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ORIGINAL PAPER

Phylogeography of two intertidal seaweeds, *Gelidium lingulatum* and *G. rex* (Rhodophyta: Gelidiales), along the South East Pacific: patterns explained by rafting dispersal?

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Abstract Rafting on floating seaweeds facilitates dispersal of associated organisms, but there is little information on how rafting affects the genetic structure of epiphytic seaweeds. Previous studies indicate a high presence of seaweeds from the genus *Gelidium* attached to floating bull kelp *Durvillaea antarctica* (Chamisso) Hariot. Herein, we analyzed the phylogeographic patterns of *Gelidium lingulatum* (Kützing 1868) and *G. rex* (Santelices and Abbott 1985), species that are partially co-distributed along the Chilean coast (28°S–42°S). A total of 319 individuals from *G. lingulatum* and 179 from *G. rex* (20 and 11 benthic localities,

respectively) were characterized using a mitochondrial marker (COI) and, for a subset, using a chloroplastic marker (*rbc*L). *Gelidium lingulatum* had higher genetic diversity, but its genetic structure did not follow a clear geographic pattern, while *G. rex* had less genetic diversity with a shallow genetic structure and a phylogeographic break coinciding with the phylogeographic discontinuity described for this region (29°S–33°S). In *G. lingulatum*, no isolation-by-distance was observed, in contrast to *G. rex*. The phylogeographic pattern of *G. lingulatum* could be explained mainly by rafting dispersal as an epiphyte of *D. antarctica*, although other mechanisms cannot be completely ruled out (e.g., human-mediated dispersal). The contrasting pattern observed in *G. rex* could be attributed to other factors such as intertidal distribution (i.e., *G. rex* occurs in the lower zone compared to *G. lingulatum*) or differential efficiency of recruitment after long-distance dispersal. This study indicates that rafting dispersal, in conjunction with the intertidal

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distribution, can modulate the phylogeographic patterns of seaweeds.

Introduction

The dispersal ability of marine species is a major trait determining the genetic structure of their benthic populations (Weersing and Toonen 2009; Selkoe and Toonen 2011; Haye et al. 2014). In general, species with high dispersal ability (i.e., presence of planktonic larvae, swimming or crawling structures in adults) tend to have lower genetic structure due to higher gene flow between geographically distant populations compared to species with direct development (absence of larvae) or low mobility (e.g., Dawson et al. 2014; Haye et al. 2014). However, other factors such as oceanographic, geological, geographical and ecological features can also affect connectivity, and therefore, the distribution of genetic diversity (Palumbi 1994). In particular, on rocky shores, the tidal height where the organisms are distributed might influence the genetic structure of local populations, with species from medium and high tidal levels having greater genetic structure than species from the low intertidal or subtidal zone (Kelly and Palumbi 2010). This is frequently assumed to be due to the patchiness and greater variety of environmental stresses in the high- to mid-intertidal zones that may generate differential natural selection than in lower zones where the conditions tend to be more homogeneous. Several studies have reported this pattern, which tends to be more prevalent in seaweeds and sessile invertebrates (Engel et al. 2004; Billard et al. 2005; Valero et al. 2011; Krueger-Hadfield et al. 2013; Robuchon et al. 2014).

Seaweeds from intertidal or shallow subtidal habitats are considered good models for phylogeographic studies (Hu et al. 2016). This is due to the complex reproductive cycles (alternation of haploid and diploid phases) of numerous species from all seaweed divisions that may affect the genetic structure of their populations (Krueger-Hadfield and Hoban 2016), coupled with the low dispersal capacity of spores (Santelices 1980; Destombe et al. 1992). However, other mechanisms such as rafting permit dispersal over long distances (Thiel and Haye 2006; Muhlin et al. 2008; Fraser et al. 2009a; 2010; Coyer et al. 2011a, b). For example, some buoyant seaweeds, such as the bull kelp *Durvillaea antarctica* (Fraser et al. 2010) and the giant kelp *Macrocystis pyrifera* (Macaya and Zuccarello 2010a, b) can float over extensive distances (>1000 km) after detachment from the primary substratum, and occasionally even cross entire ocean basins (e.g., over 5000 km, between the coasts of New Zealand and Chile), disrupting the potential for genetic differentiation among distant populations (Thiel and Gutow 2005a; Fraser et al. 2010; Coyer et al. 2011b). Rafting may not only facilitate gene flow among benthic populations

of floating species, but also of their epibiont communities (Thiel and Haye 2006).

Only a few studies have evaluated the effects of rafting on the genetic diversity and structure of epibionts (also called secondary rafters), focusing mostly on animals associated with floating kelps (see Nikula et al. 2010, 2011a, b, 2013; Cumming et al. 2014). In their recent review of phylogeographic studies on non-buoyant seaweeds associated with floating substrata, Macaya et al. (2016) have shown that most of these epibionts present low genetic structure and high genetic connectivity among populations. Nevertheless, in most cases the authors of the genetic studies only suggested this connectivity via rafting of floating seaweeds and could not completely exclude other vectors of dispersal (e.g., floating marine litter, see Kiessling et al. 2015).

A good choice to study the phylogeography of epibionts is conducting research in areas where there is extensive prior information about abundances and environmental factors that could affect the persistence of floating substrata, especially detached seaweeds. In particular, one of the oceans where there have been several studies on rafting and phylogeography of seaweeds is the South East Pacific coast (SEP, ~14°S to 56°S) (Thiel and Gutow 2005b; Fraser et al. 2010; Macaya and Zuccarello 2010a, b; see also for review Guillemin et al. 2016a). In this zone, phylogeographic studies of benthic species (invertebrates and seaweeds) have focused on testing the concordance between the proposed biogeographic boundaries (at 30°S and 42°S) and phylogeographic breaks (for recent reviews see Haye et al. 2014; Guillemin et al. 2016a). In particular, seaweed species with low dispersal ability presented notorious phylogeographic breaks, suggesting that evolutionary lineages constitute distinct phylogenetic species, as in the intertidal macroalgae *Lessonia nigrescens* (now separated into *L. berteroana* and *L. spicata*; Tellier et al. 2009; González et al. 2012) and *Mazzaella laminarioides* (Montecinos et al. 2012). On the other hand, seaweeds with high dispersal ability have shallow phylogeographic breaks and a low genetic structure, such as the floating kelp *Macrocystis pyrifera* (Macaya and Zuccarello 2010a, b). A distinct phylogeographic pattern (i.e., strong genetic structure and high values of genetic diversity) has been reported for the bull kelp *Durvillaea antarctica*, a species with a high dispersal potential by rafting, along the continental coast of Chile (Fraser et al. 2010). This has been attributed to ineffective long-distance dispersal, either due to low effectiveness in recruitment of new individuals in resident populations or because bull kelp supplies are highly variable in certain areas (Fraser et al. 2010). More than 40 species of seaweeds, mainly Rhodophyta, have been found attached to holdfasts of stranded specimens of *D. antarctica* along the continental coast of Chile (Macaya et al. 2016). Therefore, dispersal as secondary rafter could also modulate the genetic structure of these epiphytic algae as suggested

for other non-buoyant seaweeds with low genetic differentiation among distant populations (Boo et al. 2014a; Guillemin et al. 2014).

Gelidium lingulatum (Kützing 1868) and *G. rex* (Santelices and Abbott 1985) are two endemic red seaweeds from the SEP (Santelices 1990). They form monospecific beds at wave-exposed sites (Ortega et al. 2001), mainly in the intertidal zone, where they grow attached to rocks and calcareous shells, but also to holdfasts of large kelps (Santelices 1990; Macaya et al. 2016). Particularly, *G.*

lingulatum is present at 1–2 m above MLLW (mean lower low water) and *G. rex* is most often found at lower intertidal heights, about 0–0.5 m above MLLW (Santelices 1986). The reported geographical distribution of *G. lingulatum* extends from Antofagasta (23°S) to Tierra del Fuego (56°S) (Ramírez and Santelices 1991; Hoffmann and Santelices 1997; Fig. 1). However, the current distribution of the species is not clearly established, because identification was based solely on morphological characters (Santelices 1990). Since *G. lingulatum* features high

