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

3
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15
16 **Abstract**

17
18 The distribution of the Southern Ocean (SO) biota is the result of major geologic, oceanographic and climate
19 changes during the last 50 million years (Ma). Several groups of marine benthic organisms exhibit marked
20 taxonomic similarities between Antarctic Peninsula and southern South America where families, genera and
21 even species are currently co-distributed in these continents. Several species of macroalgae such as *Gigartina*
22 *skottsbergii*, *Plocamium cartilagineum*, *Iridaea cordata*, are currently found at both sides of the Drake
23 Passage. Advances in molecular techniques have allowed to determine their phylogenetic relationships and
24 level of divergence between populations from these continents in order to determine whether they constitute
25 separate evolutionary units. In this study we determine whether *Iridaea cordata* represents the same
26 evolutionary unit in southern South America and the Antarctic Peninsula or if populations at both sides of the
27 Drake Passage, separated by the Antarctic Polar Front (APF), **represent putative cryptic species**. According to
28 our results, *I. cordata* populations from Antarctic Peninsula and South America are clearly distinguishable
29 evolutionary units with a 8.31% and a 3.17% mtDNA and cpDNA molecular divergence, respectively. The
30 separation between Antarctic and South American populations of *I. cordata* occurred at the end of the
31 Miocene between 5 Ma (rbcL) and 9 Ma (COI-5P). These results are similar to those recorded in *G.*
32 *skottsbergii* on both sides of the Drake Passage. Accordingly, *I. cordata* populations at both sides of the
33 Drake Passage include two cryptic species. In this context, cryptic speciation plays an important role in the
34 evolution of the Southern Ocean and accordingly, the systematic, biogeography and biodiversity of the region
35 require major revisions.

36
37 **Keywords:** Southern Ocean, Rhodophyte, biogeography, Antarctic Circumpolar Current, cryptic speciation,
38 vicariance.

39

40 **Introduction**

41 The Southern Ocean (SO) covers an area of around 35×10^6 km² encircling the Antarctic continent. It
42 represents 8% of the world's ocean surface and is considered as a major driver of global oceanic circulation
43 (Rintoul et al. 2001). This vast region harbors ~ 5% of the marine biodiversity (Barnes et al. 2009) and the
44 distribution of its biota mainly reflects the dynamic geologic, oceanographic, and climate history (Crame
45 1999; Aronson et al. 2007; Clarke 2008; Saucède et al. 2014). Marine benthic communities in the SO are
46 unique and exhibit particular characteristics that are probably associated to ecological and evolutionary
47 responses to low temperatures, strong seasonal variations in light conditions, and to short periods of primary
48 production making them particularly vulnerable to climate change (Barnes & Peck 2008; Griffiths et al. 2017).
49 Biogeographers recognize three periods that dramatically affected the distribution of the biota in the region
50 (Mackensen 2004; Poulin et al. 2014). First, the Eocene/Oligocene boundary (~34 Ma) related to major
51 oceanic gateway openings, the onset of the Antarctic isolation, and the initiation of the Antarctic Circumpolar
52 Current (ACC) (Zachos et al. 2001). The middle Miocene (~14 Ma) represents a second period of major
53 oceanographic and climatic changes that affected the intensity of the ACC and thermal latitudinal gradients
54 (Zachos et al. 2001). Finally, the Quaternary characterized by the alternation between glacial and interglacial
55 periods strongly influenced the seasonality and the intensity of sea-ice formation (Gersonde et al. 2005; Kemp
56 et al. 2010).

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

69 Integrative biogeographic studies in SO marine benthic organisms have helped to understand [the](#) relative role
70 of vicariance versus dispersal in the biogeography of the region and have helped for taxonomic revisions
71 showing the presence of hidden cryptic diversity (Krabbe et al. 2008; Dornburg et al. 2016; Billard et al.
72 2015). Several groups of marine organisms including invertebrates (Patarnello et al. 1996), vertebrates
73 (Clarke and Johnston 1996), and macroalgae (Hommersand et al. 1994; Silberfeld et al. 2010) exhibit major
74 levels of genetic divergence between SO provinces supporting the role of vicariance. Nevertheless, new
75 molecular studies are showing that the origin and diversification of several marine groups occurred long after

