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Molecular divergence between *Iridaea cordata* (Turner) Bory de Saint-Vincent 1826 populations from Antarctic Peninsula and the Magellan Region

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Abstract

The distribution of the Southern Ocean (SO) biota is the result of major geologic, oceanographic and climate changes during the last 50 million years (Ma). Several groups of marine benthic organisms exhibit marked taxonomic similarities between Antarctic Peninsula and southern South America where families, genera and even species are currently co-distributed in these continents. Several species of macroalgae such as *Gigartina skottsbergii*, *Plocamium cartilagineum*, *Iridaea cordata*, are currently found at both sides of the Drake Passage. Advances in molecular techniques have allowed to determine their phylogenetic relationships and level of divergence between populations from these continents in order to determine whether they constitute separate evolutionary units. In this study we determine whether *Iridaea cordata* represents the same evolutionary unit in southern South America and the Antarctic Peninsula or if populations at both sides of the Drake Passage, separated by the Antarctic Polar Front (APF), represent putative cryptic species. According to our results, *I. cordata* populations from Antarctic Peninsula and South America are clearly distinguishable evolutionary units with a 8.31% and a 3.17% mtDNA and cpDNA molecular divergence, respectively. The separation between Antarctic and South American populations of *I. cordata* occurred at the end of the Miocene between 5 Ma (rbcL) and 9 Ma (COI-5P). These results are similar to those recorded in *G. skottsbergii* on both sides of the Drake Passage. Accordingly, *I. cordata* populations at both sides of the Drake Passage include two cryptic species. In this context, cryptic speciation plays an important role in the evolution of the Southern Ocean and accordingly, the systematic, biogeography and biodiversity of the region require major revisions.

Keywords: Southern Ocean, Rhodophyte, biogeography, Antarctic Circumpolar Current, cryptic speciation, vicariance.

Introduction

The Southern Ocean (SO) covers an area of around $35 \times 10^6 \text{ km}^2$ encircling the Antarctic continent. It represents 8% of the world's ocean surface and is considered as a major driver of global oceanic circulation (Rintoul et al. 2001). This vast region harbors ~ 5% of the marine biodiversity (Barnes et al. 2009) and the distribution of its biota mainly reflects the dynamic geologic, oceanographic, and climate history (Crame 1999; Aronson et al. 2007; Clarke 2008; Saucède et al. 2014). Marine benthic communities in the SO are unique and exhibit particular characteristics that are probably associated to ecological and evolutionary responses to low temperatures, strong seasonal variations in light conditions, and to short periods of primary production making them particularly vulnerable to climate change (Barnes & Peck 2008; Griffiths et al. 2017). Biogeographers recognize three periods that dramatically affected the distribution of the biota in the region (Mackensen 2004; Poulin et al. 2014). First, the Eocene/Oligocene boundary (~34 Ma) related to major oceanic gateway openings, the onset of the Antarctic isolation, and the initiation of the Antarctic Circumpolar Current (ACC) (Zachos et al. 2001). The middle Miocene (~14 Ma) represents a second period of major oceanographic and climatic changes that affected the intensity of the ACC and thermal latitudinal gradients (Zachos et al. 2001). Finally, the Quaternary characterized by the alternation between glacial and interglacial periods strongly influenced the seasonality and the intensity of sea-ice formation (Gersonde et al. 2005; Kemp et al. 2010).

In spite of the complex oceanographic and tectonic settings there are strong biogeographic links between the biota from Antarctic Peninsula and the Magellan Province (Arntz 1999; Arntz et al. 2005). Families, genera, and even species of marine near-shore benthic organisms are shared between these areas and the general explanation of this “Antarctic-Magellanic Connection” is that these provinces were once contiguous and progressively drifted apart through the opening of the Drake Passage (Crame 1999). Currently, the ACC is delimited by two main fronts: i) the Antarctic Polar Front (APF) and the sub-Antarctic Front (SAF) and their respective positions have major influence over the biogeography of the region. However, several studies have demonstrated that larvae and rafted organisms may travel across the APF using eddies or intrusions of sub-Antarctic waters masses through the ACC (Clarke et al. 2005). New evidence from observations of floating kelps at sea indicate that the APF can actually be crossed by some marine organisms suggesting that the absence of many sub-Antarctic taxa in the Antarctic might be largely due to environmental differences at both sides of the front more than a complete APF impermeability (Fraser et al. 2017).

Integrative biogeographic studies in SO marine benthic organisms have helped to understand [the](#) relative role of vicariance versus dispersal in the biogeography of the region and have helped for taxonomic revisions showing the presence of hidden cryptic diversity (Krabbe et al. 2008; Dornburg et al. 2016; Billard et al. 2015). Several groups of marine organisms including invertebrates (Patarnello et al. 1996), vertebrates (Clarke and Johnston 1996), and macroalgae (Hommersand et al. 1994; Silberfeld et al. 2010) exhibit major levels of genetic divergence between SO provinces supporting the role of vicariance. Nevertheless, new molecular studies are showing that the origin and diversification of several marine groups occurred long after

