Comparative phylogeography of six red algae along the Antarctic Peninsula: extreme genetic depletion linked to historical bottlenecks and recent expansion

Marie-Laure Guillemin1,2,3 · Hélène Dubrasquet1,2 · Janette Reyes1 · Myriam Valero2

Abstract
In the Southern Ocean, rapid climatic fluctuations during the Quaternary are thought to have induced range contractions and bottlenecks, thereby instigating genetic divergence and potentially even speciation of marine species. Specifically, ice scouring during glacial events may have had drastic impacts on seaweed communities, thus leading to genetic diversification between algal populations that persisted on the Antarctic shelf in small isolated refugia. Using the mitochondrial Cytochrome c Oxidase I (COI) gene and 279 individual macroalgal specimens collected from five geographic areas along the coasts of the Antarctic Peninsula and the South Shetland Islands, we studied the genetic diversity of six commonly encountered species of red algae. All six algae were characterized by very low genetic diversity, and we found a significant signature of recent population expansion of a single haplotype encountered over more than 450 km. These results reflect the drastic impact of historical perturbations on populations of Antarctic seaweeds. We propose that genetic drift during a glacial bottleneck had a strong effect and could have been amplified by gene surfing effects during spatial expansion after ice sheet retreat. This led to the rapid spread of a single haplotype in the recolonized region. Unfortunately, the very low level of genetic diversity encountered did not allow us to precisely pinpoint the putative location of the glacial refugium inhabited by Antarctic seaweeds. Despite this, we propose that future studies should test the role of active volcanic areas, such as Deception Island, as long-term refugia in the region.

Keywords Antarctic Peninsula · South Shetland · COI · Rhodophyta · Glaciation · Pleistocene · Refugia

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Introduction

The ‘species pump’ or ‘biodiversity pump’ model (Haffer 1969) poses that past climatic cycles could have led to rapid divergence and speciation by promoting range fragmentation and allopatric speciation. In particular, the importance of the periodic changes in the earth’s orbit, known as Milankovitch oscillations, that generated repeated 10–100 kyr glacial–interglacial shifts during the Pliocene and Pleistocene has been acknowledged (Hewitt 2004; Allcock and Strugnell 2012). These rapid climatic fluctuations produced changes in species ranges, population size, and connectivity. Furthermore, during contractions of populations in refugia, altered selective regimes and increased drift could have promoted incipient speciation (i.e., ‘species pump’ hypothesis, Haffer 1969; see also Avise 2000). Glacial–interglacial shifts have been characterized not only by large and rapid changes in the volume of global ice but also by variation in sea level, temperature, and precipitation regimes (Haffer 1969; Hewitt
While the amplitude of the effect of repeated glacial–interglacial shifts on divergence and allopatric speciation is still debated (Knapp and Mallet 2003), the ‘species pump’ is believed to have played an important role in the diversification of terrestrial (alpine: Schoville et al. 2012; boreal: Weir and Schluter 2004; Antarctic: Convey et al. 2009; and equatorial: Haffer 1969), freshwater (April et al. 2013), and marine (Clarke et al. 1992; Wilson et al. 2009) taxa.

During glacial periods in Antarctica, ice shelves have extended far from the continent likely destroying most available habitat for benthic biota and forcing remnant populations down the continental slope into deep-water refugia (Thate et al. 2005). However, for organisms restricted to shallow waters, such as photosynthetic macroalgae or their associated fauna, survival in deep-water refugia is not possible; thus, the effect of glaciations could have led to complete eradication of some species from Antarctic coasts. Indeed, at the present time, ice scouring has an extreme impact on shallow water communities (Gutt 2001), and it has been postulated that ice caps had eliminated algal populations in sub-Antarctic regions covered by ice during the Last Glacial Maximum (Fraser et al. 2012). However, the presence of polypinous on the continental shelf edge (Thate et al. 2008) and diachrony of ice sheet extensions (i.e., regional variation in timing of ice sheet formation; Anderson et al. 2002) suggest that ice-free regions persisted during glacial periods along Antarctic coasts. These two phenomena could have provided small refugia scattered around the Antarctic continental shelf edge, where shallow water communities could have survived during glaciation (Allcock and Strugnell 2012). At least 38 glacial–interglacial cycles were suggested to have occurred over the last 5 million years (Myr) (see Box1 in Allcock and Strugnell 2012), and repeated events of diversification could have affected organisms persisting on the Antarctic shelf (Clarke et al. 1992). Recent phylogeographic studies have revealed the existence of numerous cryptic species or deep genetic lineages in a wide array of marine animals (e.g., anenid polychaetes, nemerteans, molluscs, arthropods, and echinoderms; see Janosik and Halanych 2010; Allcock and Strugnell 2012; Riesgo et al. 2015 for review). The existence of these deep genetic lineages has been reported even in organisms for which only a limited regional sampling was performed (Janosik and Halanych 2010; Allcock and Strugnell 2012; Riesgo et al. 2015). Speciation linked to isolation in small refugia along the Antarctic shelf has been hypothesized to be the source of the unexpectedly high species diversity in many taxa, particularly in sea slugs (Wilson et al. 2009) and sea cucumbers (O’Loughlin et al. 2011).