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

95

96 **Material and Methods**

97

98 *Samplings*

99 Individuals of *Iridea cordata* (Rhodophyta; Fig. 1) were collected between 2011-2016 from five localities
100 across Antarctic Peninsula and the Magellanic Province. Sampling localities are as follows: 1) Avian Island,
101 Marguerite Bay (67°45'S; 68°52'W, n = 2); 2) Hannah Point, Livingstone Island, South Shetland Islands
102 (62°41'S; 60°52'W, n = 4); 3) Fildes Bay, King George Island, South Shetland Islands (62°11'S; 58°56'W, n
103 = 4); 4) Diego Ramírez Island, Cape Horn (56°27'S; 68°43'W, n = 5); and 5) Otway Sound, Strait of
104 Magellan (52°58'S; 71°13'W, n = 5). Fronds were sampled from distinct holdfasts to avoid the analyses of
105 genetically identical ramets (Billard et al. 2015). Samplings were conducted in the intertidal during low tides
106 and healthy fronds were cut and placed into a plastic bag filled with silica beads for rapid desiccation of the
107 tissue and DNA preservation.

108

109 *DNA preparation, PCR amplification and sequence edition*

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

114 time, a partial fragment of the chloroplastic gene Ribulose-1,5-biphosphate carboxylase/oxygenase (*rbcL*)
115 was amplified using specific primers F-*rbcL* and R-*rbcL* (Guillemin et al. 2015). PCR amplifications were
116 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
117 mM MgCl₂, 200 mM dNTPs, 1.25 ul of each primer (10 pg/ul), 1 ul DMSO, 1 U Taq polymerase
118 (Invitrogen), 15.6 ul of double-distilled water and 50 ng of DNA. Thermal cycling parameters for COI-5P
119 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
120 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
121 7 min. Thermal cycling parameters for *rbcL* included an initial denaturation step at 96°C for 4 min, 5 cycles
122 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
123 72° (30 sec), and a final extension at 72°C for 7 min. PCR amplicons were purified and sequenced in both
124 directions with an [ABI3730](#) Automatic Sequencer at Macrogen Inc. (Seoul, South Korea). Chromatograms
125 were inspected and edited using Proseq v.3.5 (Filatov 2009), and multiple alignments were obtained
126 independently for each molecular marker using Muscle (Edgar 2004). Base composition of nucleotide
127 sequences was analyzed independently for each marker using MEGA 7.0 (Kumar et al. 2016) and codon
128 usage was determined using the effective number of codon value (ENC; Wright 1990) with DnaSP 5.0
129 (Librado and Rozas 2009). New COI-5P and *rbcL* sequences in *I. cordata* have been deposited in Genbank
130 under the Accession Numbers XXXXX-XXXXX and XXXXX-XXXXX, respectively.

131

132 *Phylogenetic reconstructions, maximum parsimony networks and divergence time estimations*

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

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

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

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

161 Divergence time estimations were performed in BEAST v.1.6.2 (Drummond et al. 2012). The best-fit model
162 for the mtDNA COI-5P and *rbcL* data sets was a relaxed molecular-clock analyses with an uncorrelated
163 lognormal (ucln) model of evolutionary rate heterogeneity using the GTR + G and the XXX substitution
164 models, respectively. A birth-death speciation prior was used for branching rates in the phylogeny, four
165 chains were run twice for 100×10^6 generations, and trees were sampled every 1000 generations. Because of
166 the absence of clear fossil records in rhodophytes we used conservative mutation rates (0.5% for COI-5P and
167 0.2% for *rbcL*), following previous studies in the group (Kamiya et al. 2004; Billard et al. 2015).
168 Convergence of model parameters was estimated by plotting the marginal posterior probabilities versus the
169 generations in TRACER. Effective sample-size values were estimated for each parameter to ensure adequate
170 mixing of the MCMC (ESSs > 1000).