Fig. 1 Geographic location of the coast of Chile, showing the main biogeographic zones (provinces and districts) and breaks (30°S–33°S and 41°S–42°S) (modified from Camus 2001). The sampled distributions of *Gelidium lingulatum* and *G. rex* along the Chilean coast are also indicated (*shaded bars*), as well as the geographic distribution according to the literature (*lines*). Also, local strandings (stranded biomass and length) of floating bull kelp *Durvillaea antarctica* in different biogeographic districts are shown (correspondence between *circle sizes* and stranded biomasses, and kelp *sizes* and lengths are indicated) (extracted from López et al. 2017)
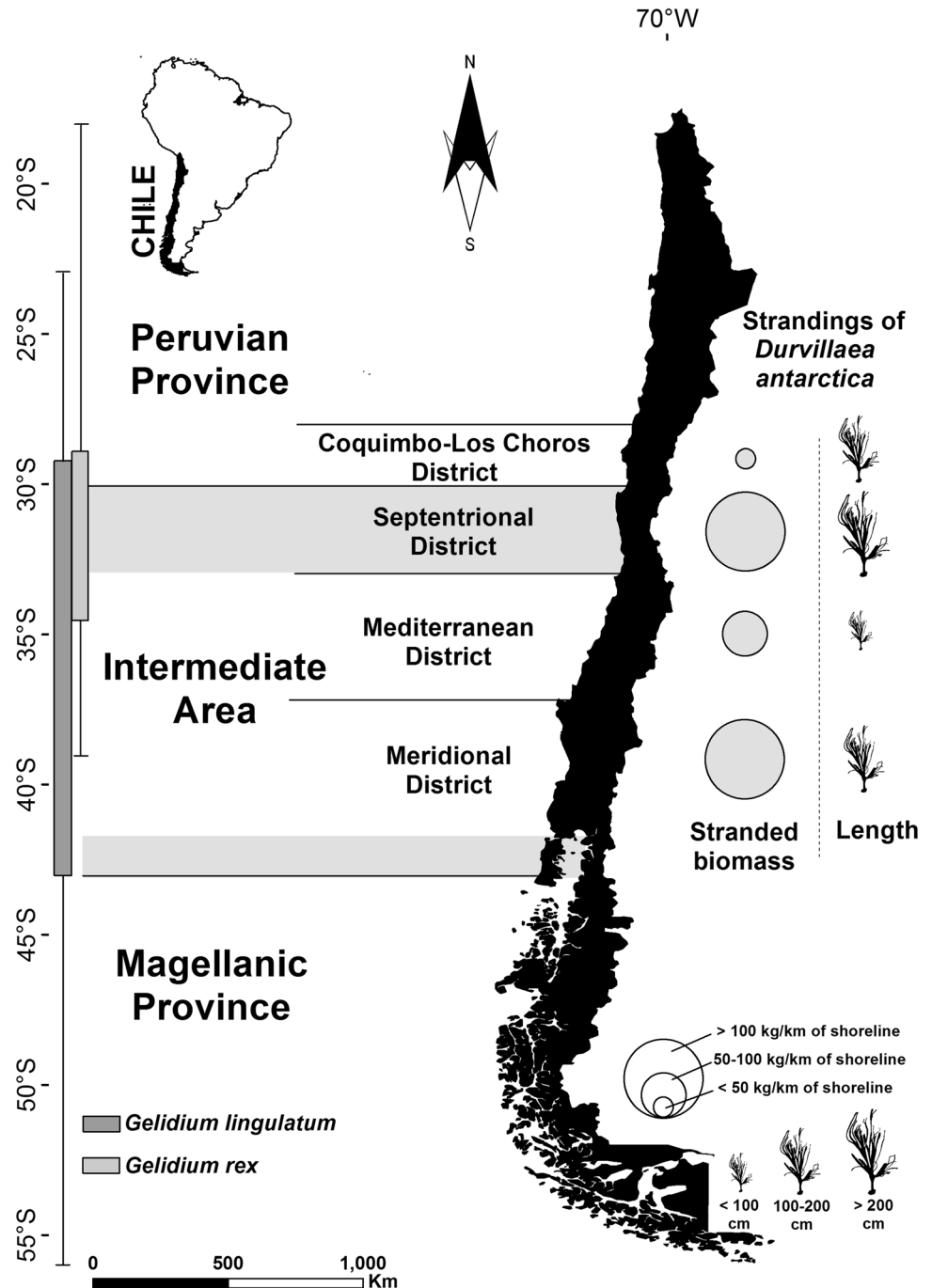
phenotypic plasticity and juveniles are morphologically very similar to other species of the genus, there is a certain risk of erroneous identifications. On the other hand, *G. rex* has morphological features facilitating identification in the field. This species is distributed more narrowly, between Coquimbo (30°S) and Concepción (36°S) (Hoffmann and Santelices 1997), although it has been suggested that its northern and southern distribution could extend to 16°S and 39°S, respectively (Santelices and Abbott 1985; Fig. 1).

Both species of *Gelidium* have a reproductive cycle with an alternation of haploid and diploid phases (Hernández 1997), thalli that can re-attach to the substratum (Rojas et al. 1996), and their spores only survive for short time periods in the water so that the dispersal potential via spores is limited (Bobadilla and Santelices 2005). Also, these turf-forming seaweeds are ecologically important as settlement and nursery area for small invertebrates (González et al. 1991). Moreover, they are economically important for agar extraction (Matsuhiro and Urzúa 1990, 1991; Melo 1998). Within their geographic ranges individuals of both species are frequently found in holdfasts of floating bull kelp *Durvillaea antarctica* (i.e., >10% in the case of *G. lingulatum* and 1–10% in *G. rex*, Macaya et al. 2016), and while intrinsic dispersal ability is strongly limited in these species, dispersal on floating bull kelps could potentially enhance connectivity between their populations. However, this could also be modulated by the distribution across the tidal gradient, where more structure would be expected in *G. lingulatum* from the mid-intertidal zone compared to *G. rex*, which grows in the low intertidal zone.

Genetic studies in Gelidiales have revealed high species diversity within the group and also important limitations of the morphological identification of species (e.g., Nelson et al. 2006; Boo et al. 2013, 2014b, 2016). Currently, few phylogeographic studies are available for species from the genus *Gelidium*. For example, both *G. canariense* in the Canary Islands (Bouza et al. 2006) and *G. elegans* on the coast of Korea, China and Japan (Kim et al. 2012) have high genetic variability between populations, numerous private haplotypes, and low genetic connectivity. This high level of genetic structure among populations has also been observed for species with a wide geographical range, such as *G. vagum* (Yoon et al. 2014), *G. crinale* and *G. pusillum* (Kim and Boo 2012).

Using two molecular markers (COI and *rbc*L), the present study aimed to determine the geographical distribution of genetic diversity for two species from the genus *Gelidium*, which are partially co-distributed along the Chilean coast and occur at distinct tidal levels. Based on these results, this study also aimed to evaluate whether the observed phylogeographic patterns might be influenced by rafting dispersal via floating seaweeds.

Materials and methods

Biogeographical features of the study area

The SEP coast (~14°S to 56°S) is characterized by a linear topography and no major topographical discontinuities between 14°S and 42°S, south of where it becomes a coast characterized by the presence of channels and fjords (Camus 2001; Thiel et al. 2007; Försterra 2009). Ocean circulation in this area is mainly determined by the Humboldt Current with south–north orientation, and by the southward Cape Horn Current in the southernmost area (Thiel et al. 2007). Also, it is characterized by a latitudinal temperature gradient in surface waters (Tapia et al. 2014) where the occurrence of seasonally persistent upwelling events affect the biogeographic structure of the coastal zone (Lachkar and Gruber 2012; Aravena et al. 2014). Two major biogeographic provinces have been described for the continental coast of Chile: the Peruvian Province (18°S–30°S) and the Magellanic Province (42°S–56°S), which are separated by a broad transition zone, the Intermediate Area, between 30°S and 42°S (Camus 2001) (Fig. 1). A recent study had reported a strong pattern of stranded biomass and length of beach-cast bull kelps (*Durvillaea antarctica)* in different biogeographical districts (i.e., subdivisions of the biogeographic provinces), particularly within the Intermediate Area (López et al. 2017, Fig. 1), suggesting areas where the connectivity of their populations and that of their secondary rafters could be greater than in others.

Sampling of *Gelidium lingulatum* and *G. rex*

Species identification

Both species were identified using morphological traits as described by Santelices and Montalva (1983), Santelices and Stewart (1985), Vargas and Collado-Vides (1996), and Hoffmann and Santelices (1997). For *G. lingulatum* some difficulties in visual species identification were encountered due to its close morphological similarity with other co-occurring *Gelidium* species (e.g., *G. chilense*), particularly in the northern part of the described distribution range of the species. Fully developed individuals consist of a crawling and an erect portion. The creeping axes adhere to the substratum by short discoidal rhizoids, while the erect axes are cylindrical with tongue-like blades and sparsely branched at the base (Hoffmann and Santelices 1997) (Fig. 2). While *G. lingulatum* is supposed to occur as far north as 23°S (Ramírez and Santelices 1981), no individuals with the morphological characteristics of *G. lingulatum* were found in eight locations from the northern part of our study area (~20°S to 28°S, Fig. 2, Online Resource 1). In locations at 28°S (i.e., BURR and APOL), we found

individuals with typical traits of the genus *Gelidium*, but not of *G. lingulatum*, and molecular characterization confirmed the distinctiveness from *G. lingulatum* (unpubl. data). This suggests that *G. lingulatum* does not occur north of 29°S, where other, morphologically similar species have been found; consequently, the distribution range of *G. lingulatum* seems to be more restricted than reported by Ramírez and Santelices (1991) and Hoffmann and Santelices (1997). On the other hand, a clear morphological distinction of *G. rex* is possible because of the cylindrical axes at the base and flattened middle and upper parts with toothed margins. Also, this species lacks branchlets along the main axis and has a rigid, crispate and cartilaginous thallus (Fig. 3). In addition, *G. rex* is the largest species from the genus *Gelidium* present in Chile (Santelices and Abbott 1985). No individuals of *G. rex* were found in surveys north of 28°S (Online Resource 1) and south of 34°S (Fig. 3).