In the Southern Ocean, most studies using molecular approaches to determine the existence of divergent lineages and cryptic species have focused on fishes and marine invertebrates (Allcock and Strugnell 2012). Surprisingly, until now, genetic structure of macroalgae has been largely neglected (but see Fraser et al. 2012, 2013; Billard et al. 2015; Fraser 2016) despite the fact that they represent an important part of benthic communities both as resources (i.e., primary producers) and as community structural components (Amsler et al. 2014). The diversity pump has been proposed to be particularly relevant in Antarctic organisms with a limited capacity for dispersal since populations located in refugia could easily be thoroughly isolated, leading to allopatric divergence (Clarke et al. 1992; Wilson et al. 2009; Allcock and Strugnell 2012; Verheye et al. 2016). Macroalgae lacking specialized floating structures are generally considered very poor dispersers compared to other marine organisms (Kinlan and Gaines 2003). Indeed, strong spatial structure of genetic diversity can be observed at small scales (i.e., less than 10 km; Valero et al. 2011 and Durrant et al. 2014). Thus, the small population sizes and restrictive dispersal (Montecinos et al. 2012 and references therein) of macroalgae could lead to an increased susceptibility to neutral processes of genetic differentiation, and genetic divergence could arise rapidly even between neighboring populations (Neiva et al. 2012). However, contrary to our expectations, a recent study focusing on the red macroalga, Gigartina skottbergii, and utilizing two genetic markers (the mitochondrial intergenic region Cox2–3 and the chloroplastic Rubisco large subunit gene) showed a complete absence of genetic structure over 1600 km of coast sampled in the Antarctic region (Billard et al. 2015). The authors suggest that genetic homogeneity of G. skottbergii has resulted from a strong demographic bottleneck during the last Quaternary glaciations (i.e., range contraction) followed by sudden recolonization during post-glacial expansion.

In this study, we sought to determine the impact of habitat reduction during glacial periods on genetic diversity in six species of red macroalgae commonly encountered along the Antarctic Peninsula and the South Shetland Islands. Depending on the distribution of refugia during the Last Glacial Maximum, two different outcomes could be expected for these organisms: (1) if a single, small-sized refugium has acted as the origin of a recent expansion wave, this should be reflected in our genetic data by high genetic homogeneity and low genetic diversity over the whole sampled area or (2) if macroalgae have been isolated in various disjoint refugia, this should lead to the observation of highly differentiated genetic lineages, each mainly restricted to a single location or geographic area (see Fig. 1 in Allcock and Strugnell 2012).