the physical separation of the continental landmasses (Near et al. 2012; Poulin et al. 2014; Billard et al. 2015). This study aims at estimating patterns of genetic divergence between co-distributed Antarctic and Magellanic populations of the rhodophyte *Iridaea cordata*, a cold adapted species broadly distributed in different provinces of the SO (Wiencke 1990; Wiencke and Clayton 2002). This species is a member of the Gigartinae and common in shallow sub-tidal communities but can also be found down to a depth of 30 m (Wiencke and Amsler 2012). The species produces large quantities of carrageenans (Craigie 1990) have economic importance and is harvested in southern Chile [jointly](#) with other carragenophytes (i.e. *G. skottsbergii*, *Mazzaella laminarioides* and *Sarcothalia crispata*). Economic incomes from carrageenan extraction is particularly important in Patagonia and Tierra del Fuego and have been affected by the steady decline of *G. skottsbergii* natural stands due to over exploitation (Buschmann et al. 2001). A shift through complementary exploitation of other carragenophytes genera, including *Iridea* has been propose as a mechanism to allow the recovery of the *G. skottsbergii* stands by diversification of exploited resources. Nevertheless, apart from *Gigartina*, higher latitude carragenophytes genera have not been intensely studied and key information concerning taxonomy, distribution of genetic diversity, and potential ecological adaptation are strongly required. Preliminary phylogenetic analyses in *I. cordata* recorded a 3.4% of cpDNA divergence between Antarctic and Magellanic populations (Hommersand et al. 1999; Hommersand and Fredericq 2003). In order to corroborate these results, we performed molecular comparisons using cpDNA (*rbcL*) and mtDNA (COI-5P) sequences to determine the actual number of evolutionary units and to determine the divergence time between populations of the species from both sides of the Drake Passage.

Material and Methods

Samplings

Individuals of *Iridea cordata* (Rhodophyta; Fig. 1) were collected between 2011-2016 from five localities across Antarctic Peninsula and the Magellanic Province. Sampling localities are as follows: 1) Avian Island, Marguerite Bay (67°45'S; 68°52'W, *n* = 2); 2) Hannah Point, Livingstone Island, South Shetland Islands (62°41'S; 60°52'W, *n* = 4); 3) Fildes Bay, King George Island, South Shetland Islands (62°11'S; 58°56'W, *n* = 4); 4) Diego Ramírez Island, Cape Horn (56°27'S; 68°43'W, *n* = 5); and 5) Otway Sound, Strait of Magellan (52°58'S; 71°13'W, *n* = 5). Fronds were sampled from distinct holdfasts to avoid the analyses of genetically identical ramets (Billard et al. 2015). Samplings were conducted in the intertidal during low tides and healthy fronds were cut and placed into a plastic bag filled with silica beads for rapid desiccation of the tissue and DNA preservation.

DNA preparation, PCR amplification and sequence edition

Dried algal tissue was grounded using a Bead beater and DNA was prepared following two protocols: i) a phenol-chlorophorm methodology (Faugeron et al. 2001) and b) a cetyl trimethylammonium bromide (CTAB) methodology (Martinez et al. 2003). A partial fragment of the mitochondrial gene cytochrome c oxidase subunit I (COI-5P) was amplified using the specific primers GazF1 and GazR1 (Saunders 2005). At the same

time, a partial fragment of the chloroplastic gene Ribulose-1,5-biphosphate carboxylase/oxygenase (*rbcL*) was amplified using specific primers F-*rbcL* and R-*rbcL* (Guillemin et al. 2015). PCR amplifications were done in a 25 ul reaction containing 2.5 ul 10X Buffer (50 mM KCl, 10 mM Tris-HCl, pH 8.0). 0.7 ul of 50 mM MgCl₂, 200 mM dNTPs, 1.25 ul of each primer (10 pg/ul), 1 ul DMSO, 1 U Taq polymerase (Invitrogen), 15.6 ul of double-distilled water and 50 ng of DNA. Thermal cycling parameters for COI-5P included an initial denaturation step at 94°C for 5 min, 5 cycles at 94°C (30 sec), 40°C (30 sec), and 72°C (30 sec), followed by 30 cycles of 94°C (30 sec), 56°C (30 sec) and 72° (30 sec), and a final extension at 72°C for 7 min. Thermal cycling parameters for *rbcL* included an initial denaturation step at 96°C for 4 min, 5 cycles of 94°C (30 sec), 45°C (30 sec), and 72°C (30 sec), followed by 30 cycles of 94°C (30 sec), 56°C (30 sec), and 72° (30 sec), and a final extension at 72°C for 7 min. PCR amplicons were purified and sequenced in both directions with an ABI3730 Automatic Sequencer at Macrogen Inc. (Seoul, South Korea). Chromatograms were inspected and edited using Proseq v.3.5 (Filatov 2009), and multiple alignments were obtained independently for each molecular marker using Muscle (Edgar 2004). Base composition of nucleotide sequences was analyzed independently for each marker using MEGA 7.0 (Kumar et al. 2016) and codon usage was determined using the effective number of codon value (ENC; Wright 1990) with DnaSP 5.0 (Librado and Rozas 2009). New COI-5P and *rbcL* sequences in *I. cordata* have been deposited in Genbank under the Accession Numbers XXXXX-XXXXX and XXXXX-XXXXX, respectively.

Phylogenetic reconstructions, maximum parsimony networks and divergence time estimations

Phylogenetic reconstructions included *I. cordata* populations from Antarctic Peninsula and the Magellan region. For comparative purposes we also included in the analyses available COI-5P and *rbcL* sequences of other rhodophytes such as *Chondrus*, *Chondracanthus*, *Gigartina*, *Mazzaella*, and *Sarcothalia* (Table 1). For *rbcL* reconstructions we used two outgroups (*Mastocarpus stellatus* and *Phyllophora crispa*) following Hommersand et al. (1994). Similarly, in the case of COI-5P we used two outgroups *Dumontia contorta* and *Asteromenia bermudensis* following Saunders (2005).