Sampling locations

Individuals of *G. lingulatum* and *G. rex* were collected in winters and summers of 2012–2015 from natural populations in the mid–lower intertidal zone (0.5–1 m) of wave-exposed rocky shores. Sampling was performed in a total of 11 locations (28°S–34°S; 790 km of coastline) for *G. rex*, covering 68% of the described geographic range, and in a total of 20 locations (29°S–42°S; 1770 km of coastline) for *G. lingulatum* (45% of the initially described geographic range) (Table 1; Figs. 2, 3). For both *G. lingulatum* and *G. rex,* we collected at least 15 individuals per locality (for this study, an individual was composed of one or several erect axes that arise from stoloniferous thalli, Santelices 1986), except in those locations of low species abundance, such as in the north of the study range (Table 1). A total of 319 and 179 specimens were analyzed for *G. lingulatum* and *G. rex*, respectively.

Sample manipulation

For each sample, several branches of small and well-identified patches of *G. lingulatum* or *G. rex* were collected. Samples were only taken from patches that had a minimum distance of 1 m apart, since vegetative propagation occurs by prostrate stoloniferous thalli (Santelices 1986). Samples were carefully cleaned from epibionts, then stored in individual plastic bags filled with silica gel beads for rapid dehydration, and transported to the laboratory for further genetic analysis.

DNA extraction, PCR amplification, sequencing and sequences alignment

For each sample, a small piece of dry tissue (50 mg) was finely ground using the Tissue Lyser® (Rotsch, Hilden, Germany) at 240 rpm for 5 min. The subsequent DNA extraction was performed using the EZNA® Tissue DNA Kit (Bio-Tek OMEGA, Atlanta, USA), according to the manufacturer's specifications.

Polymerase chain reaction (PCR) amplification of the partial Cytochrome Oxidase c subunit I gene (COI) was performed using primers designed by Saunders (2005) for red seaweeds (GazF1: 5′ TCAACAAATCATAAAGATATTGG 3′ and GazR2: 5′ ACTTCTGGATGTCCAAAAAAYCA 3′) and using the same conditions for PCR concentrations and program as Fraser et al. (2009b). Reactions were done using dNTPs and DNA polymerase GoTaq, Fermelo Biotec (Promega, Madison, USA), and PCR reactions were performed in a thermocycler Veriti (Applied Biosystems, Foster City, USA).

In order to compare the results of the COI marker with a marker with a slower evolving rate, a subset of 22 individuals (10 *G. lingulatum* and 12 *G. rex*) was selected for the *rbc*L sequencing, considering primarily the specimens having different COI haplotypes and trying to cover the maximum of the species distribution range. It is important to note that a single marker may not be representative of the species history, and therefore, the combination of multiple markers facilitates the detection of different processes occurring at different time scales (Ballard and Whitlock 2004). The chloroplast-encoded *rbc*L corresponds to the large subunit of the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo). PCR amplifications of *rbc*L were performed using two primer combinations, F7–R753 (F7: 5′AACTCT GTAGAACGNACAAG 3′; R753: 5′ GCTCTTTCATAC ATATCTTCC 3′; Freshwater and Rueness 1994; Gavio and Fredericq 2002) and F645–R*rbc*Sstart (F645: 5′ ATGCGT TGG AAAGAAAGATTCT 3′ and R*rbc*Sstart: 5′ TGTGTT GCGGCCGCCCTTGTGTTAGTCTCAC 3′; Freshwater and Rueness 1994; Lin et al. 2001). The conditions for PCR concentrations and program were identical to Boo et al. (2013). The PCR reagents used were similar to those described for the COI marker.

PCR products were purified and then sequenced using the reverse amplification primers (GazR2 for COI, R753 and R*rbc*Sstart for *rbc*L) by Macrogen Inc. (Seoul, South Korea: http://www.macrogen.com). Sequences were visualized and edited in Chromas v2.5.1 (Technelysium Pty Ltd 2016) and multiple sequence alignment was performed using CLUSTALW function of BioEdit 7.2.5 (Hall 1999) for each species and marker dataset. Final alignments were checked visually. The resulting datasets for *G. lingulatum* consisted of a 622-base pair (bp) alignment for the mitochondrial DNA region and of a 1484-bp alignment for the chloroplastic DNA region, while *G. rex* datasets consisted of a 628-bp alignment and a 1543-bp alignment, respectively. All haplotype sequences were deposited in GenBank (Accession Numbers KX961986–KX962024) and analyzed by BLAST

analysis to identify matches with other sequences (Altschul et al. 1990).

Genetic diversity and genetic differentiation

Estimations of standard genetic diversity indices per location and per species

The following molecular diversity indices were computed at the species-level only for the *rbc*L dataset and at the species- and location-levels for COI, using Arlequin v 3.5.2.2 (Excoffier and Lischer 2010): the number of haplotypes (*h*), the number of private haplotypes (i.e., haplotypes found at a single sampled location, h_{priv}), the number of polymorphic sites (*S*), haplotype diversity (*H*, based on haplotype frequency, the probability that two randomly chosen haplotypes are different; Excoffier and Lischer 2010) and nucleotide diversity (π, the probability that two randomly chosen homologous nucleotide sites are different, expressed as %π; Excoffier and Lischer 2010). For each COI dataset, considering the different sample sizes, a rarefaction method was used with the Contrib program (Petit et al. 1998) to calculate the standardized haplotype diversity at location (excluding the locations with less than 14 individuals) and overall (species-level). Since sample size of *G. lingulatum* (*n* = 319 samples) is about twice as large as that of *G. rex* (*n* = 179), we considered a sample size of rarefaction of 179 individuals for the case of *G. lingulatum* in order to compare between the two species.

Estimations of pairwise and overall φ_{ST}

Population differentiation between populations of *G. lingulatum* and *G. rex,* and within species was inferred by calculating pairwise and overall (species-level) φ_{ST}-statistics (F_{ST}-like taking into account haplotype frequencies and amount of differences among haplotype pairs). Only locations with a minimum of 14 individuals were included in this analysis. Computing values and tests for significance were done using non-parametric permutation tests (1000 permutations, with Arlequin). Sequential Bonferroni correction was used for multiple comparisons.

Geographic structure

We evaluated whether locations of *G. lingulatum* and *G. rex* were geographically structured through spatial analysis of molecular variance (SAMOVA) test using SAMOVA v2.0 software (Dupanloup et al. 2002). Genetic differentiation was investigated using a hierarchical analysis of the genetic variance by partitioning F_{ST} into F_{SC} and F_{CT} indicating the genetic differentiation of populations within groups and between groups, respectively. For each COI dataset,

locations with less than 14 samples were excluded and each combination of groups was tested using 500 permutations.

Isolation by distance

The isolation-by-distance model (Slatkin 1993) was tested using a Mantel test in Arlequin with 1000 permutations, testing for a positive correlation between pairwise geographic distance (in km) and raw (*D*) average pairwise differences for COI datasets, excluding locations with less than 14 samples. Linearized population pairwise φ_{ST} values could not be used in the Mantel test because several locations were genetically monomorphic for different haplotypes, and pairwise comparisons between such fixed populations gave an φ_{ST} of 1.0. The geographical distance between location pairs was measured as distance along the coast for continental locations and taken as the straight-line distance for the island locations (Chiloé Island: MBRA, CUCA and SBA), using the 'path ruler' tool in Google Earth (http://earth.google.com/).

Haplotype network reconstruction and historical demography

To represent the genealogical relationship between haplotypes, a network of COI haplotypes was constructed for each species, using the median-joining algorithm implemented in NETWORK v5.0 (Bandelt et al. 1999). This method is based on a maximum parsimony algorithm to simplify the complex branching pattern and to represent the most parsimonious intraspecific phylogenies (Polzin and Daneshmand 2003).

To infer the historical demography of *G. lingulatum* and *G. rex*, we first calculated neutrality tests, Tajima's *D* (Tajima 1989), and Fu's F_s (Fu 1997) statistics for each COI dataset, in order to detect significant past changes in population size. Significant departure from selection-drift equilibrium was tested by 1000 bootstrap replicates in Arlequin. Under the assumption of neutrality, negative values characterize populations in expansion while positive values, associated to the loss of rare haplotypes, are considered as a signature of recent bottlenecks.