Materials and methods

Study models

All our six study models correspond to fleshy red macroalgae with thallus size varying from some centimeters
(e.g., *Iridaea cordata* (Turner) Bory) to up to several dozen centimeters (e.g., *Gigartina skottsbergii* Setchell & N.L. Gardner) in length and/or diameter (see Fig. 1b). None possesses floating structures. *Georgiella confluens* (Reinsch) Kylin, *Curdiea racovitzae* Hariot, and *Palmaria decipiens* (Reinsch) Ricker are reported as mostly Antarctic but have also been observed in some sub-Antarctic Islands (*C. racovitzae* and *G. confluens* in South Georgia, and *P. decipiens* in South Georgia, Macquarie Island, and Kerguelen Island; Wiencke and Clayton 2002; Wiencke et al. 2014). *Iridaea cordata* and *G. skottsbergii* have been registered in Antarctica, South Georgia, Falkland Islands, Tierra del Fuego, and the Southern part of the Chilean and Argentinian Patagonia in studies using classical taxonomy (Wiencke et al. 2014; Pellizzari et al. 2017). However, molecular studies support that specimens sampled on both sides of the Antarctic Circumpolar Current correspond to different cryptic species (Hommersand et al. 2009; Billard et al. 2015). *Plocamium cartilagineum* (Linnaeus) Dixon has been reported on most Antarctic and sub-Antarctic coasts although these observations are based on taxonomical characteristics only, and the existence of cryptic species could be suspected in this highly variable morphospecies (Wiencke et al. 2014; specimens reported as *P. aff. cartilagineum* in Pellizzari et al. 2017). The six study species are fairly common and can be encountered forming mats mostly in the intertidal down to the shallow subtidal for *I. cordata*.
G. skottsbergii, C. racovitzae, and P. decipiens, or deeper, as understory of large brown macroalgae, for G. confluens and P. cartilagineum. Most Antarctic macroalgae studied have also proven to be highly stenothermic. Thus, their spore production, settlement, and survival are highly limited by temperature, and characteristics such as growth and reproduction often follow a strong seasonal pattern, mirroring changes in abiotic conditions (e.g., the growth of G. confluens, P. cartilagineum, and I. cordata occurs between 0 °C and 5 °C, with an upper survival temperature of 11–16 °C; Wiencke et al. 2014).

**Sampling**

For G. confluens, G. skottsbergii, and P. cartilagineum, samples were collected by scuba diving from shallow subtidal zones down to 30 m. Samples of C. racovitzae, I. cordata, and P. decipiens were obtained from both intertidal rock pools and the shallow subtidal (i.e., mostly at depth of 0 to 15 m). In order to sample individuals corresponding to distinct genotypes and coming from sexual reproduction and through spore settlement, only one thallus sample was taken from each macroalgal holdfast, and all holdfasts were sampled well separated on the rocky substrate. Samples were collected in five distinct areas (see Fig. 1a), two located in the South Shetland Islands (GEO: King George Island, 62°12′S/58°57′W and PRA: Greenwich Island, 62°28′S/59°40′W) and three located along the Antarctic Peninsula (OHI: O’Higgins, 63°18′S/57°53′W; PAR: Paradise Bay, 64°50′S/62°52′W; and MAR: Marguerite Bay, 67°45′S/68°52′W). Specimens were pressed as vouchers after removing a small portion of the thallus stored in silica gel for subsequent DNA analysis. Voucher specimens are housed in the herbarium of the Universidad Austral de Chile and are available from the contact author on request. In total, 42 specimens were collected for both G. confluens, 28 for G. skottsbergii, 90 for I. cordata, 35 for P. decipiens, and 64 for P. cartilagineum (Table 1; Fig. 2).

**DNA extraction, PCR amplification, and sequencing**

DNA extraction was undertaken according to the methods described in Faugeron et al. (2001). DNA amplification of the 5′ part of the mitochondrial Cytochrome c Oxidase I gene (COI) was done following the amplification protocols of Saunders (2005) using the primer pair GazF1 (5′-TCA ACA AAT CAT AAA GAT ATT GG-3′) and GazR1 (5′-ACT TCT GGA TGT CCA AAA AAY CA-3′). Purified PCR products (UltraCleanTM kit, MO BIO Laboratories, Carlsbad, USA) were sequenced (Macrogen Inc., Seoul, South Korea). The 279 generated COI sequences (632 bp) have been archived with the GENBANK accession numbers KY559671-KY559712, KY559727-KY559746, KY559753-KY559780, KY559817-KY559905, KY559935-KY559947, KY559949-KY559970, KY560012-KY560065, and KY560067-KY560076. For each accession, information about the region, sampling locality, and voucher code (i.e., given under the “organism” category) has been provided. Sequences were aligned using the CLUSTAL function of MEGA v.5 (Tamura et al. 2011).