171

172 **Results**

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

183 Reconstructions using different sources of DNA (mtDNA and cpDNA) corroborated previous molecular
184 analyses in rhodophytes and discriminated major taxonomic groupings (Hommersand et al. 1999; Saunders
185 2005) with high bootstrap values and posterior probabilities (Fig. 2A and 2B). All the methods (MP, ML, and
186 BA) and markers showed that *I. cordata* populations from both sides of the Drake Passage represent different
187 evolutionary units and sister species (Fig. 2A and 2B). Uncorrected p-values between these units are 8.31%
188 and 3.17% for COI-5P and *rbcL* (Fig. 3A and 3B), respectively. Divergence time estimates based on COI-5P
189 sequences, under a 95% Bayesian confidence credible interval for BCI for relative divergence times (Fig. 4),

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

194

195 **Discussion**

196 Recent advances in molecular technologies have allowed to further understand the evolution and
197 biogeography of the SO biota (Allcock and Strugnell 2012; Poulin et al. 2014; Billard et al. 2015). During the
198 last decade, SO macroalgae have been subjected to several studies that generated key advances in the
199 comprehension of phylogenetic relationships, systematics, biogeographies and actual patterns of diversities
200 (Hommersand et al. 2009; Wiencke et al. 2014; Guillemain et al. 2018). Macroalgae exhibit a remarkably wide
201 range of life cycles and several species represent important resources with a wide range of uses in the food,
202 cosmetic, and fertilizer industry (Craigie 1990). Accordingly, they represent interesting models for
203 evolutionary biology, physiological, and induced environmental adaptation studies (Coelho et al. 2010). At
204 the same time, macroalgae represent suitable sentinels for global warming-induced processes such as ocean
205 acidification, atmospheric CO₂ rise, increased ultraviolet B (UVB) irradiance, and temperatures (Ji et al.
206 2016).

207 In this study, multi-locus phylogenetic reconstructions support previous molecular studies (Hommersand et al.
208 1999) in *Iridaea cordata* and recovered the presence of two sister species at each side of the Drake Passage.
209 Patterns of molecular differentiation and divergence time estimates between Antarctic and South American
210 lineages of *Iridaea* suggest that they have been separated for several million of years. [Indeed, divergence](#) time
211 estimates suggest that the effective separation between South American and Antarctic populations of *I.*
212 *cordata* occurred between 5 (cpDNA) and 9 (mtDNA) Ma, long after the physical separation of these
213 continental landmasses estimated between 41 Ma (Livermore et al. 2005) and 23.9 [Ma](#) (Pfuhl and McCave
214 2005) and the initiation of the ACC (Zachos et al. 2001). Divergence time estimations in *I. cordata* are
215 consistent with recent molecular studies in notothenioid fishes (Near et al. 2012), invertebrates (Page and
216 Linse 2002; Wilson et al. 2009), and macroalgae (Billard et al. 2015) showing that the effective separation
217 between Antarctic and sub-Antarctic populations of several marine benthic organisms occurred no more than
218 10 Ma [ago](#) (Poulin et al. 2014). Accordingly, several studies have demonstrated that the separation between
219 Antarctic and South American populations of near-shore marine benthic organisms occurred near the Mio-
220 Pliocene boundary and the onset of these divergences does not seem to be a direct consequence of continental
221 drift processes (Poulin et al. 2014 and references therein).

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

228 Zuccarello 2010; Nikula et al. 2010; Cumming et al. 2014; Moon et al. 2017; González-Wevar et al. 2018).
229 The disruption of connectivity between Antarctic and sub-Antarctic populations seems to be related to more
230 recent oceanographic and climatic changes [that have](#) occurred in the Southern Ocean after the Middle
231 Miocene Climatic Transition (MMCT). Sea Surface Temperatures (SST), salinity and ice-volume
232 accumulation after the MMCT support the occurrence of major changes in ocean circulation that triggered
233 global cooling, the initiation of sub-zero conditions in the Southern Ocean and the intensification of the ACC
234 (Shevenell et al. 2004; Lewis et al. 2008). The intensification of the ACC after the MMCT is supported by
235 different sources of data including the strengthening of the westerly winds, atmospheric circulation shifts,
236 $\delta_{18}\text{O}$ signatures (Heinrich et al. 2011) and by faunal isotopic changes (Lewis et al. 2008; Verducci et al. 2009).
237 Recent studies in the Central Scotia Sea indicate that a remnant, currently-submerged volcanic arc may have
238 formed a barrier to deep eastward oceanic circulation until the mid-Miocene, 11.2 Ma (Dalziel et al. 2013)
239 when the full establishment of a deep ACC was achieved, ultimately separating Antarctic and South
240 American benthos. In this context, *I. cordata* as other higher latitude rhodophytes, exhibit low dispersive
241 potential with free-living stages ([i.e. spores](#)) lasting only for a couple of hours (Hansen 1977). However,
242 oceanographic conditions could have favoured connectivity between Antarctic and South America through
243 rafting [of adult fronds](#) until the mid-Miocene, even for this non-buoyant species (Fraser et al. 2013; Billard et
244 al. 2015). In summary, as proposed for other Southern Ocean marine organisms (González-Wevar et al. 2017),
245 changes in the latitudinal position of the ACC and the development of a strengthened current system may
246 constitute key mechanisms explaining the recent Mio-Pliocene separation of Antarctic and sub-Antarctic
247 lineages of red algae. As recorded in other macroalgae [groups](#), after the separation, the resulting evolutionary
248 lineages at both sides of the Drake Passage, followed different evolutionary pathways (Lin et al. 2001; Billard
249 et al. 2015).