As a complementary approach to infer the historical demography of each species, we compared the observed mismatch distributions of the number of differences between pairs of sequences to estimated values under a model of sudden pure demographic expansion (Rogers and Harpending 1992) and a model of spatial expansion (Excoffier 2004) using Arlequin. For each expansion model and each species, the fit between observed and estimated mismatch distributions was calculated through a generalized least squares approach and tested by 1000 permutations. A multimodal distribution generally indicates a population in demographic

Table 1 Sampling sites of benthic populations of *Gelidium lingulatum* and *G. rex*. The code used to identify each sampling site, coordinates (latitude and longitude), indices of genetic diversity found for the mitochondrial marker COI, results of neutrality tests and their significance are indicated

Sampling site	Code	Coordinates Latitude	Coordinates Longitude	N	h	h_{priv}	S	H (±SD)	%π (±SD)	D	P value	F_s	P value
Gelidium lingulatum													
Punta de Choros	PTCH	29°13'S	71°27'W	1	1	0	0	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
El Arrayán	ARRA	29°41'S	71°19'W	4	2	1	1	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
La Pampilla	PAM	29°57'S	71°21'W	15	4	3	3	0.467 (±0.148)	0.098 (±0.092)	−1.010	0.165	−1.420	0.062
Zapallar	ZAP	32°33'S	71°28'W	9	3	2	2	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Maitencillo	MAIT	32°37'S	71°25'W	7	1	0	0	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Montemar	MONT	32°57'S	71°33'W	28	5	2	6	0.384 (±0.113)	0.167 (±0.128)	−0.941	0.190	−0.598	0.323
La Boca	LBO	33°54'S	71°50'W	15	3	1	2	0.257 (±0.142)	0.043 (±0.056)	−1.491	0.055	**−1.546**	0.021
Pichilemu	PCH	34°22'S	72°00'W	17	5	2	6	0.507 (±0.140)	0.222 (±0.161)	−0.742	0.246	−0.523	0.355
Constitución	CON	35°19'S	72°25'W	22	4	0	6	0.463 (±0.120)	0.201 (±0.147)	−0.743	0.290	0.635	0.659
Curanipe	CUR	35°50'S	72°38'W	19	2	0	4	0.456 (±0.085)	0.293 (±0.197)	1.750	0.972	4.866	0.978
Cobquecura	COB	36°10'S	72°49'W	16	1	0	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
Lota	LOT	37°09'S	73°11'W	26	2	0	1	0.077 (±0.070)	0.012 (±0.027)	−1.156	0.118	−1.094	0.082
Quidico	QICO	37°22'S	73°39'W	20	2	1	3	0.442 (±0.088)	0.213 (±0.155)	1.333	0.917	3.792	0.935
Curiñanco	CRNC	39°49'S	73°24'W	15	2	0	3	0.133 (±0.112)	0.064 (±0.071)	**−1.685**	0.034	0.834	0.508
Pucatrihue	PUCA	40°31'S	73°42'W	18	4	1	5	0.601 (±0.111)	0.292 (±0.197)	0.791	0.805	1.345	0.794
Bahía Mansa	BAM	40°34'S	73°44'W	13	4	0	5	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Hua-Huar	HUAR	41°18'S	73°50'W	14	5	1	7	0.593 (±0.144)	0.267 (±0.187)	−0.908	0.207	−0.384	0.416
Mar Brava	MBRA	41°56'S	74°01'W	20	4	1	6	0.558 (±0.113)	0.243 (±0.170)	−0.341	0.413	0.999	0.737
Cucao	CUCA	42°40'S	74°07'W	25	2	0	1	0.105 (±0.092)	0.017 (±0.033)	−1.165	0.146	−0.838	0.095
Santa Bárbara	SBA	42°51'S	72°47'W	21	3	0	5	0.186 (±0.110)	0.118 (±0.102)	−1.424	0.061	0.580	0.574
Mean COI								0.348 (±0.203)	0.150 (±0.106)				
Overall COI				319	24	15	21	0.781 (±0.013)	0.352 (±0.216)	−0.853	0.223	**−6.287**	0.039
Gelidium rex													
Los Burros	BURR	28°54'S	71°31'W	19	4	3	3	0.380 (±0.134)	0.065 (±0.070)	−1.422	0.059	**−2.070**	0.013
El Apolillado	APOL	29°10'S	71°29'W	20	1	0	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
El Sauce	SAUC	30°31'S	71°41'W	23	3	2	2	0.534 (±0.097)	0.094 (±0.087)	0.210	0.685	0.217	0.476
Fundo Agua Dulce	FUAD	31°30'S	71°34'W	14	1	1	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
Chigualoco	CHLO	31°45'S	71°31'W	18	1	0	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
Playa Amarilla	PAMA	31°51'S	71°30'W	17	1	0	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
Quintay	QTAY	33°11'S	71°42'W	15	1	0	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
Punta Tralca	PTTR	33°24'S	71°42'W	18	2	1	1	0.426 (±0.110)	0.047 (±0.058)	0.022	0.724	0.463	0.384
La Boca	LBO	33°54'S	72°25'W	2	1	0	0	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Pichilemu	PCH	34°25'S	72°02'W	19	1	0	0	N.A.	N.A.	0.000	1.000	0.000	N.A.
Bucalemu	BUCA	34°38'S	72°02'W	14	3	2	2	0.484 (±0.142)	0.084 (±0.027)	−0.438	0.293	−0.388	0.273

Table 1 (continued)

Sampling site	Code	Coordinates		N	h	h_{priv}	S	H (±SD)	%π (±SD)	D	P value	F_s	P value
		Latitude	Longitude										
Mean COI								0.165 (±0.225)	0.029 (±0.039)				
Overall COI				179	11	9	10	0.628 (±0.029)	0.136 (±0.107)	−1.208	0.103	**−5.085**	0.027
Overall COI north				76	7	6	6	0.533 (±0.059)	0.097 (±0.086)	−1.179	0.119	**−3.295**	0.048
Overall COI north-f				62	6	5	5	0.344 (±0.076)	0.059 (±0.064)	**−1.509**	0.037	**−4.090**	0.005
Overall COI south				103	4	3	3	0.134 (±0.046)	0.022 (±0.036)	**−1.368**	0.047	**−3.514**	0.004

N number of individuals sequenced, h number of haplotypes, h_{priv} number of private haplotypes, S number of polymorphic sites, H standardized haplotype diversity and SD (after rarefaction); %π percentage of nucleotide diversity and SD, D Tajima's test, F_s Fu's test. Mean and overall values correspond to the average values of the locations and the total for each species, respectively. Significant values ($P < 0.05$) are shown in bold. N.A. = not available or uncalculated (locations with $N < 14$)

equilibrium, while a unimodal distribution is associated with a recent pure demographic expansion or a range expansion.

In the particular case of *G. rex*, in both approaches, the COI dataset was separated into three groups, according to the results of the geographic distribution of haplotypes (see "Results"), those locations from 28°S to 31°S (including FUAD named "*G. rex* north"), the same locations without FUAD (i.e., 28°S to 30°S named "*G. rex* north-f"), and those locations of the southern range (between ~31°S and 34°S, called "*G. rex* south").

Results

Sequence characteristics

A 622-bp portion of COI was analyzed from 319 individual *G. lingulatum*, detecting 24 haplotypes with 21 polymorphic sites (Table 1). On the other hand, the 628-bp portion of COI sequenced for 179 individual *G. rex* revealed 11 haplotypes, with 10 polymorphic sites (Table 1). From the 10 individuals of *G. lingulatum* sequenced also for the *rbc*L marker (1484-bp alignment), three haplotypes were detected, differing by 2 polymorphic sites (Online Resource 2), while sequencing of 12 individuals *G. rex* (1543-bp portion of *rbc*L) revealed only one single haplotype.

A query of sequences for the COI haplotypes of *G. rex*, using a BLAST search, revealed a 100% identity between two of our haplotypes (GR4 and GR9, query cover: 516 bp) and a reference sequence identified as *G. rex*, from Tongoy Bay, Chile (30°15′S; 71°29′W; GenBank Accession Number: HM629875; Kim et al. 2011). Similarly, the unique *rbc*L haplotype recovered for *G. rex* (GR701) presented a 94–100% match with the two reference sequences for the species, both identified as *G. rex* from Tongoy Bay (GenBank Accession Number: AF305801, query cover: 1430 bp, Thomas and Freshwater 2001; GenBank Accession Number: HM629835, query cover: 1353 bp, Kim et al. 2011). The taxonomic unit *G. lingulatum* was absent from GenBank, but some of our haplotypes presented a 100% identity with sequences registered as *Gelidium* sp., from Chile (Chungungo: 29°26′S; 71°18′W and Caleta Horcón: 32°42′S; 71°29′W). The sequences from Chungungo matched with GL5 and GL702 haplotypes, for COI and *rbc*L, respectively, while sequences from Caleta Horcón matched with GL3 and GL703 haplotypes, respectively (GenBank accession numbers: COI, JX891593–JX891594; *rbc*L, JX89619–JX891622; query cover: COI, 511 bp; *rbc*L: 1354 bp; Boo et al. 2013).