Phylogenetic relationships in rhodophytes were estimated using different reconstruction methods including maximum parsimony (MP), maximum likelihood (ML), and bayesian analysis (BA). MP and ML reconstructions were performed using MEGA. For maximum parsimony reconstructions we used the following assumptions: characters were treated as equally weighted using a tree bisection and reconnection (TBR) heuristic search with the branch swapping option. Non-parametric bootstrap (bs) values were estimated to infer nodal support for both the MP and the ML with 1000 pseudo-replicates (Felsenstein 1981). Nucleotide substitution models for ML and BA were determined with jModelTest (Darriba et al. 2012) through the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), respectively. The TN93 + G (*rbcL*) and the GTR + G (COI-5P) substitution models were used for ML and BA reconstructions using MEGA and MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001), respectively. Bayesian inference posterior probabilities were estimated using the Metropolis coupled Markov chain Monte Carlo (MCMC) algorithm running four chains for 50 x 10⁶ generations with tree sampled every 1000 generations. Stationarity of the analyses was inferred when the average standard deviation of split frequencies was less

than 0.01 following Huelesenbeck and Ronquist (2001). The first 10% of the trees were discarded (burn-in) and posterior probabilities were estimated as the fraction of trees showing a particular nodal association. Posterior probability densities were summarized as a Maximum Clade Credibility Tree (MCCT) using Treeannotator v.1.6.1. (<http://beast.bio.ed.ac.uk/TreeAnnotator>) and visualized with Figtree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree>).

For comparative purposes, we also reconstructed mtDNA and cpDNA genealogical relationships within Antarctic and South American *I. cordata* populations using maximum parsimony networks in Hapview (Salzburger et al. 2011). This method allows the simple reconstruction of phylogenetic relationships based on intra- and inter-specific molecular data sets.

Divergence time estimations were performed in BEAST v.1.6.2 (Drummond et al. 2012). The best-fit model for the mtDNA COI-5P and *rbcL* data sets was a relaxed molecular-clock analyses with an uncorrelated lognormal (ucln) model of evolutionary rate heterogeneity using the GTR + G and the XXX substitution models, respectively. A birth-death speciation prior was used for branching rates in the phylogeny, four chains were run twice for 100×10^6 generations, and trees were sampled every 1000 generations. Because of the absence of clear fossil records in rhodophytes we used conservative mutation rates (0.5% for COI-5P and 0.2% for *rbcL*), following previous studies in the group (Kamiya et al. 2004; Billard et al. 2015). Convergence of model parameters was estimated by plotting the marginal posterior probabilities versus the generations in TRACER. Effective sample-size values were estimated for each parameter to ensure adequate mixing of the MCMC (ESSs > 1000).

Results

Mitochondrial DNA (COI-5P) alignments in *Iridaea cordata* populations (609 bp) coded for 203 amino acids and included 50 variable positions (8.21%) of which 49 (98%) were parsimoniously informative. Chloroplast DNA (*rbcL*) sequences in the species (869 bp) coding for 289 amino acids, were more conserved with only 24 variable positions (2.76%), and all of them (100%) parsimoniously informative. Mitochondrial and chloroplast sequences were A-T rich. Mitochondrial and nuclear sequences were not saturated at any position and no evidence for codon bias was detected for COI-5P (ENC = 43.23) and *rbcL* (ENC = 39.47). No indels or stop codons were identified within the analyzed *I. cordata* populations. In the case of COI-5P we found five amino acid changes (positions 1, 48, 143, 149, and 164) between Antarctic and Magellan populations. In contrast, just a single amino acid change was recorded for the *rbcL* between Antarctic and Magellan populations.

Reconstructions using different sources of DNA (mtDNA and cpDNA) corroborated previous molecular analyses in rhodophytes and discriminated major taxonomic groupings (Hommersand et al. 1999; Saunders 2005) with high bootstrap values and posterior probabilities (Fig. 2A and 2B). All the methods (MP, ML, and BA) and markers showed that *I. cordata* populations from both sides of the Drake Passage represent different evolutionary units and sister species (Fig. 2A and 2B). Uncorrected p-values between these units are 8.31% and 3.17% for COI-5P and *rbcL* (Fig. 3A and 3B), respectively. Divergence time estimates based on COI-5P sequences, under a 95% Bayesian confidence credible interval for BCI for relative divergence times (Fig. 4),

suggest that the separation between *I. cordata* populations from Antarctic Peninsula and the Magellan region occurred during the Miocene around 9.0 Ma (16 – 7 Ma). Similarly, divergence time estimates based on *rbcL* sequences suggest that the separation between Antarctic Peninsula and South American populations of *I. cordata* occurred approximately 5 Ma (4 – 6 Ma).

Discussion

Recent advances in molecular technologies have allowed to further understand the evolution and biogeography of the SO biota (Allcock and Strugnell 2012; Poulin et al. 2014; Billard et al. 2015). During the last decade, SO macroalgae have been subjected to several studies that generated key advances in the comprehension of phylogenetic relationships, systematics, biogeographies and actual patterns of diversities (Hommersand et al. 2009; Wiencke et al. 2014; Guillemin et al. 2018). Macroalgae exhibit a remarkably wide range of life cycles and several species represent important resources with a wide range of uses in the food, cosmetic, and fertilizer industry (Craigie 1990). Accordingly, they represent interesting models for evolutionary biology, physiological, and induced environmental adaptation studies (Coelho et al. 2010). At the same time, macroalgae represent suitable sentinels for global warming-induced processes such as ocean acidification, atmospheric CO₂ rise, increased ultraviolet B (UVB) irradiance, and temperatures (Ji et al. 2016).

