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Unexpected absence of island endemics: Long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species

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Abstract

Aim: We assess biogeographical patterns, population structure and the range of species in the pulmonate genus *Siphonaria* across the sub-Antarctic. We hypothesized that locally endemic cryptic species will be found across the distribution of these direct-developing limpets in the sub-Antarctic.

Location: The sub-Antarctic coasts of the Southern Ocean including South America, the Falkland/Malvinas, South Georgia, Kerguelen and Macquarie Islands.

Methods: Multi-locus phylogenetic reconstructions, mtDNA time-calibrated divergence time estimations and population-based analyses of *Siphonaria* populations were used at the scale of the Southern Ocean.

Results: We resolve two widely distributed lineages of *Siphonaria* (*S. lateralis* and *S. fuegiensis*) across the sub-Antarctic. MtDNA divergence time estimates suggest that they were separated around 4.0 Ma (3.0 to 8.0 Ma). Subsequently both species followed different evolutionary pathways across their distributions. Low levels of genetic diversity characterize the populations of both species, reflecting the role of Quaternary glacial cycles during their respective demographic histories, suggesting high levels of dispersal among geographically distant localities.

Main conclusions: *Siphonaria lateralis* and *S. fuegiensis* constitute sister and broadly co-distributed species across the sub-Antarctic. Unexpected transoceanic similarities and low levels of genetic diversity in both these direct-developing species imply recurrent recolonization processes through long-distance dispersal to isolated sub-Antarctic islands. For such groups of Southern Ocean invertebrates, rafting may be more effective for long-distance dispersal than a free-living planktotrophic larval stage. This biogeographical model may explain why many marine species lacking a dispersal phase exhibit broad distributions, low genetic diversity and low population structure over thousands of kilometres.

KEYWORDS
Antarctic circumpolar current, direct developers, long-distance dispersal, oceanic biogeography, pulmonate, rafting, *Siphonaria*, sub-Antarctic

1 | INTRODUCTION

Biogeographical mechanisms explaining the distribution of southern temperate taxa have been debated for more than a century (Crame, 1999; Darwin, 1845; Dell, 1972; Knox, 1960; Strugnell, Rogers, Prodöhl, Collins, & Allcock, 2008). Recently, the literature has been characterized by disagreement over the relative importance of vicariance versus dispersal in the biogeography of the Southern Ocean biota but consensus has emerged about the combined significance of these processes (Clarke, Barnes, & Hodgson, 2005; Fraser, Nikula, Spencer, & Waters, 2009; González-Wevar, Nakano, Cañete, & Poulin, 2010; Gonzalez-Wevar et al., 2017; Moon, Chown, & Fraser, 2017; Nikula, Fraser, Spencer, & Waters, 2010; Nikula, Spencer, & Waters, 2012; Poulin, Gonzalez-Wevar, Díaz, Gérard, & Hüne, 2014; Saucède, Pierrat, Danis, & David, 2014; Waters, 2008).

In the marine realm, dispersal plays a central role in the evolution of species with spatially structured populations, resulting in genetic cohesion, global persistence despite local extinction and the tracking of favourable environments in a changing world (Ayre, Minchinton, & Perrin, 2009; Cowen & Sponaugle, 2009; Puritz et al., 2017; Ronce, 2007). The presence of pelagic dispersive larval stages in species with low autonomous vagility is often considered a valuable proxy for dispersal potential (Haye, Varela, & Thiel, 2012; Puritz et al., 2017; Thorson, 1950). Species with free-living planktonic stages (broadcast-spawners) are expected to be more effective dispersers than those lacking larval stages (direct developers) and to exhibit less population differentiation (Haye et al., 2012; Marko, 2004). Nevertheless, meta-analyses and comparative studies, particularly in the Southern Ocean, have challenged such assumptions (Cumming, Nikula, Spencer, & Waters, 2014; Helmuth, Veit, & Holberton, 1994; Nikula et al., 2010; Weersing & Toonen, 2009).

The role of long-distance dispersal by rafting has been especially controversial (Gillespie et al., 2012; Thiel & Haye, 2006), with its rarity and unpredictability often hindering the development of testable hypotheses (Cowie & Holland, 2006; Crisp, Trewick, & Cook, 2011). In the sub-Antarctic, rafting events are mainly associated with buoyant kelps, which facilitate dispersal of different groups from invertebrates (Cumming et al., 2014; Gonzalez-Wevar et al., 2017; Helmuth et al., 1994; Nikula et al., 2010) to non-buoyant kelps (Fraser et al., 2013).