250 Even though *I. cordata* populations from Antarctic Peninsula and southern South America are recognized as
251 the same nominal species, the levels of molecular divergence recorded between populations [located on these](#)
252 [two](#) continents raises questions about its taxonomy (pairwise percent of divergence: 8.31% for COI-5P and
253 3.17% for *rbcL*). These values are well above the threshold generally used to discriminate between species in
254 red algae, including rhodophytes of the order Gigartinales (Le Gall and Saunders 2010, Calderon and Boo
255 2016). In fact, several studies in Southern Ocean marine organisms have demonstrated the presence of
256 genetically distinct species that have not been previously distinguished through morphological criteria (Held
257 and Wägele, 2005; Allcock et al. 2011; Billard et al. 2015). Cryptic speciation seems to constitute a common
258 evolutionary process in the Southern Ocean and a plausible explanation for the high degree of divergence
259 recorded between Antarctic and South American population of marine organisms (see for example Poulin et
260 al. 2014). In this context, islands of the Scotia Sea seems to have played a major role in the evolution of the
261 Southern Ocean biota (Linse et al. 2007). These islands constitute hotspots of biodiversity and currently
262 represent the northernmost limit of many Antarctic species, as well as the southernmost distribution of several
263 South American ones. Future studies should attempt to elucidate the phylogenetic and phylogeographic
264 affinities of Scotia Arc islands populations of *I. cordata* in order to better understand the role of the geologic

265 and oceanographic processes separating Antarctic and sub-Antarctic populations of this rhodophyte.
266 Preliminary mtDNA phylogeographic results in *Iridaea* populations (Figure 3a) suggest the presence of a
267 single genetic unit in Antarctic Peninsula across more than 700 km, from Fildes Bay, South Shetland Island to
268 Avian Island, Marguerite Bay. These results corroborate a recent phylogeographic study in the species
269 including more individuals (n = 90) from five study sites that showed a complete absence of genetic structure
270 across its distribution in Antarctic Peninsula and the South Shetland Island (Guillemin et al. 2018). Moreover,
271 low levels of genetic diversity and absence of population structure have also been recorded in other Antarctic
272 macroalgae including *G. skottsbergii* (Billard et al. 2015), and other rhodophytes (Guillemin et al. 2018).
273 These results could reflect the drastic effect of historical perturbations on Antarctic macroalgae where genetic
274 drift during glacial bottlenecks were followed by rapid recolonization following the deglaciation process
275 (Billard et al. 2015). In contrast, the two analyzed South American populations of *Iridaea* showed marked
276 levels of genetic differentiation. In southern South America, fragmentation of populations and subsequent
277 divergence may have been promoted by isolation in various in-situ microrefugia during glacial maxima, a
278 trend reported in different Magellanic freshwater (Zemlak et al. 2010), terrestrial (Sérsic et al. 2011) and
279 marine organisms (Vianna et al. 2011). Nevertheless, our results in *Iridaea* contrast with previous studies on
280 macroalgae phylogeography; where recent recolonization from a single source has been proposed to explain
281 the high genetic homogeneity of populations in southern South America (review in Guillemin et al. 2016b).
282 These results has been related to the biological characteristics of the intertidal, low subtidal macroalgae
283 studied to the date for which perturbations by glacial cycles and associated ice-scouring seem to have
284 completely whipped out southernmost populations along the coast of Chile (Fraser et al. 2009). Nevertheless,
285 highly isolated Gulfs as the Otway Sound, which basically exhibits an estuarine circulation pattern
286 (Valdenegro and Silva 2003), have not been included in previous macroalgae studies (Guillemin et al. 2016b).
287 Future studies should perform more expanded phylogeographic analyses in South American populations of
288 *Iridaea*, including fjord areas where high endemism's has been reported for macroalgae (Guillemin et al.
289 2016a) and possible periglacial refugia as islands of the Scotia Sea (Linse et al. 2006), in order to better
290 understand the legacy of the Quaternary glacial cycles over its patterns of genetic diversity and structure.

