work has revealed red bladed species of macroalgae growing in deep water tropical habitats; for instance, *Cryptonemia abyssalis* C. W. Schneider & Popolizio is a recently described species collected from a depth of 90 m off the coast of Bermuda (Schneider et al. 2018). The patterns observed here seem tenable to the first hypothesis (i.e., no contemporary connectivity between North and South populations) (Table 1, Fig. 2).

Conclusion

Introductions of marine algal species are a concern worldwide. Though the Southeast Pacific coastline is relatively “pristine” compared to other areas (Thomsen et al. 2016), it has not been exempt from human-mediated introductions of species (Castilla et al. 2005, Castilla and Neill 2010). The results presented here have demonstrated that the amphitropical *C. variegata* has a natural distribution across both hemispheres, and that contemporary North and South populations were likely established during the late Pleistocene, possibly via rafting on *M. pyrifera* (Coyer et al. 2001). Regardless of how *C. variegata* managed to cross the tropical barrier during the Pleistocene, it serves as a rare example of a species of algae with a non-human mediated amphitropical distribution.

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SUPPLEMENTARY MATERIAL

Supplementary Table S1. Specimen list and collection information for *Callophyllis variegata* (<https://www.e-algae.org>).

Supplementary Table S2. Log-likelihood ratio tests for simplified IMA2 models (<https://www.e-algae.org>).

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