In this study, multi-locus phylogenetic reconstructions support previous molecular studies (Hommersand et al. 1999) in *Iridaea cordata* and recovered the presence of two sister species at each side of the Drake Passage. Patterns of molecular differentiation and divergence time estimates between Antarctic and South American lineages of *Iridaea* suggest that they have been separated for several million of years. Indeed, divergence time estimates suggest that the effective separation between South American and Antarctic populations of *I. cordata* occurred between 5 (cpDNA) and 9 (mtDNA) Ma, long after the physical separation of these continental landmasses estimated between 41 Ma (Livermore et al. 2005) and 23.9 Ma (Pfuhl and McCave 2005) and the initiation of the ACC (Zachos et al. 2001). Divergence time estimations in *I. cordata* are consistent with recent molecular studies in notothenioid fishes (Near et al. 2012), invertebrates (Page and Linse 2002; Wilson et al. 2009), and macroalgae (Billard et al. 2015) showing that the effective separation between Antarctic and sub-Antarctic populations of several marine benthic organisms occurred no more than 10 Ma ago (Poulin et al. 2014). Accordingly, several studies have demonstrated that the separation between Antarctic and South American populations of near-shore marine benthic organisms occurred near the Miocene boundary and the onset of these divergences does not seem to be a direct consequence of continental drift processes (Poulin et al. 2014 and references therein).

As proposed by Poulin et al. (2014), an explanation for the incongruence in the molecular divergence between Antarctic and sub-Antarctic benthic organisms and the expected separation based on geologic evidence may be a consequence of populations from Antarctica and South America maintaining connectivity after the physical separation of these continents through passive dispersal of pelagic larval stages or rafting. Connectivity between geographically separated populations plays a key role in the biogeography of the Southern Ocean, particularly between sub-Antarctic provinces (Fraser et al. 2009, 2011; Macaya &

Zuccarello 2010; Nikula et al. 2010; Cumming et al. 2014; Moon et al. 2017; González-Wevar et al. 2018). The disruption of connectivity between Antarctic and sub-Antarctic populations seems to be related to more recent oceanographic and climatic changes [that have](#) occurred in the Southern Ocean after the Middle Miocene Climatic Transition (MMCT). Sea Surface Temperatures (SST), salinity and ice-volume accumulation after the MMCT support the occurrence of major changes in ocean circulation that triggered global cooling, the initiation of sub-zero conditions in the Southern Ocean and the intensification of the ACC (Shevenell et al. 2004; Lewis et al. 2008). The intensification of the ACC after the MMCT is supported by different sources of data including the strengthening of the westerly winds, atmospheric circulation shifts, $\delta_{18}\text{O}$ signatures (Heinrich et al. 2011) and by faunal isotopic changes (Lewis et al. 2008; Verducci et al. 2009). Recent studies in the Central Scotia Sea indicate that a remnant, currently-submerged volcanic arc may have formed a barrier to deep eastward oceanic circulation until the mid-Miocene, 11.2 Ma (Dalziel et al. 2013) when the full establishment of a deep ACC was achieved, ultimately separating Antarctic and South American benthos. In this context, *I. cordata* as other higher latitude rhodophytes, exhibit low dispersive potential with free-living stages ([i.e. spores](#)) lasting only for a couple of hours (Hansen 1977). However, oceanographic conditions could have favoured connectivity between Antarctic and South America through rafting [of adult fronds](#) until the mid-Miocene, even for this non-buoyant species (Fraser et al. 2013; Billard et al. 2015). In summary, as proposed for other Southern Ocean marine organisms (González-Wevar et al. 2017), changes in the latitudinal position of the ACC and the development of a strengthened current system may constitute key mechanisms explaining the recent Mio-Pliocene separation of Antarctic and sub-Antarctic lineages of red algae. As recorded in other macroalgae [groups](#), after the separation, the resulting evolutionary lineages at both sides of the Drake Passage, followed different evolutionary pathways (Lin et al. 2001; Billard et al. 2015).

Even though *I. cordata* populations from Antarctic Peninsula and southern South America are recognized as the same nominal species, the levels of molecular divergence recorded between populations [located on these two](#) continents raises questions about its taxonomy (pairwise percent of divergence: 8.31% for COI-5P and 3.17% for *rbcL*). These values are well above the threshold generally used to discriminate between species in red algae, including rhodophytes of the order Gigartinales (Le Gall and Saunders 2010, Calderon and Boo 2016). In fact, several studies in Southern Ocean marine organisms have demonstrated the presence of genetically distinct species that have not been previously distinguished through morphological criteria (Held and Wägele, 2005; Allcock et al. 2011; Billard et al. 2015). Cryptic speciation seems to constitute a common evolutionary process in the Southern Ocean and a plausible explanation for the high degree of divergence recorded between Antarctic and South American population of marine organisms (see for example Poulin et al. 2014). In this context, islands of the Scotia Sea seems to have played a major role in the evolution of the Southern Ocean biota (Linse et al. 2007). These islands constitute hotspots of biodiversity and currently represent the northernmost limit of many Antarctic species, as well as the southernmost distribution of several South American ones. Future studies should attempt to elucidate the phylogenetic and phylogeographic affinities of Scotia Arc islands populations of *I. cordata* in order to better understand the role of the geologic