Overall, for COI the nucleotide diversity (%π) was 0.352 ± 0.216 and 0.131 ± 0.112 in *G. lingulatum* and *G. rex*, respectively, while standardized haplotype diversity was 0.781 ± 0.013 and 0.628 ± 0.029 after rarefaction, being in both cases greater in *G. lingulatum* than in *G. rex* (see Table 1). On the other hand, for the *rbc*L marker, nucleotide

diversity and standardized haplotype diversity in *G. lingulatum* were $\%\pi = 0.059 \pm 0.051$ and $H = 0.711 \pm 0.086$, respectively. In the case of *G. rex*, no genetic diversity was observed for this marker.

Phylogeographical patterns

For *G. lingulatum*, 15 of 24 COI haplotypes were private (62.5%) (i.e., haplotypes found at a single location), most of

them (12 haplotypes) being unique (i.e., haplotypes found only in one single individual), while for *G. rex*, 9 of 11 haplotypes were private (81.5%), but only two of them were unique.

A contrasting pattern among species was observed regarding the distribution of the frequent haplotypes. The three most frequent COI haplotypes of *G. lingulatum* were widespread and shared among geographically distant locations (GL3: 11 locations distributed along the complete study range ~29°S–42°S, 2000 km distance; GL5:

Fig. 2 Geographic distribution of haplotypes and haplotype networks of *Gelidium lingulatum* for mitochondrial COI and chloroplastic *rbc*L markers. Sampling locations where no individuals of the species were found from the northern part of the study area are also indicated. Photographs of a specimen and intertidal patches of species are shown in the *lower right*. The within-location diversity and the geographical extent of each haplotype are shown. On the map each *circle* represents a location and the proportion of *pie chart* indicates the frequency of individuals for each haplotype. The *pie chart color-code* corresponds to the one used in haplotype networks of each marker. In the networks, each *circle* represents a haplotype and its *size* is proportional to the frequency in which the haplotype was encountered (correspondence between *circle sizes* and *numbers* of individuals is indicated). *Perpendicular bars* between each haplotype pair correspond to the number of mutational steps among them. Abbreviations for location codes are as in Table 1
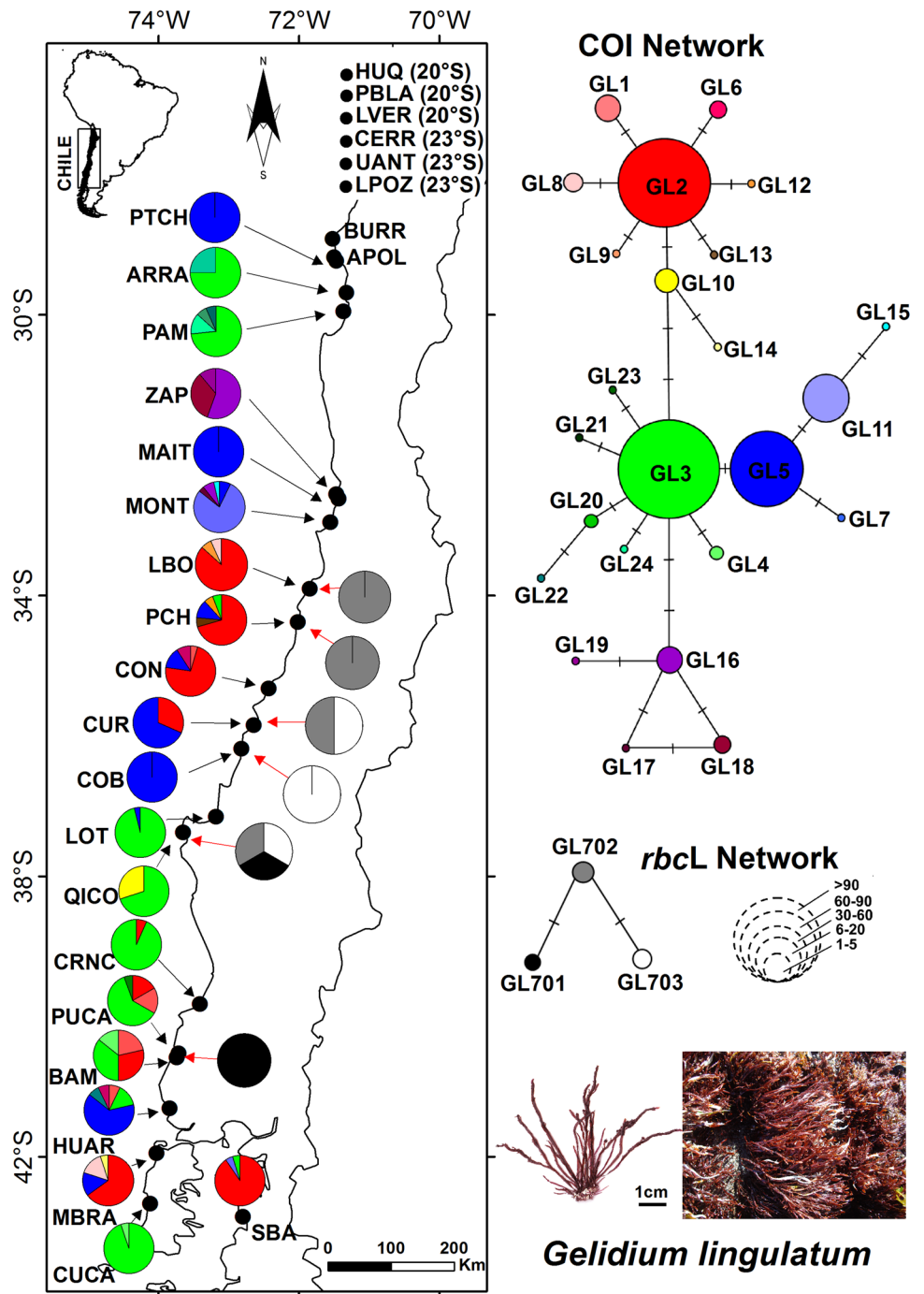
Fig. 3 Geographic distribution of haplotypes and haplotype networks of *Gelidium rex* for mitochondrial COI and chloroplastic *rbc*L markers. Sampling locations where no individuals of the species were found from the northern and southern sites of the study area are also indicated. Photographs of a specimen and intertidal patches of species are shown in the lower right. See legend of Fig. 2 for details
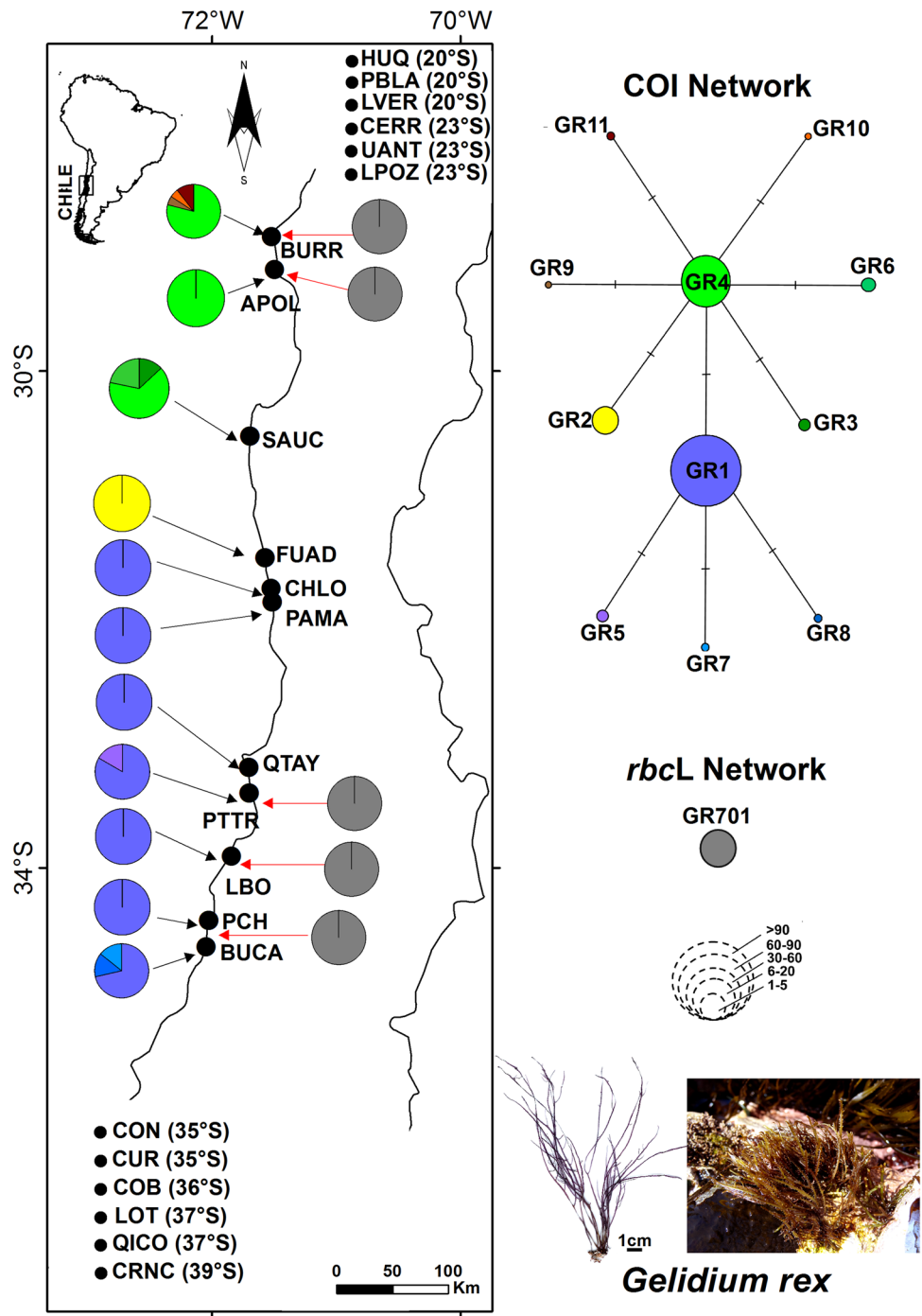
10 locations between ~29°S and 41°S, 1800 km distance; GL2: 9 locations between ~33°S and 42°S, 1550 km distance; Table 1; Fig. 2). On the other hand, the two most frequent COI haplotypes of *G. rex* presented disjunct geographic distributions, with GR4 exclusively found at the three northernmost locations (~28°S to 30°S) and GR1 only at the seven southernmost locations (~31°S to 34°S; Fig. 3). In between, the location FUAD presented a singular pattern, as all sampled individuals (i.e., 14) shared the GR2 haplotype, which is private from this location.