**Data analysis**

For each species, levels of polymorphism over the whole sampled area were calculated using the following standard genetic diversity indices: number of sampled haplotypes (k), number of polymorphic sites (S), haplotype diversity (H), average number of pairwise differences (Π), and nucleotide diversity (π). These indices were calculated using DnaSP v.4 (Rozas et al. 2003). Haplotype networks were reconstructed using the median joining algorithm implemented in NETWORK v.4 (Bandelt et al. 1999). Haplotype frequencies, for each species in each area, were calculated using DnaSP v.4 (Rozas et al. 2003).

Three tests were performed to assess whether each species is at mutation–drift equilibrium or if there was a signature of post-glacial recent expansion. Tajima’s D (Tajima 1989) and Fu’s FS (Fu 1997) neutrality tests were conducted using DnaSP v.4 (Rozas et al. 2003). Significance for these

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>k</th>
<th>S</th>
<th>H</th>
<th>Π</th>
<th>π · 10−2</th>
<th>Tajima’s D</th>
<th>Fu’s FS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curdinea racovitae</td>
<td>42</td>
<td>2</td>
<td>1</td>
<td>0.048</td>
<td>0.048</td>
<td>0.008</td>
<td>−1.120**</td>
<td>−1.491**</td>
</tr>
<tr>
<td>Georgiella confluens</td>
<td>20</td>
<td>4</td>
<td>4</td>
<td>0.363</td>
<td>0.489</td>
<td>0.077</td>
<td>−1.638*</td>
<td>−1.613**</td>
</tr>
<tr>
<td>Gigartina skottsbergii</td>
<td>28</td>
<td>2</td>
<td>1</td>
<td>0.071</td>
<td>0.071</td>
<td>0.011</td>
<td>−1.151**</td>
<td>−1.155**</td>
</tr>
<tr>
<td>Iridaea cordata</td>
<td>90</td>
<td>7</td>
<td>5</td>
<td>0.398</td>
<td>0.623</td>
<td>0.102</td>
<td>−0.797**</td>
<td>−2.882**</td>
</tr>
<tr>
<td>Palmaria decipiens</td>
<td>35</td>
<td>7</td>
<td>6</td>
<td>0.318</td>
<td>0.343</td>
<td>0.054</td>
<td>−2.103***</td>
<td>−7.041***</td>
</tr>
<tr>
<td>Plocamium cartilagineum</td>
<td>64</td>
<td>4</td>
<td>4</td>
<td>0.122</td>
<td>0.155</td>
<td>0.025</td>
<td>−1.759***</td>
<td>−3.466**</td>
</tr>
</tbody>
</table>

N number of sampled specimens, k number of haplotypes, S polymorphic sites, H haplotype diversity, Π average number of nucleotide differences, π nucleotide diversity, ns nonsignificant. * p < 0.05; ** p < 0.01; *** p < 0.001

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Two neutrality tests was obtained by simulating 1000 samples using the coalescent approach developed in DnaSP v.4 (Rozas et al. 2003). Negative and significant values for Tajima’s D and Fu’s FS neutrality tests reflect an excess of rare polymorphisms in a population, which indicates either positive selection or a recent increase in population size (Aris-Brosou and Excoffier 1996). Moreover, we tested the frequency distribution of pairwise differences between haplotypes (i.e., mismatch analysis) against a model of sudden expansion (Roger and Harpending 1992). This was done using 1000 replicates in the program ARLEQUIN v.3.5 (Excoffier and Lisher 2010). The goodness-of-fit between the observed and estimated distributions was assessed by calculating the sum of squared differences (SSD) between the observed and expected distributions and the Harpending’s raggedness index (Rag) (Harpending 1994). Calculations were performed in ARLEQUIN v.3.5 (Excoffier and Lisher 2010), and significance was assessed by bootstrapping (1000 replicates).