and oceanographic processes separating Antarctic and sub-Antarctic populations of this rhodophyte. Preliminary mtDNA phylogeographic results in *Iridaea* populations (Figure 3a) suggest the presence of a single genetic unit in Antarctic Peninsula across more than 700 km, from Fildes Bay, South Shetland Island to Avian Island, Marguerite Bay. These results corroborate a recent phylogeographic study in the species including more individuals ($n = 90$) from five study sites that showed a complete absence of genetic structure across its distribution in Antarctic Peninsula and the South Shetland Island (Guillemin et al. 2018). Moreover, low levels of genetic diversity and absence of population structure have also been recorded in other Antarctic macroalgae including *G. skottsbergii* (Billard et al. 2015), and other rhodophytes (Guillemin et al. 2018). These results could reflect the drastic effect of historical perturbations on Antarctic macroalgae where genetic drift during glacial bottlenecks were followed by rapid recolonization following the deglaciation process (Billard et al. 2015). In contrast, the two analyzed South American populations of *Iridaea* showed marked levels of genetic differentiation. In southern South America, fragmentation of populations and subsequent divergence may have been promoted by isolation in various in-situ microrefugia during glacial maxima, a trend reported in different Magellanic freshwater (Zemlak et al. 2010), terrestrial (Sérsic et al. 2011) and marine organisms (Vianna et al. 2011). Nevertheless, our results in *Iridaea* contrast with previous studies on macroalgae phylogeography; where recent recolonization from a single source has been proposed to explain the high genetic homogeneity of populations in southern South America (review in Guillemin et al. 2016b). These results have been related to the biological characteristics of the intertidal, low subtidal macroalgae studied to the date for which perturbations by glacial cycles and associated ice-scouring seem to have completely whipped out southernmost populations along the coast of Chile (Fraser et al. 2009). Nevertheless, highly isolated Gulfs as the Otway Sound, which basically exhibits an estuarine circulation pattern (Valdenegro and Silva 2003), have not been included in previous macroalgae studies (Guillemin et al. 2016b). Future studies should perform more expanded phylogeographic analyses in South American populations of *Iridaea*, including fjord areas where high endemism's has been reported for macroalgae (Guillemin et al. 2016a) and possible periglacial refugia as islands of the Scotia Sea (Linse et al. 2006), in order to better understand the legacy of the Quaternary glacial cycles over its patterns of genetic diversity and structure.

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Conflict of interest

The authors declare no conflict of interest.

Figure Captions

Fig. 1 Sampling localities of *Iridaea cordata* in Antarctic Peninsula and the Magellan region. Shapefiles of the coastlines available in the database GEODas (NOAA) were filtered using GEODas Coastline Extractor v.1.1.3.1 (<https://www.ngdc.noaa.gov/mgg/geodas/geodas.html>).

Fig. 2 Bayesian maximum credibility tree of rhodophytes relationships with special emphasis in *Iridaea cordata* populations from the Antarctic Peninsula and the Magellan region. **a)** phylogenetic reconstructions based on mtDNA COI-5P sequences. **b)** phylogenetic reconstructions based on cpDNA *rbcL* sequences. Bootstrap support values (MP and ML) and BPP are shown above the nodes (in that order).

Fig. 3 Maximum parsimony haplotype Networks in Antarctic and Magellanic populations of *Iridaea cordata*. **a)** Mitochondrial COI-5P sequences. **b)** Chloroplast DNA *rbcL* sequences. Each haplotype is represented by a circle, color indicated the collection site. The size of the circles is proportional to its frequency in the whole sampling effort.

Fig. 4. Bayesian maximum clade credibility tree based on mtDNA (COI-5P) showing divergence time estimates within rhodophytes and particularly between *Iridaea cordata* populations from [the](#) Antarctic Peninsula and the Magellanic region. Posterior probabilities are shown above the clades. Grey boxed regions depict 95% Bayesian credibility intervals (BCIs) for relative divergence times.

Table Captions

Table 1. [Species name, collection](#) location or reference, and GenBank numbers for [rhodophyte sequences](#) used in this study.

Table 1 Species name, collection location or reference, and GenBank numbers for rhodophyte sequences used in this study