In the case of the *rbc*L marker, the three haplotypes in *G. lingulatum* were distributed from ~33°S to 40°S, co-occurring in some locations (CUR and QICO, Fig. 2, see Online Resource 2), whereas for *G. rex* the single haplotype was observed from ~28°S to 34°S (Fig. 3; see Online Resource 2).

For the *G. lingulatum* COI dataset, average values per sampled location of standardized haplotype diversity (*H*) and nucleotide diversity (%π) were 0.348 ± 0.203 and 0.150 ± 0.106, respectively (Table 1). Of the 20 sampled
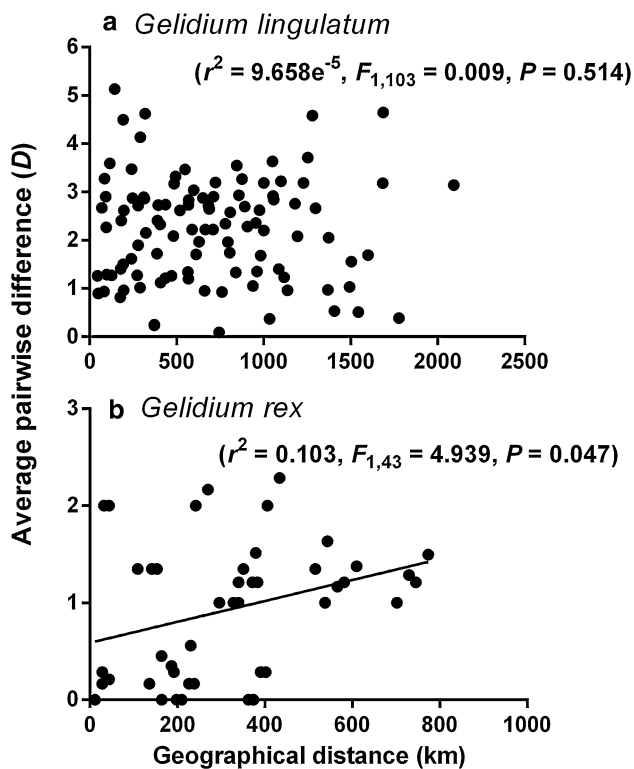
Fig. 4 Scatter plot of genetic differentiation and geographic distance of pairwise locations for COI marker. **a** *Gelidium lingulatum* and **b** *G. rex*. Pairwise genetic distances, represented as *D*, are plotted against pairwise geographic distances (km). *Each point* corresponds to a pairwise comparison of locations. The results of the statistical analyses and the regression *line* for significant relationship (*G. rex*) are also shown. Locations with $N < 14$ were excluded from analyses

locations, 17 were polymorphic with up to 5 haplotypes per location (Fig. 2; Table 1). The haplotype network showed that private haplotypes differed from one of the three most frequent haplotypes mostly by 1 (and up to 3) mutational steps and the maximum pairwise difference among *G. lingulatum* haplotypes is 7 steps (Fig. 2).

A lower diversity was observed for the *G. rex* COI dataset, with average values per sampled location of standardized haplotype diversity (*H*) and nucleotide diversity ($\%\pi$) of 0.165 ± 0.225 and 0.029 ± 0.039, respectively (Table 1). Most of the locations were monomorphic (7 of 11) and polymorphic locations showed up to 4 haplotypes (Table 1; Fig. 3). The haplotypes differed by 1–3 mutational steps in the haplotype network, with all private haplotypes found at 1 single step from one of the two most frequent haplotypes (Fig. 3).

Within-species genetic structure (COI datasets)

The SAMOVA revealed eight different groups for *G. lingulatum*, with only two groups formed by several locations

which are distributed interspersed along the latitudinal gradient covered by the study (i.e., group 1: PAM, LOT, CRNC, CUCA, 1770 km distant between the most extreme sites; group 8: LBO, PCH, CON, MBRA, SBA, 1550 km distant between the most extreme sites; see Fig. 2 and Online Resource 3). In contrast, in *G. rex* the three detected groups coincide completely with the disjunct distribution of the three most frequent haplotypes, as described above (Online Resource 3). The groups corresponded to (1) northern locations (BURR, APOL and SAUC), (2) the single site FUAD, and (3) southern locations (from CHLO to BUCA).

According to the Mantel test, in *G. lingulatum* the correlation between genetic distance and geographic distance was not significant ($r^2 = 9.658 \text{ e}^{-5}$, $F_{1,103} = 0.009$, $P = 0.514$; Fig. 4a), while in *G. rex* the correlation was significant ($r^2 = 0.103$, $F_{1,43} = 4.939$, $P = 0.047$), indicating an isolation-by-distance pattern for the latter species (Fig. 4b). However, no isolation-by-distance was observed when the three geographic groups were considered separately, *G. rex* north ($r^2 = 0.199$, $F_{1,6} = 2.339$, $P = 0.177$), *G. rex* north-f ($r^2 = 0.835$, $F_{1,4} = 2.861$, $P = 0.166$), and *G. rex* south ($r^2 = 1.441 \text{ e}^{-4}$, $F_{1,37} = 0.283$, $P = 0.598$).

The overall φ_{ST} (at species-level) for *G. lingulatum* was 0.629. Most pairwise φ_{ST}-values were significant, indicating differentiation among locations. Interestingly, similarities between geographically distant (over 1000 km) locations were observed (e.g., LBO, PCH, CON, MBRA and SBA) (Fig. 2, Online Resource 4). On the other hand, the overall φ_{ST} for *G. rex* was 0.859. The φ_{ST}-values were significant for all pairwise comparisons among locations from distinct groups. Likewise, genetic differentiation was evidenced among all location pairs from the group *G. rex* north (i.e., BURR, APOL, SAUC and FUAD), whereas within the group *G. rex* south, only the location BUCA was significantly different from the other sampled locations of that zone (Fig. 3; Online Resource 5).

Historical demography (COI datasets)

The mismatch distribution for the *G. lingulatum* COI dataset was fitted to the sudden demographic expansion model (SSD = 0.017, $P = 0.398$), and the spatial expansion model (SSD = 0.015, $P = 0.496$; Fig. 5a). Neutrality tests on overall *G. lingulatum* COI data also supported partially a demographic expansion, with a negative Tajima's *D* index (although not significant: $D = -0.853$, $P = 0.223$) and a negative and significant Fu's F_s index ($F_s = -6.287$, $P = 0.039$; Table 1).