291

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298

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503

504 **Conflict of interest**

505 The authors declare no conflict of interest.

506

507 **Figure Captions**

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

511

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

516

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

521

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

526

527 **Table Captions**

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

530

531

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

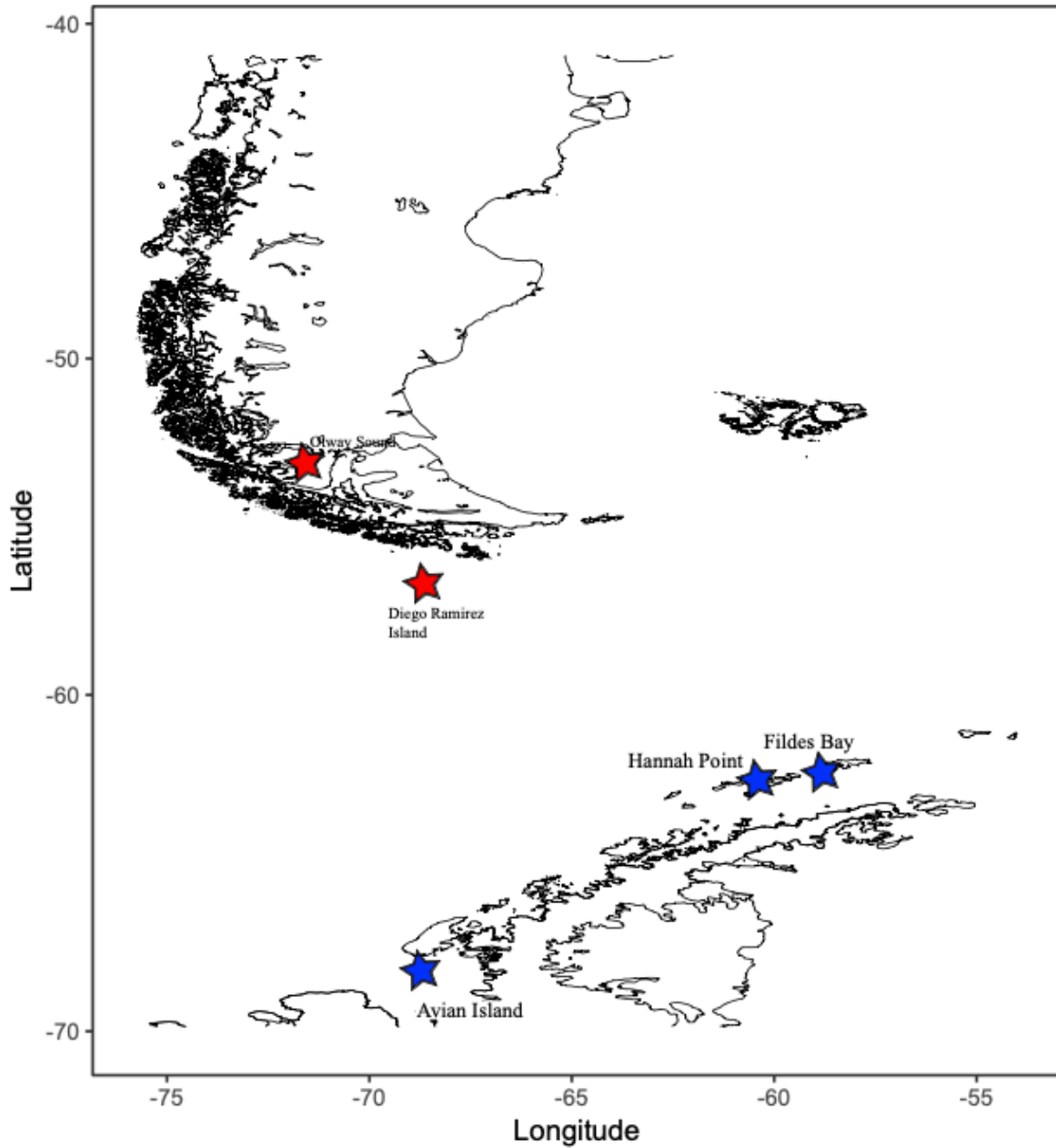


Fig. 1 Sampling localities of *Iridaea cordata* in Antarctic Peninsula and South America. Shapefiles of the coastlines available in the database GEODas (NOAA) were filtered using GEODas Coastline Extractor v.1.1.3.1 (<https://www.ngdc.noaa.gov/mgg/geodas/geodas.html>)

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

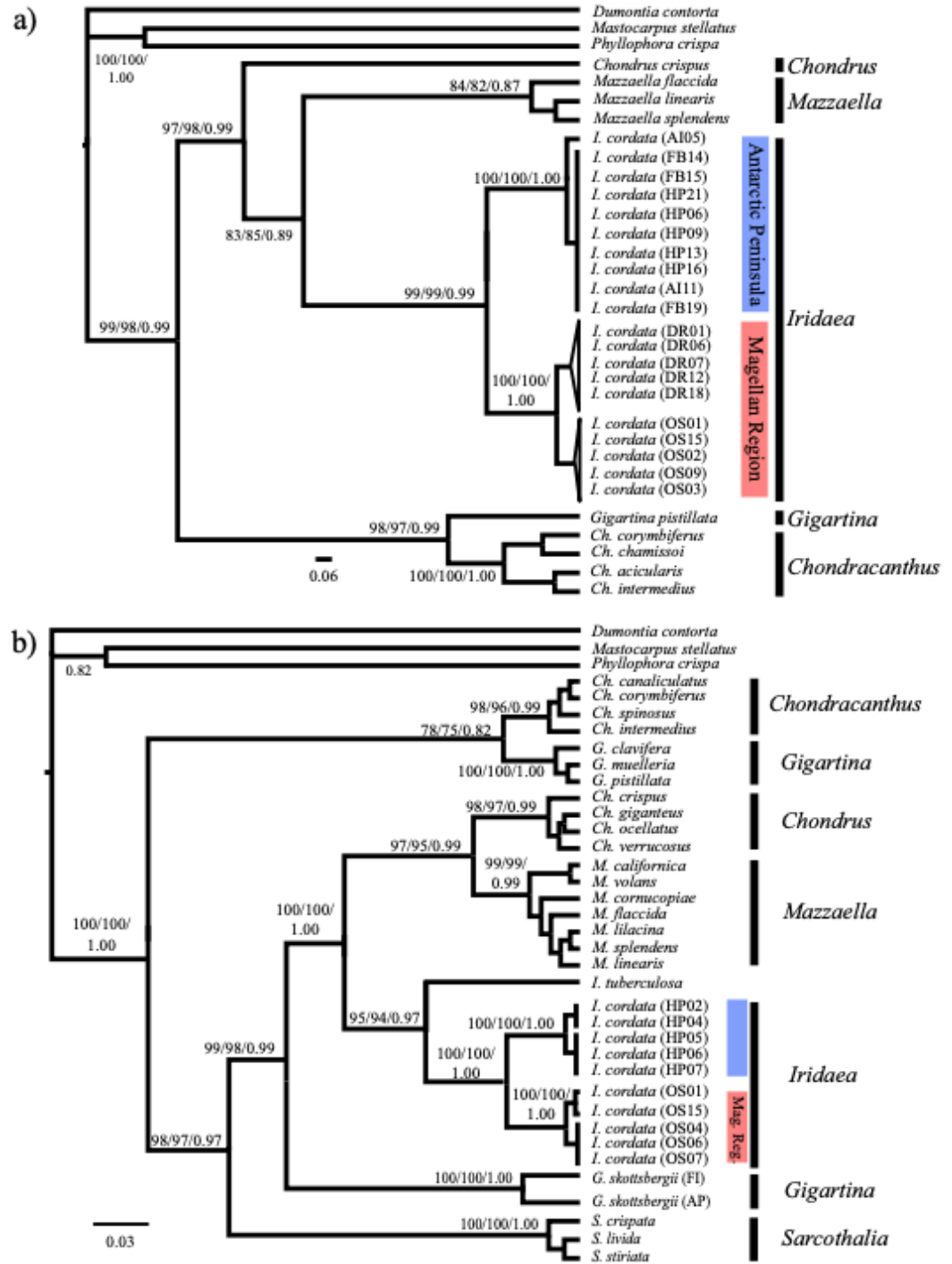
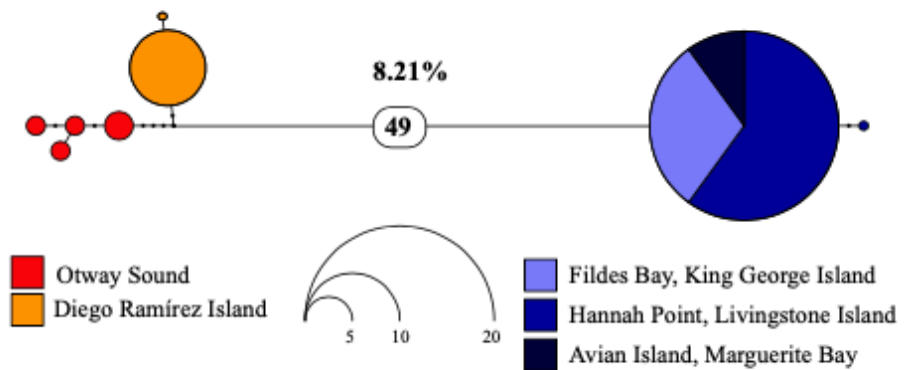