Species	<i>rbcL</i>	Reference	COI-5P	Reference
<i>Dumontia contorta</i>	N/A	N/A	AY970583	Saunders 2005
<i>Mastocarpus stellatus</i>	U02992	Hommersand et al. 1994	KY572683	Bringloe and Saunders 2018
<i>Phyllophora crispa</i>	U02990	Hommersand et al. 1994	KJ960955	Robuchon et al. 2015
<i>Chondracanthus acicularis</i>	N/A	N/A	KR909521	Saunders 2005
<i>Chondracanthus canaliculatus</i>	U02939	Hommersand et al. 1994	N/A	N/A
<i>Chondracanthus chamissoi</i>	N/A	N/A	KP059072	Saunders 2005
<i>Chondracanthus corymbiferus</i>	U02941	Hommersand et al. 1994	GQ398090	Le Gall and Saunders 2010
<i>Chondracanthus intermedius</i>	U02942	Hommersand et al. 1994	KR909534	Saunders 2005
<i>Chondracanthus sp.</i>	N/A	N/A	KR909524	Saunders 2005
<i>Chondracanthus spinosus</i>	U02943	Hommersand et al. 1994	N/A	N/A
<i>Chondrus crispus</i>	U02984	Hommersand et al. 1994	AY970567	Saunders 2005
<i>Chondrus giganteus</i>	U02986	Hommersand et al. 1994	N/A	N/A
<i>Chondrus ocellatus</i>	U02987	Hommersand et al. 1994	N/A	N/A
<i>Chondrus verrucosus</i>	U02988	Hommersand et al. 1994	N/A	N/A
<i>Gigartina clavifera</i>	U03424	Hommersand et al. 1994	N/A	N/A
<i>Gigartina muelleriana</i>	U03427	Hommersand et al. 1994	N/A	N/A
<i>Gigartina pistillata</i>	U03429	Hommersand et al. 1994	KJ960715	Robuchon et al. 2015
<i>Gigartina skottsbergii</i> (FAK)	AF146206	Billard et al. 2015	N/A	N/A
<i>Gigartina skottsbergii</i> (ANT)	U03432	Billard et al. 2015	N/A	N/A
<i>Mazzaella affinis</i>	N/A	N/A	AY970577	Saunders 2005
<i>Mazzaella californica</i>	U03082	Hommersand et al. 1994	N/A	N/A
<i>Mazzaella cornucopiae</i>	U03377	Hommersand et al. 1994	N/A	N/A
<i>Mazzaella flaccida</i>	U03378	Hommersand et al. 1994	AY970574	Saunders 2005
<i>Mazzaella lilacina</i>	U03382	Hommersand et al. 1994	N/A	N/A
<i>Mazzaella linearis</i>	U03383	Hommersand et al. 1994	AY970584	Saunders 2005
<i>Mazzaella rosea</i>	N/A	N/A	AY970600	Saunders 2005
<i>Mazzaella sanguinea</i>	N/A	N/A	AY970599	Saunders 2005
<i>Mazzaella splendens</i>	U03385	Hommersand et al. 1994	AY970594	Saunders 2005
<i>Mazzaella volans</i>	U03386	Hommersand et al. 1994	N/A	N/A
<i>Sarcothalia crispata</i>	U03085	Hommersand et al. 1994	N/A	N/A
<i>Sarcothalia livida</i>	U03087	Hommersand et al. 1994	N/A	N/A
<i>Sarcothalia stiriata</i>	U03089	Hommersand et al. 1994	N/A	N/A
<i>Iridaea tuberculosa</i>	AF146208	Hommersand et al. 1999	N/A	N/A
<i>Iridaea cordata</i> (ICPH01)	N/A	N/A	MH892484	Our sequence
<i>Iridaea cordata</i> (ICPH05)	MH892495	Our sequence	N/A	N/A
<i>Iridaea cordata</i> (ICPH07)	MH892496	Our sequence	N/A	N/A
<i>Iridaea cordata</i> (ICBF19)	N/A	N/A	MH892485	Our sequence
<i>Iridaea cordata</i> (ICDR01)	N/A	N/A	MH892486	Our sequence
<i>Iridaea cordata</i> (ICDR11)	N/A	N/A	MH892487	Our sequence
<i>Iridaea cordata</i> (ICSO01)	MH892492	Our sequence	MH892488	Our sequence
<i>Iridaea cordata</i> (ICSO03)	N/A	N/A	MH892489	Our sequence
<i>Iridaea cordata</i> (ICSO04)	MH892493	Our sequence	N/A	N/A
<i>Iridaea cordata</i> (ICSO09)	N/A	N/A	MH892491	Our sequence
<i>Iridaea cordata</i> (ICSO15)	MH892494	Our sequence	N/A	N/A
<i>Iridaea cordata</i> (ICSO16)	N/A	N/A	MH892490	Our sequence