For *G. rex* north and *G. rex* north-f, a demographic population expansion was not or only poorly supported by both tested models (*G. rex* north: sudden demographic

Fig. 5 Mismatch distribution for COI datasets for *Gelidium lingulatum* (**a**), *G. rex* north (**b**), *G. rex* north-f (**c**) and *G. rex* south (**d**), according to spatial expansion models. The observed distributions of the number of pairwise differences (*bars*) are contrasted to their expected distributions (*solid lines*) under a model of spatial expansion
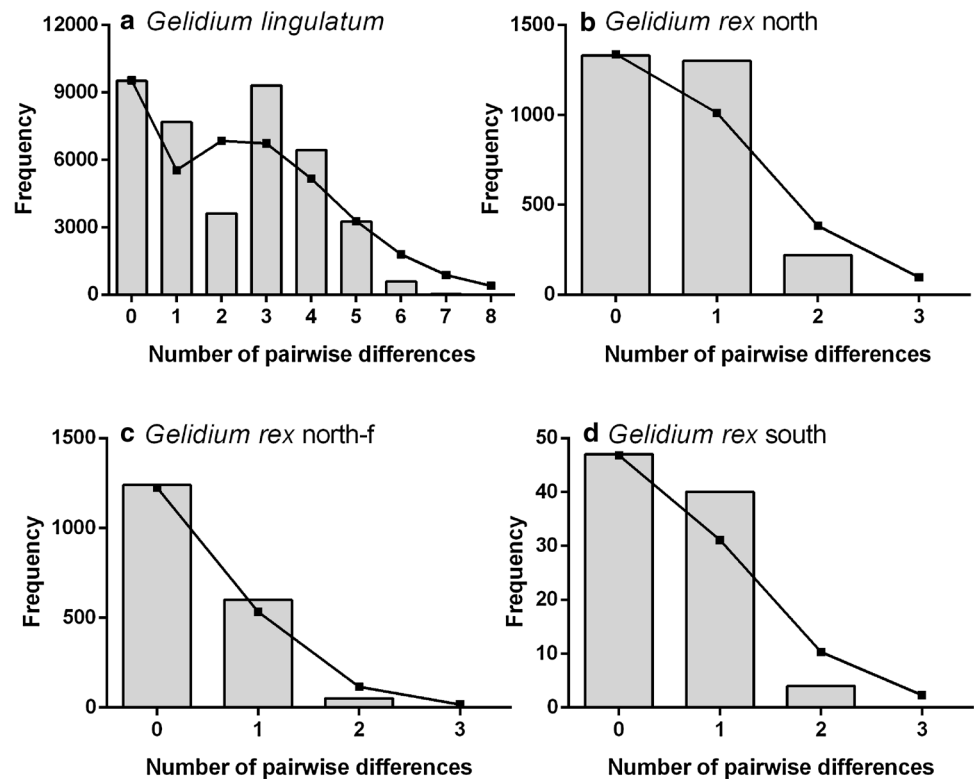
expansion, SSD = 0.013, P = 0.045 and spatial expansion, SSD = 0.013, P = 0.001; *G. rex* north-f: sudden demographic expansion, SSD = 0.002, P = 0.025 and spatial expansion, SSD = 0.002, P = 0.089; Fig. 5b, c). Tajima's D was not significant for *G. rex* north, while Fu's F_s indicated a demographic expansion (D = −1.179, P = 0.119; F_s = −3.295, P = 0.048). In the case of *G. rex* north-f, both indices showed a demographic expansion (D = −1.509, P = 0.037; F_s = −4.090, P = 0.005). In contrast, for *G. rex* south stronger evidence was found for population expansion both from mismatch analysis (with a higher support for the sudden demographic expansion: SSD = 0.014, P = 0.309; compared to the spatial expansion model: SSD = 0.014, P = 0.162; Fig. 5d), and from neutrality tests, both significant (D = −1.368, P = 0.047; F_s = −3.514, P = 0.004; Table 1).

Discussion

The two seaweed species presented contrasting genetic diversity and structure. *Gelidium lingulatum* had higher genetic diversity, but genetic structure did not follow a clear geographic pattern, while *G. rex* had low genetic diversity, a phylogeographic break, but shallow genetic structure. In particular, the phylogeographic pattern of *G. lingulatum* is not consistent with that observed for other intertidal red seaweeds described for the coast of Chile, using the same

mitochondrial marker and partially sharing the same geographic area of study (Montecinos et al. 2012; Guillemin et al. 2016b). On the other hand, the *G. rex* pattern has similarities to the shallow genetic structure of *M. pyrifera* (Macaya and Zuccarello 2010a).

Contrasts in genetic diversity and structure

Our results for genetic diversity in *G. lingulatum* and *G. rex* are within the observed range of previous studies done for other *Gelidium* species, using the COI marker (e.g., *G. elegans*: h = 34, H = 0.711, %π = 0.734, Kim et al. 2012; *G. vagum*: h = 17, S = 16, H = 0.844, %π = 0.173, Yoon et al. 2014; H values not standardized by rarefaction), revealing a high genetic diversity at species-level, particularly in the case of *G. lingulatum*, and after standardizing the H values to the smaller sample size of *G. rex*. Another red seaweed (*Mazzaella laminarioides*) from the coast of Chile showed higher genetic diversity indices (h = 24, S = 62, H = 0.871, %π = 3.42, H value not standardized) compared with *G. lingulatum* and *G. rex*, although that study covered a larger geographic area (29°S–54°S) (Montecinos et al. 2012). These three red seaweed species (*G. lingulatum*, *G. rex*, *M. laminarioides*) share some characteristics of their habitat (cohabiting in the rocky intertidal shore, partially co-distributed along the Chilean coast) and of their life history (low autonomous dispersal capacity, triphasic isomorphic life cycle). Nevertheless, they present contrasting genetic diversity;

these differences could be associated with the distribution in the intertidal zone (i.e., *M. laminarioides* lives higher in the intertidal zone than both *Gelidium* species) or with the type of vegetative reproduction found in the genus *Gelidium* (i.e., fragmentation and re-attachment to the substratum, Santelices and Varela 1994; Rojas et al. 1996; Perrone et al. 2006). In particular *G. lingulatum* tends to monopolize the rocky substratum, which could suppress local genetic diversity, in contrast to the individual and unconnected thalli of *Mazzaella* (Gómez and Westermeier 1991).

The amplitude of the latitudinal range could also have implications in the genetic diversity, because a wider geographic range is related to a larger effective population size and a higher gradient of environmental variability, which can lead to selection and local adaptation (Alberto et al. 2010). This could explain the differences in genetic diversity between the two species studied, considering the wider geographic range of *G. lingulatum* compared to *G. rex*. Therefore, our results suggest that the amplitude of the geographic range contribute to the differences in genetic diversity observed for both species, and other red seaweeds from the Chilean coast.

In the case of *G. lingulatum*, genetic structure was evidenced throughout its range, but without a clear geographical pattern (i.e., haplotypes disappear and reappear repeatedly throughout its geographic range and no phylogeographic break was detected), and there was no genetic isolation-by-distance. On the other hand, *G. rex* compared to *G. lingulatum* showed a different pattern with a disjunct haplotype distribution where a separation occurs at ~31°S between the northern, FUAD, and southern populations of its geographic range. This coincides with the biogeographic break at 30°S (Camus 2001) and is also consistent with the phylogeographic breaks described for that region for many intertidal species of invertebrates and macroalgae with limited dispersal abilities (i.e., 29°S–33°S, Tellier et al. 2009; Sánchez et al. 2011; Montecinos et al. 2012; Haye et al. 2014; Guillemin et al. 2016a). However, unlike other intertidal seaweeds (e.g., *Lessonia nigrescens* complex, Tellier et al. 2011; *M. laminarioides*, Montecinos et al. 2012), this geographical subdivision is not based on a strong genetic difference, since the separation between populations is only one mutational step, similar to the shallow genetic structure described for *M. pyrifera*, a kelp species with high dispersal potential via rafting (Macaya and Zuccarello 2010a).

Indeed, the *rbc*L marker, despite the low sample sizes, revealed no indication for a phylogeographic break due to the complete absence and lower polymorphism for this marker in *G. rex* and *G. lingulatum*, respectively. This is consistent with the generally lower mutation rate of this marker, compared to COI (Engel et al. 2008; Grant 2016). Therefore, all these results suggest that *G. lingulatum* and *G. rex* (more evident in *G. lingulatum*) have a long-distance

dispersal mechanism, which cannot be explained by intrinsic dispersal abilities alone due to limited autonomous dispersal potential via spores/gametes.

Gelidium rex is a species found in the very low intertidal zone compared to *G. lingulatum*, which grows closer to the mid-intertidal zone (Santelices 1986). In general, species that are distributed in an area with less environmental variability (e.g., longer immersion times below the tidal gradient as for *G. rex*) tend to have less genetic structure (Kelly and Palumbi 2010). This might be due to less patchy distributions and larger population sizes in the low intertidal or subtidal zones (i.e., distribution width effect, Robuchon et al. 2014), which would reduce the selection pressure and the action of genetic drift observed in upper intertidal zone (although the distribution of *G. rex* in the lower intertidal zone tends to be very patchy rather than being a continuous fringe; Santelices and Abbott 1985). For example, for two sister species of laminarian kelps co-distributed along the coast of France, Robuchon et al. (2014) showed that populations of the species inhabiting the shallow subtidal zone (*Laminaria hyperborea*) had less genetic structure than those of the intertidal species (*L. digitata*). In addition, this is congruent with the observed pattern of *M. laminarioides* from the mid-intertidal zone, which has a much stronger genetic structure than both *Gelidium* species, showing two strongly differentiated haplogroups (separated by 15–45 bp for COI) between 29°S and 37°S, and up to 3 haplogroups considering locations up to 42°S (Montecinos et al. 2012). However, if both species of *Gelidium* are compared, genetic structure of *G. lingulatum* did not follow a clear geographic pattern in contrast to *G. rex* and overall (species-level) φ_{ST}-value is lower for *G. lingulatum* (0.629) than *G. rex* (0.859). Therefore, our results do not support the hypothesis that seaweed species from the mid-intertidal zone have more genetic structure compared with organisms from lower zones and it suggests that other factors may be important. A trend of less genetic structure in species from the upper intertidal zone has also been observed in two intertidal barnacles (*Jehlius cirratus* and *Notochthamalus scabrosus*) from the Chilean coast (18°S–54°S) (Zakas et al. 2009; Ewers-Saucedo et al. 2016; Guo and Wares 2017). Future studies should also use complementary nuclear markers to improve understanding of the genetic structure of these species within their tidal distribution.