We approximated the timing since the beginning of the most recent population expansion using the equation $\tau = 2u t$, where $t$ is the number of years since expansion and $u$ is the per-sequence-per-year mutation rate. The parameter Tau ($\tau$) and 90% percentile values of $\tau$ were inferred directly.
from the model of sudden expansion in ARLEQUIN v.3.5 (Excoffier and Lisher 2010). Since no precise molecular clock exists for the COI in red algae, we used as an approximation of the divergence rate of 0.14% per Myr published by Muangmai et al. (2014). These authors have computed this rough estimate for COI of the genus Bostrychia using two samples of Bostrychia calliptera collected from both sides of the Isthmus of Panama, considering 2.5–3.0 Myr ago as the final closure date of the Isthmus. Since substitution rates are usually much lower than mutation rates (i.e., because natural selection tends to remove deleterious mutations), we applied the tenfold evolutionary rate correction for intraspecies time dependence of molecular rates as proposed by Ho et al. (2011); this was applied to the divergence rate proposed for COI (Muangmai et al. 2014) before estimating the timing since the beginning of population expansion (mutation rate, u = 1.4% per Myr for the COI).

Results

Over the whole sampled area (i.e., more than 450 km of sampled coast, Fig. 1a), all six red macroalgae showed very low levels of mtDNA genetic diversity (Fig. 2). Depending on the species under study, one to six polymorphic sites were detected (Table 1). The number of observed haplotypes varied from two in Curdiea racovitzae and G. skottsbergii to seven in I. cordata and P. decipiens. The highest values of mtDNA diversity were encountered in I. cordata (haplotype diversity = 0.398, average number of pairwise differences = 0.623, and nucleotide diversity = 0.001), the species with the largest sample size (N = 90; Table 1). Simple, star-like haplotype network topologies were observed for each species (Fig. 2). For all species, the central haplotype was the most frequent (from 77% of the samples in I. cordata to 98% of the samples in C. racovitzae) and was present in all localities (Fig. 2), while the remaining haplotypes were rare and private (i.e., haplotype confined to a single geographic locality). One exception to this was the I. cordata network (Fig. 2). For this species, two haplotypes (i.e., shaded in gray in Fig. 2) showed intermediate frequency (11 and 8%, respectively) and were also widely distributed in most sampled areas. These haplotypes were related to the most common I. cordata haplotype through branch length of at most two mutational steps (Fig. 2).

In all studied species, both Tajima’s D and Fu’s Fs tests gave negative values (Table 1). Associated probabilities were significant in C. racovitzae, G. confluens, P. decipiens, and P. cartilagineum for the Tajima’s D test, and in P. decipiens and P. cartilagineum for the Fu’s Fs test (Table 1). Congruent with these findings and the fact that the majority of the individuals within each species shared the same haplotype, distributions of pairwise differences between sequence pairs were L-shaped for all six species (Online Resource 1). From the results of the goodness-of-fit tests, the null hypothesis of sudden expansion could not be rejected for the six species tested (Table 2; all p values for Expected SSD > Observed SSD and Expected Rag > Observed Rag were much higher than 0.05). The population expansion was estimated to have begun during the late Quaternary. Times of expansion were estimated to range from 0–36,000 years in C. racovitzae to 0–240,000 years in I. cordata (Table 2).

Discussion

Throughout the South Shetland Islands and the Antarctic Peninsula, no differentiated genetic groups were observed within the six species studied here. On the contrary, all six red macroalgae were characterized by very low genetic diversity and a significant signature of recent population expansion of a single haplotype encountered over more than 450 km. Some limitations of our study, such as the low number of samples available for some species (mostly for G. confluens, G. skottsbergii, and P. decipiens, for which less than 40 samples were studied), the relatively limited area studied compared to the entirety of the Antarctic coast, or the fact that only one gene was sequenced (but see Billard et al. 2015, the same results observed using two different markers, more samples, and more sample locations for G.