Fig. 3 Maximum parsimony haplotype Networks in Antarctic and South American populations of *Iridaea cordata*. **a** Mitochondrial COI-5P sequences. **b** Chloroplast DNA *rbcL* sequences. Each haplotype is represented by a circle, and the colors indicate collection sites. The size of the circles is proportional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

a) COX1



b) rbcL

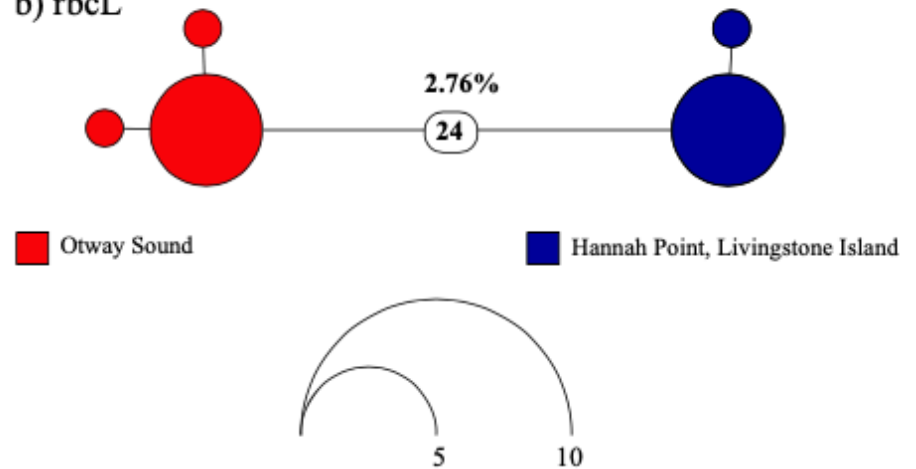


Fig. 4 Bayesian maximum clade credibility tree based on mtDNA (COI-5P) showing divergence time estimates among rhodophytes and particularly between *Iridaea cordata* populations from the Antarctic Peninsula and South America. Posterior probabilities are shown above the clades. Gray-boxed regions depict 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 Ramirez Island, Cape Horn; AP Antarctic Peninsula; SA South America