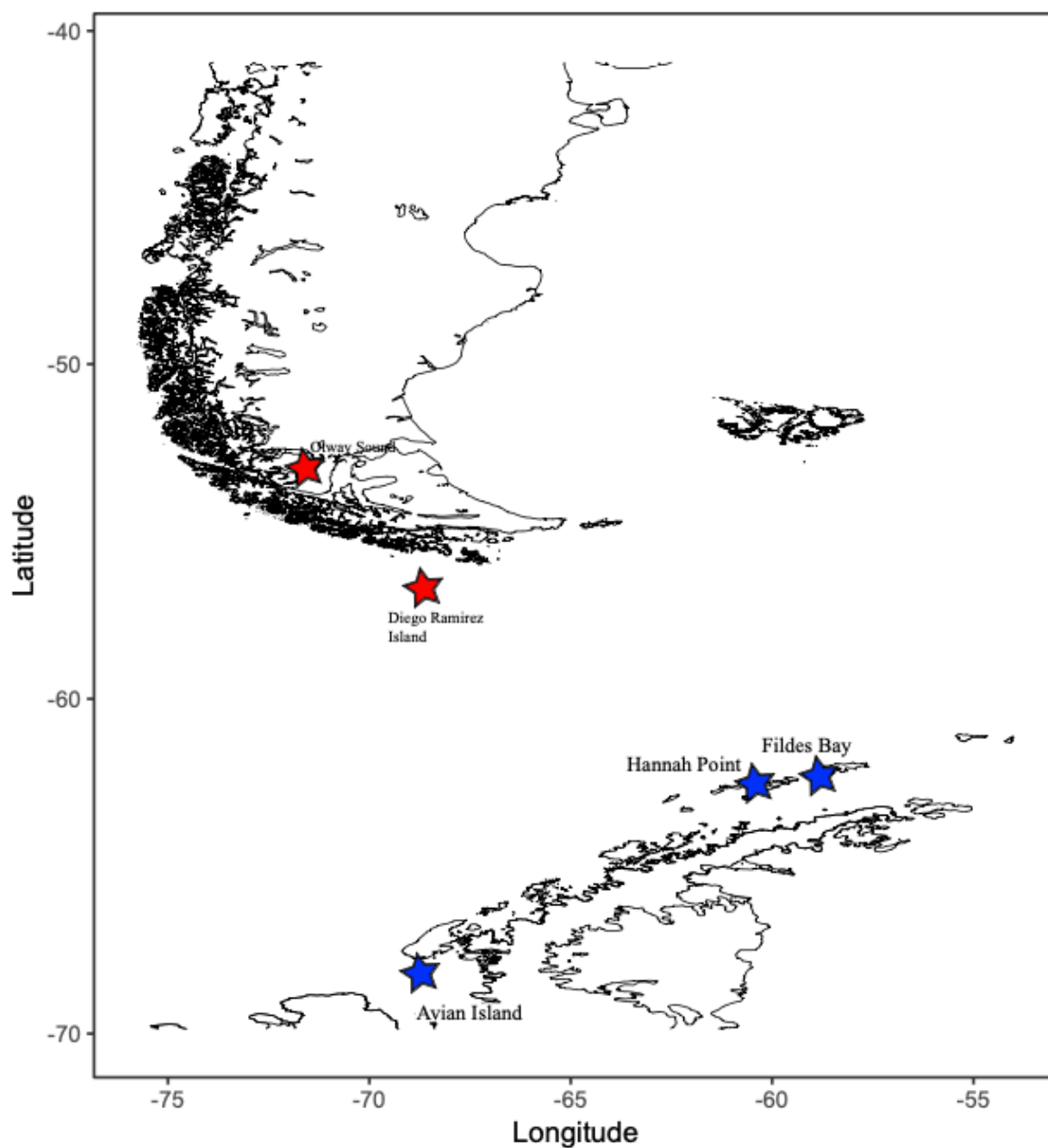


Fig. 1 Sampling localities of *Iridaea cordata* in Antarctic Peninsula and South America. Shapefiles of the coastlines available in the database GEODas (NOAA) were filtered using GEODas Coastline Extractor v.1.1.3.1 (<https://www.ngdc.noaa.gov/mgg/geodas/geodas.html>)

Fig. 2 Bayesian maximum credibility tree of rhodophyte relationships, with special emphasis on *Iridaea cordata* populations from the Antarctic Peninsula and South America. **a** Phylogenetic reconstructions based on mtDNA COI-5P sequences. **b** Phylogenetic reconstructions based on cpDNA *rbcL* sequences. Bootstrap support values (MP and ML) and BPP are shown above the nodes (in that order). AI Avian Island, FB Fildes Bay, HP Hannah Point, OS Otway Sound, DR Diego Ramirez Island, FI Falkland Islands, AP Antarctic Peninsula