Phylogeographic patterns as a result of rafting dispersal

In *G. lingulatum*, the lack of a phylogeographic break, patchy distribution of haplotypes within its geographic range and no isolation-by-distance are indications of long-distance dispersal events. Human-mediated transport (Banks et al. 2015) or rafting dispersal (e.g., wood and floating seaweeds, Thiel and Gutow 2005a) can move

organisms over long distances. In the case of human-mediated dispersal, transport through maritime traffic (ballast waters and ship hulls) has been shown to affect the phylogeographic patterns of other seaweeds (e.g., *Undaria pinnatifida*, Voisin et al. 2005; *Caulerpa cylindracea*, Piazzi et al. 2016). Although *G. lingulatum* germlings have a high tolerance to total darkness (Santelices et al. 2002), conditions in ballast waters are strongly adverse (i.e., anoxia) and maritime traffic occurs offshore and in ports, not in rocky areas, so that this transport mechanism is much less likely than through rafting dispersal by floating seaweeds. In addition, at least one species from the genus *Gelidium* has been detected on derelict aquaculture buoys in Coquimbo Bay (30°S) (Astudillo et al. 2009), and so other floating substrata cannot be completely ruled out as dispersal vehicle. Another long-distance dispersal mechanism through drifting fronds has been also reported in *G. versicolor* on the south coast of England (Dixon and Irvine 1977).

Detached seaweeds are one of the most common floating substrata along the coast of Chile (Hinojosa et al. 2010; 2011; Wichmann et al. 2012). Rafting transport could increase the gene flow between distant populations and thus modify the genetic structure, as had been described for some invertebrates inhabiting holdfasts of *D. antarctica* (Nikula et al. 2010; Haye et al. 2012). In Chile, both *G. lingulatum* and *G. rex* are often found attached to holdfasts of floating and recently stranded bull kelps *D. antarctica* (higher frequencies in *G. lingulatum* than *G. rex*, Macaya et al. 2016), but the continental clade (30°S–44°S) of this bull kelp presents a very different phylogeographic pattern (Fraser et al. 2010) than the two red seaweeds. For example, *D. antarctica* has a much more genetically structured pattern (i.e., more mutational steps among pairs of haplotypes) compared to *G. rex* and its geographical haplotype distribution is not similar to the patchy pattern of *G. lingulatum*. This suggests that other factors during, or after, along-shore rafting journeys could be affecting connectivity among distant populations. Moreover, Macaya et al. (2016) suggested that the physiological capacity to tolerate new environmental conditions at the sea surface during rafting might be directly related to the bathymetric distribution pattern of seaweeds in their benthic habitats. Particularly in turf algae, changes in solar radiation levels during transfer from the benthic to the pelagic environment (rafting at the sea surface) could affect performance and persistence of these algae. Given the intertidal distribution of the two study species, these shifts in light regime should be more critical in *G. rex* than in *G. lingulatum*. In addition, the difference in latitudinal distribution between the two species (i.e., wider in *G. lingulatum* compared to *G. rex*) could also suggest that there are different tolerance capacities to harsh conditions between them.

Long-distance dispersal could also be consistent with the historical patterns observed. For *G. lingulatum* and *G. rex* a recent population expansion was detected, although in the latter this was only observed in southern populations, while in northern populations (particularly, those from BURR to SAUC) this pattern was not so clear. This coincides with the high presence of private haplotypes in both species, which in the case of *G. rex* were detected only at the northernmost and southernmost sampling sites (i.e., BURR and BUCA). Nikula et al. (2010) reported genetic signatures of population expansion in epifaunal invertebrates (i.e., peracarids) associated with holdfasts of floating bull kelp *D. antarctica* in subantarctic areas. This suggests that rapid historical population growth might have been favored by frequent rafting events.

Successful immigration after rafting journeys is likely also influenced by other factors such as substratum availability, settlement capacity of immigrant propagules, and the density of the resident population (i.e., density blocking, Waters et al. 2013; Neiva et al. 2014). In dense local populations, new haplotypes that arrive with few immigrant individuals have a high probability of being outcompeted because of their rarity, which leads to rapid elimination of these new haplotypes by genetic drift. For example, this could be happening for *G. rex* in locations such as FUAD, where a single private haplotype was very frequent among the sampled individuals. This is congruent with records in locations adjacent to FUAD (30°S–31°S), where higher population abundances of this species have been observed in comparison to northern and southern sites (Broitman et al. 2001, Vásquez and Vega 2004). This could be because, as observed in other species of *Gelidium* (i.e., *G. arbuscula*, Sosa and García-Reina 1992; Sosa et al. 1998), stoloniferous outgrowths of creeping axes is a common way of propagation; therefore, locally adapted clones could propagate asexually and became predominant through competitive advantage, thereby minimizing the availability of unoccupied substratum and limiting opportunities for recruitment of new genotypes (via sexual reproduction). In addition, the ability of thallus reattachment of these species (Rojas et al. 1996) would favor the monopolization of the substratum. For example, Alberto et al. (1999) suggested that populations of *G. sesquipedale* from northern France to Morocco maintain the gene flow among populations (<500 km) through occasional transport of detached fronds by local currents during storm events and subsequent reattachment to new substrata.

Conversely, strong disturbances with massive local mortalities (e.g., coastal uplifts after earthquakes) could change this pattern (Castilla et al. 2010; Jaramillo et al. 2012), enhancing the possibility of successful immigration to uncolonized habitats or those with lower population density. Habitat heterogeneity could also be an important factor influencing phylogeography and population connectivity

in intertidal seaweeds. For example, the extent of sandy beaches (particularly from 36°S to 40°S on the coast of Chile, Thiel et al. 2007) could reduce the availability of primary substratum for intertidal seaweeds inhabiting rocky shores and thus, genetic drift and small effective population sizes probably contribute strongly to the divergence between their populations (Fraser et al. 2010). Therefore, our results suggest that the phylogeographic patterns of these intertidal algae are affected by rafting dispersal via floating seaweeds, although there may be differential functional capabilities during rafting journeys and/or differential efficiency of recruitment after long-distance dispersal that could explain the divergent patterns between both species. Future studies should also focus on phenology and the relationships between different phases of the life cycle in these species.

Conclusions and outlook

Our phylogeographic study confirms the presence of *G. lingulatum* along the Chilean coast at least from 29°S to 42°S (no recent records are available for the south, 42°S–56°S, John et al. 2003; Soto et al. 2012), but our surveys suggest that this species does not occur north of 29°S. Similarly, we only found individuals of *G. rex* between 28°S and 34°S, despite a reported distribution ranging from 16°S to 39°S (Santelices and Abbott 1985), thus suggesting a previous overestimation of the geographical range in both study species (Fig. 1).

Gelidium lingulatum had some genetic structure (i.e., φ_{ST} values are highly significant among several locations), but did not follow a clear geographic pattern (i.e., no phylogeographic break, and haplotypes disappear and reappear repeatedly along its geographical range), contrasting with findings for other red seaweeds with similar life histories and distribution ranges (e.g., *M. laminarioides*, Montecinos et al. 2012; *Nothogenia chilensis*, Lindstrom et al. 2015). A shallow genetic structure was observed in *G. rex*, with a phylogeographic break coinciding with the phylogeographic discontinuity described for other species between 29°S and 33°S (Tellier et al. 2009; Sánchez et al. 2011; Montecinos et al. 2012). We propose that these contrasting patterns of *G. lingulatum* and *G. rex* might be due to (1) differences in tidal level and species-specific adaptations in physiology and reproductive biology (e.g., temperatures below 10 °C are limiting for growth of these species, Oliger and Santelices 1981) and (2) differences in extrinsic dispersal capacities, with more effective rafting dispersal for *G. lingulatum* than for *G. rex*.

As previously suggested (Macaya et al. 2016), while our study provides support for efficient rafting dispersal, it also indicates that the relative contribution of rafting to contemporaneous population connectivity may vary, depending on seaweed biology (e.g., functional and reproductive characteristics of these epiphytic non-buoyant seaweeds) and population ecology (e.g., density blocking). Further studies should in particular focus on rafting routes, via genetic characterization of the source populations of stranded *D. antarctica*, particularly those holdfasts carrying *G. rex* or *G. lingulatum* individuals. Recent studies indicate that supplies of bull kelp rafts to the shore vary strongly along the coast of Chile (López et al. 2017, Fig. 1), which could affect connectivity among the populations of *D. antarctica* and of associated epibionts.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interests.

Human and animals rights This article does not contain any studies with human participants or animals performed by any of the authors.

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