<table>
<thead>
<tr>
<th>Species</th>
<th>SSD</th>
<th>p value</th>
<th>Rag</th>
<th>p value</th>
<th>τ</th>
<th>Range estimation of times of expansion (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curdiea racovitzae</td>
<td>0.000</td>
<td>0.19</td>
<td>0.821</td>
<td>0.83</td>
<td>0.16</td>
<td>(0–0.636) 0–36,000</td>
</tr>
<tr>
<td>Georgiella confluens</td>
<td>0.000</td>
<td>0.74</td>
<td>0.179</td>
<td>0.77</td>
<td>0.48</td>
<td>(0–2.263) 0–128,000</td>
</tr>
<tr>
<td>Gigartina skottsbergii</td>
<td>0.000</td>
<td>0.22</td>
<td>0.740</td>
<td>0.80</td>
<td>0.18</td>
<td>(0–0.715) 0–40,000</td>
</tr>
<tr>
<td>Iridaea cordata</td>
<td>0.007</td>
<td>0.56</td>
<td>0.244</td>
<td>0.63</td>
<td>1.47</td>
<td>(0–4.241) 0–240,000</td>
</tr>
<tr>
<td>Palmaria decipiens</td>
<td>0.001</td>
<td>0.32</td>
<td>0.224</td>
<td>0.56</td>
<td>0.39</td>
<td>(0.081–0.987) 5,000–56,000</td>
</tr>
<tr>
<td>Plocamium cartilagineum</td>
<td>0.000</td>
<td>0.38</td>
<td>0.627</td>
<td>0.74</td>
<td>0.64</td>
<td>(0–2.199) 0–124,000</td>
</tr>
</tbody>
</table>

For details about calculations of the parameter Tau (τ) and time of expansion, see details in the text.
skottsbergii) could explain the results found here. However, the fact that the same pattern was encountered in all six species allows us to assume that the genetic structure and diversity of Antarctic macroalgal populations is actually a reflection of historical glacial perturbations during the late Quaternary.

There are reports of distinct glacial refugia in the South Shetland Islands and Antarctic Peninsula harboring cryptic species that have diverged recently in micro-allopatry (marine animals: Wilson et al. 2007, 2009; Allcock et al. 2011; Verheyen et al. 2016). In other marine bioregions, like the southeastern tip of Australia (Fraser et al. 2009) or the Philippine archipelago (Payo et al. 2013), processes of divergence and speciation in marine macroalgae have also been connected to fluctuations in sea level and water temperature during glacial periods. For the six species of Antarctic red macroalgae studied here, however, no trace of an effect of a diversity pump in the western Antarctic Peninsula area was encountered.