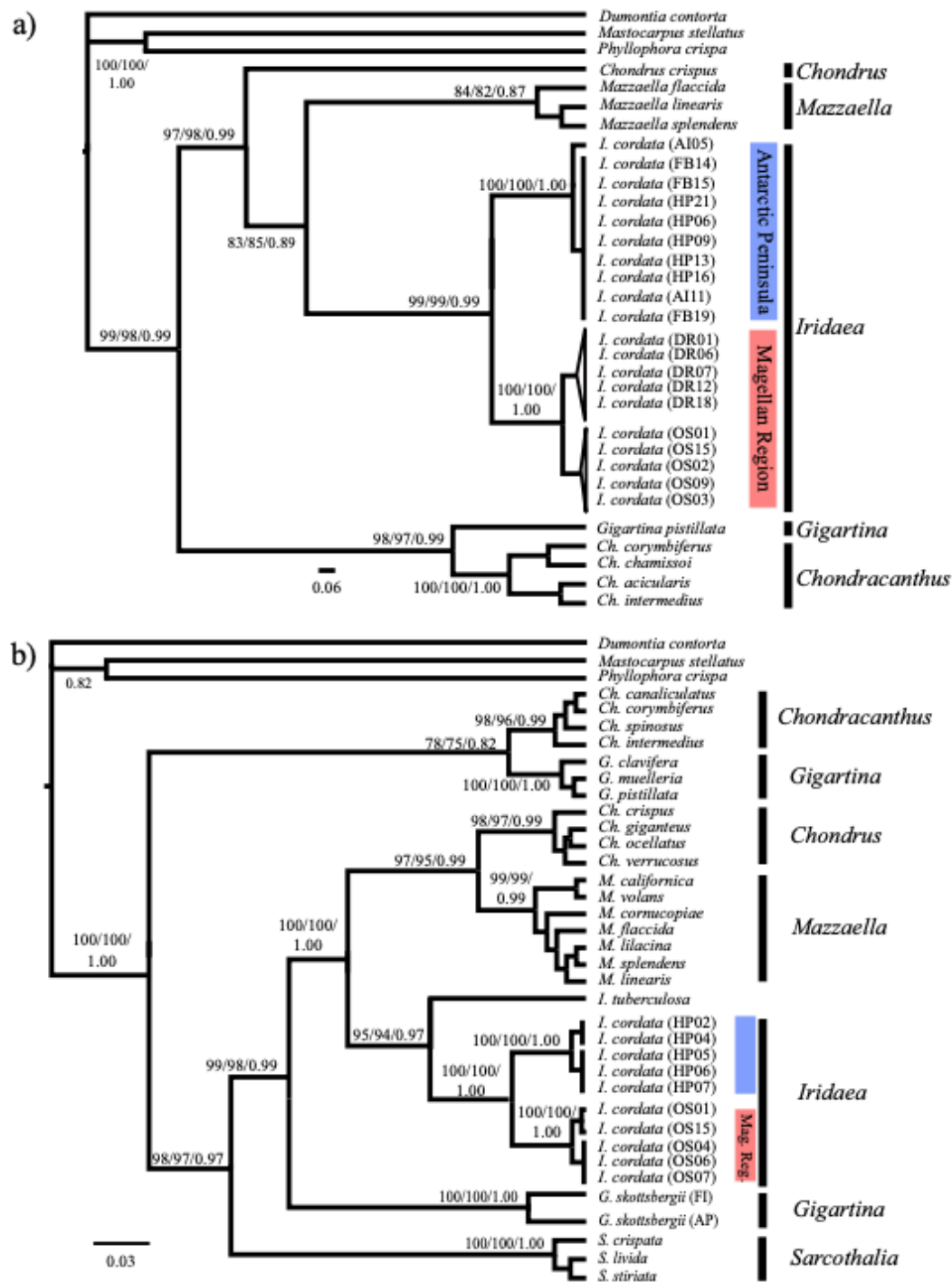


Fig. 3 Maximum parsimony haplotype Networks in Antarctic and South American populations of *Iridaea cordata*. **a** Mitochondrial COI-5P sequences. **b** Chloroplast DNA *rbcL* sequences. Each haplotype is represented by a circle, and the colors indicate collection sites. The size of the circles is proportional to the frequencies in the entire dataset

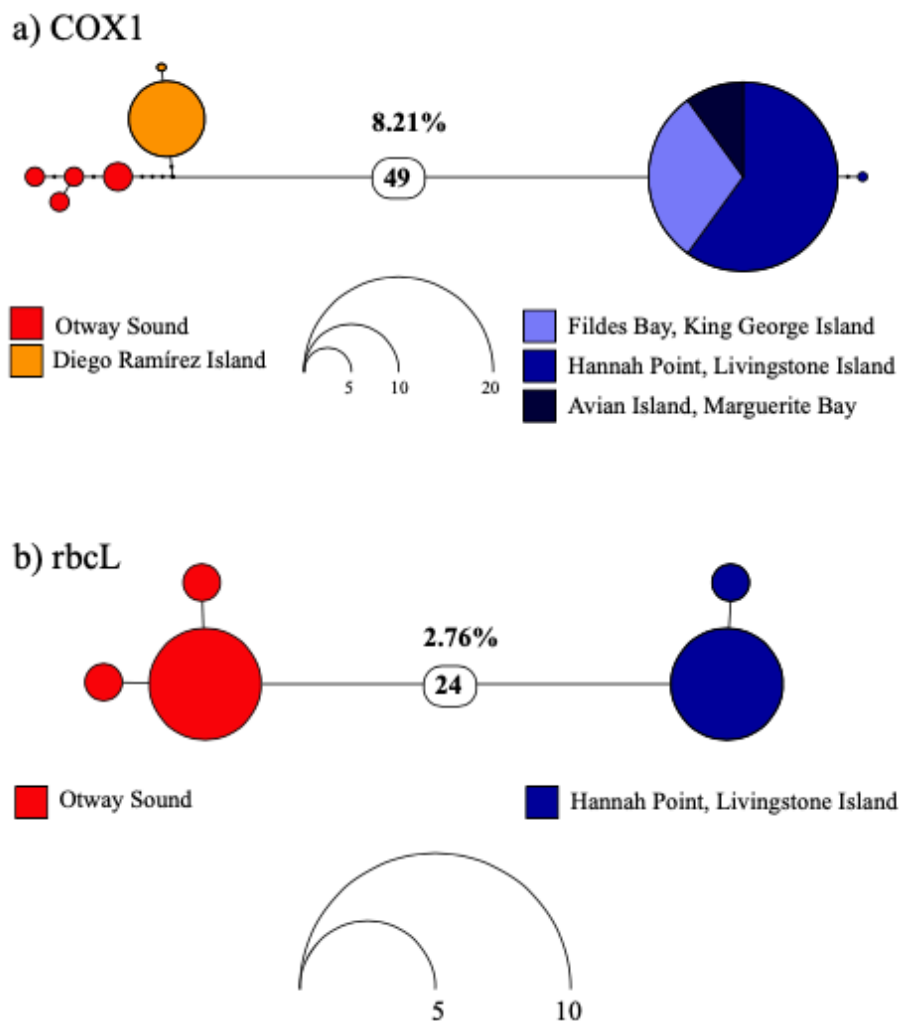


Fig. 4 Bayesian maximum clade credibility tree based on mtDNA (COI-5P) showing divergence time estimates among rhodophytes and particularly between *Iridaea cordata* populations from the Antarctic Peninsula and South America. Posterior probabilities are shown above the clades. Gray-boxed regions depict 95% Bayesian credibility intervals (BCIs) for relative divergence times. HP Hannah Point, Livingstone Island, South Shetland Islands; AI Avian Island, Marguerite Bay, Antarctic Peninsula; OS Otway Sound, Strait of Magellan; DR Diego Ramírez Island, Cape Horn; AP Antarctic Peninsula; SA South America