The existence of a single glacial refugium (Billard et al. 2015) associated with massive population size reduction during the late Quaternary and a recent recolonization of the Antarctic Peninsula and the South Shetland Islands could explain our results. Severe bottlenecks during glacial periods have been inferred for many taxa that have been studied in the Southern Ocean (Allcock and Strugnell 2012), and this includes animals with high dispersal capacities and large population sizes (e.g., the Antarctic limpet Nacella concinna: González-Wevar et al. 2011; the krill Euphausia superba: Goodall-Copestake et al. 2010; Bortolotto et al. 2011; and the shrimp Chorismus antarcticus: Raupach et al. 2010). Macroalgae are fairly limited in terms of the depth that they inhabit (as these are photosynthetic organisms that need to live close enough to the surface to get sunlight), and they are organisms that typically have restricted belt-like distributions along the coast. Differing then from pelagic or broad depth-ranging benthic animals threatened by ice scour in Antarctica (Allcock and Strugnell 2012), macroalgae cannot use refugia located in the deepest parts of the continental shelf. Indeed, a complete or nearly complete eradication of macroalgal populations from the sub-Antarctic and Antarctic coasts during the Last Glacial Maximum has been inferred based on molecular data in the Southern hemisphere (Macaya and Zuccarello 2010; Fraser et al. 2012; Montecinos et al. 2012; Billard et al. 2015), and the impact of ice scouring has been deemed to be particularly important in Antarctica during this period (Thate et al. 2005). Due to their ecological and life cycle characteristics, the dramatic impact of ice scour on Antarctic macroalgal genetic diversity is not surprising. In our study, the very low level of genetic diversity and the large-scale spread of common genetic variants prohibit us from precisely pinpointing the location of the glacial refugium of Antarctic macroalgae. Recent studies have estimated that the Last Glacial Maximum ice cap was thick and extended as far as the shelf edge around the South Shetland Islands and the Antarctic Peninsula (Simms et al. 2011; Cofaigh et al. 2014). The ice sheet retreat began earlier in the Northern part of the region, and it is very likely that Marguerite Bay, where grounded ice was hypothesized to have existed up to 14,000 years ago, is a recently colonized area (Cofaigh et al. 2014). Interestingly, the Last Glacial Maximum ice coverage proposed by Simms et al. (2011) does not include Deception Island, the largest and most active volcano in the area (see Fig. 1a). It is possible that volcanoes, like Deception Island, Penguin Island, and Bridgeman Island, have been active during the last 4 Myr and remained free of ice during glacial periods (Simms et al. 2011; Fig. 1a), thus representing potential refugia for Antarctic flora and fauna (Convey et al. 2009; Fraser et al. 2014). Except for C. racovitzae, all the macroalgae studied here have been recorded in both Deception and Penguin Islands (Pellizzari et al. 2017). Unfortunately, no sites located along these volcanic coasts were included in our work. Other glacial contraction–expansion scenarios have also proposed recolonization occurring from peri-Antarctic refugia, in sub-Antarctic Islands, to the Antarctic coasts in marine organisms (Fraser et al. 2012; González-Wevar et al. 2016). In particular, South Georgia has been reported to be located at an intermediate position between the Magellan and Antarctic biogeographic regions (i.e., representing the southernmost limit for exclusive Magellan species and the northernmost limit for exclusive Antarctic species; Arntz 2005), providing a potential glacial refugium for Antarctic marine species (González-Wevar et al. 2016). However, contrarily to what was reported by González-Wevar and collaborators (2016), a recent molecular study on Lepidonotothen nudifrons, a notothenioid fish formerly believed to be distributed from the Antarctic Peninsula up to South Georgia, has described the existence of two genetic cryptic species, one located in the northern part of the Scotia Arc (South Georgia and Sandwich Islands) and the other one restricted to more Antarctic waters, which reveals the long-term isolation of these two regions (Dornburg et al. 2016). When only taxonomical tools are taken into account, the distribution of the six macroalgae under study includes South Georgia (Wiencke and Clayton 2002; Wiencke et al. 2014); however, no sampling has been undertaken to date to resolve the genetic identity of these populations. In order to better locate glacial refugia in the region, future studies should consider identifying the genetic diversity present in populations of marine organisms collected along those regions of the Antarctic coasts that could have been less affected by ice scour during the Last Glacial Maximum (e.g., Deception Island, Penguin Island, or Bridgeman Island among others; Simms et al. 2011) and from the more northern islands of the Scotia Arc (e.g., South Georgia or the South Sandwich Islands).
In this study, the geographic spread of haplotypes of six species was determined for populations inhabiting more than 450 km of coast. Haplotypes distributed over hundreds or even thousands of kilometers has been reported in various pelagic and benthic species with long-lived pelagic larvae inhabiting the Southern Ocean (Thornhill et al. 2008; Rau-pach et al. 2010; Bortolotto et al. 2011; González-Wevar et al. 2011; Janosik et al. 2011). The wide-ranging distribution of haplotypes was attributed to the impact of strong oceanic currents and to a high degree of connectivity. However, none of the six macroalgae under study has floating structures, and their dispersal capacity should be very limited. The western Antarctic Peninsula represents a highly fragmented and isolated habitat for coastal marine species since ice-free rocky shores are rare and separated from each other by extensive areas covered by thick ice sheets, strong currents, and steep variation in shelf topography (e.g., Bransfield Strait). These physical properties likely limit gene flow between coastal populations, especially for organisms with low dispersal potential, such as macroalgae that lack buoyant structures (Hoffman et al. 2011). Nevertheless, extreme mtDNA monomorphism along the South Shetland Islands and the coasts of the Antarctic Peninsula has been observed in other species with limited dispersal ability (brooding invertebrates: the brittle star Astrotoma agassizii, Hunter and Halanych 2008; the sea spider Nymphon austrole, Mahon et al. 2008; sea slug with direct development: Doris kerguelenensis, Wilson et al. 2009). For these species as well as for red macroalgae, the strong effect of genetic drift during population contraction in glacial refugia could have been amplified by gene surfing effects during spatial expansion, after ice sheet retreat; this, in turn, would lead to the rapid spread of a dominant haplotype in the recolonized region. Indeed, during interglacial recolonization, random sampling of haplotypes through successive founder events can result in the drastic reduction of genetic diversity; thus, a single haplotype can easily spread over vast geographic areas at expanding range margins (Excoffier and Ray 2008). An emblematic example of gene surfing in macroalgae is the case of the post-glacial, European northwards range expansion of introgressed organelle lineages of Fucus vesiculo-sus with the F. ceranoides nuclear gene pool (Neiva et al. 2010). Moreover, passive transport of detached fronds by ocean currents can explain how even macroalgae characterized by low autonomous dispersal ability can quickly colonize newly available habitats stripped bare by ice during the Last Glacial Maximum (Macaya et al. 2016). Rare events of long-distance colonization by rafting have been documented even among macroalgae lacking floating structures (Fraser et al. 2013; Fraser 2016; Macaya et al. 2016). Antarctic macroalgae fronds enclosed in drift ice have been observed at sea (Guillemin M-L pers. obs.), and these fronds can also be recovered far away from the coasts (e.g., frond of a Desmarestia sp. sampled at a 2500 m depth in the Weddell Sea more than 250 km away from the closest coast; Fahr-bach 2006). In the particular case of recolonization of newly available substrates (e.g., recently deglaciated substrates), the installation of few migrants arriving to the coast can be enhanced since these recruits do not have to compete with established, locally adapted communities (Waters et al. 2013). It is interesting to note that G. skottsbergii, I. cordata, P. decipiens, and P. cartilagineum are among the first macroalgae colonizing new areas available after glacial retreat (Quartino et al. 2013). West of the Antarctic Peninsula, complex oceanic circulation patterns have been described (Moffat et al. 2008; Savidge and Amft 2009; see also Fig. 1a) that likely played a role in the post-glacial expansion of regional marine flora and fauna. Spatial expansion from refugia could have been facilitated by fronds drifting on one of the strong currents present in the region (Moffat et al. 2008; Savidge and Amft 2009; Fig. 1a), specifically, by the Antarctic Circumpolar Current, which flows northeastward from the Bellingshausen Sea through the South Shetland Islands and follows the western shelf-edge limb, and by the Antarctic Slope Front, which flows westward along the whole Antarctic continental shelf entering the Bransfield Strait near the South Scotia Ridge (Fig. 1a). Moreover, the cyclonic circulation inside the Bransfield Strait and the Antarctic Peninsula Coastal Current (APCC) that connect the Bransfield Strait to Marguerite Bay during spring and summer could easily lead to recurring connectivity in our study region (Moffat et al. 2008; Savidge and Amft 2009; Fig. 1a). The strength of the APCC is tightly linked to the amount of melt-water fluxes from the coast, and since global warming affects these fluxes (i.e., affecting glacier melting rates and snowfall rates among others), one can only wonder how connectivity of marine organisms along the Antarctic Peninsula will be altered in the near future (Moffat et al. 2008).

In summary, even if the effects of population contraction on genetic diversity were particularly drastic, a rich flora and fauna assemblage has clearly survived through the Pliocene and Pleistocene glacial and interglacial cycles (Hommersand et al. 2009; Convey et al. 2009; Clarke and Crame 2010; Alcock and Strugnell 2012; Fraser et al. 2014; Billard et al. 2015). The strong water currents in the region likely played a prominent role in the rapid recolonization that took place at the end of the Quaternary. However, in the six macroalgae under study, the presence of one dominant haplotype over the whole studied area could simply be linked to the past glacial demographic history and might not necessarily imply the existence of actual homogenizing gene flow between the Antarctic Peninsula and the South Shetland Islands. Indeed, recent studies have reported strong dissimilarities between genetic diversity and structure encountered in marine species depending on the genetic markers used (e.g., in the flathead mullet; Durand et al. 2013). Differences in patterns of
genetic structure have been linked to the fact that organelle DNA is more sensitive to introgression and/or rapid sweeps (due to selection or strong genetic drift) compared to nuclear DNA (Dowling et al. 2008; Durand et al. 2013). In order to test for the existence of current gene flow between localities within the region, it is imperative to develop new nuclear markers (e.g., microsatellites or SNPs) in macroalgae species of interest. Since the common species of macroalgae in Antarctica grow in widely heterogeneous habitats in terms of salinity and turbidity (for example, see Savidge and Amft 2009; Quartino et al. 2013), it could also be of interest to test for the existence of local adaptation using recently developed genomics and transcriptomics tools (see Riesgo et al. 2015 for a review).

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References

Due to the nature of the text, it is not suitable for conversion into a plain text representation.