Members of the pulmonate limpet genus *Siphonaria* occur on rocky intertidal shores worldwide, except in the Arctic. In a recent revision, Dayrat, Goulding, and White (2014) evaluated species richness through molecular and morphological analyses, recording a total of 41 genetic units (species), although many of them were morphologically cryptic and could not be reliably identified by shell characters. Together with this, they showed that no *Siphonaria* species was broadly distributed across the Indo-West Pacific. Three clades were recorded in southern South America: *S. lessonii* and two sister cryptic species which had previously been considered as *S. lateralis* (Dayrat et al., 2014), also known as *Kerguelenella lateralis* (White & Dayrat, 2012). These cryptic species showed 6.9% mtDNA divergence (Dayrat et al., 2014), and were recognized by Güller, Zelaya, and Ituarte (2015) as *S. lateralis* and the newly described *S. fuegiensis*.

Based on morphology, *S. lateralis* is broadly distributed across the sub-Antarctic from southern South America to Macquarie Island where it is dominant in intertidal rocky environments (Simpson & Harrington, 1985; Griffiths & Waller, 2016; Figure 1a). Published mtDNA sequences for *S. lateralis* include individuals from southern South America ($n = 10$) and South Georgia ($n = 2$) (Dayrat et al., 2014; Güller et al., 2015). Genetically identified individuals of *S. fuegiensis* ($n = 6$) have only been recorded from the southern tip of South America (Dayrat et al., 2014; Güller et al., 2015). However, on the basis of subtle differences in shell shape, other specimens have been assigned to *S. fuegiensis* from the Strait of Magellan, the Falkland/Malvinas Islands and Isla de los Estados in southern Argentina (Güller et al., 2015), where the two species are sympatric (Figure 1b).

Like many marine invertebrates in the sub-Antarctic, *S. lateralis* and probably *S. fuegiensis* are direct developers, with benthic development and low dispersal capacity (Chambers & Harrington, 1994; Simpson & Harrington, 1985). Direct development is considered a key evolutionary trait in Southern Ocean marine invertebrates enhancing potential for speciation (Pearse, Mooi, Lockhart, & Brandt, 2009; Thatje, 2012). Consequently, and as demonstrated in several marine invertebrate groups in this region (Allcock et al., 2011; Janosik, Mahon, & Halanych, 2011; Leese, Kop, Wägele, & Held, 2008; Wilson, Schrödl, & Halanych, 2009), molecular comparisons of widely separated populations might be expected to reveal additional unrecognized cryptic species. Nevertheless, both species are commonly associated with buoyant and broadly dispersing kelps, often being encased in the holdfasts of *Durvillaea antarctica* (Cumming et al., 2014; Figure 1c–e), and might have a high potential for rafting. As recently demonstrated in crustaceans and gastropods, rafting can be a major biogeographical process shaping patterns of genetic diversity and structure in direct developers across distant areas of the Southern Ocean (Cumming et al., 2014; Nikula et al., 2010, 2012). Such long-distance dispersal could contribute to the broad geographical distribution of *Siphonaria* at high latitudes.

Here we present phylogenetic and population-based analyses of high-latitude *Siphonaria* populations from South America, the Falkland/Malvinas Islands, South Georgia, Kerguelen and Macquarie Islands. We provide a clear picture of (1) the evolutionary relationships among the sub-Antarctic *Siphonaria* species and (2) the geographical distribution of each taxon, to depict biogeographical patterns of the genus at high latitudes. As a consequence of direct development in these higher latitude pulmonates, the main biogeographical patterns in *Siphonaria* across the Indo-West Pacific (Dayrat et al., 2014), and patterns recorded in Southern Ocean near-shore marine molluscs including *Nacella* (Gonzalez-Wevar et al., 2017) and *Doris* (Wilson et al., 2009), we expected to find closely related cryptic species, endemic to each island group. Alternatively, long-distance dispersal mediated by rafting could play a key role in the biogeography of direct developers like *Siphonaria*

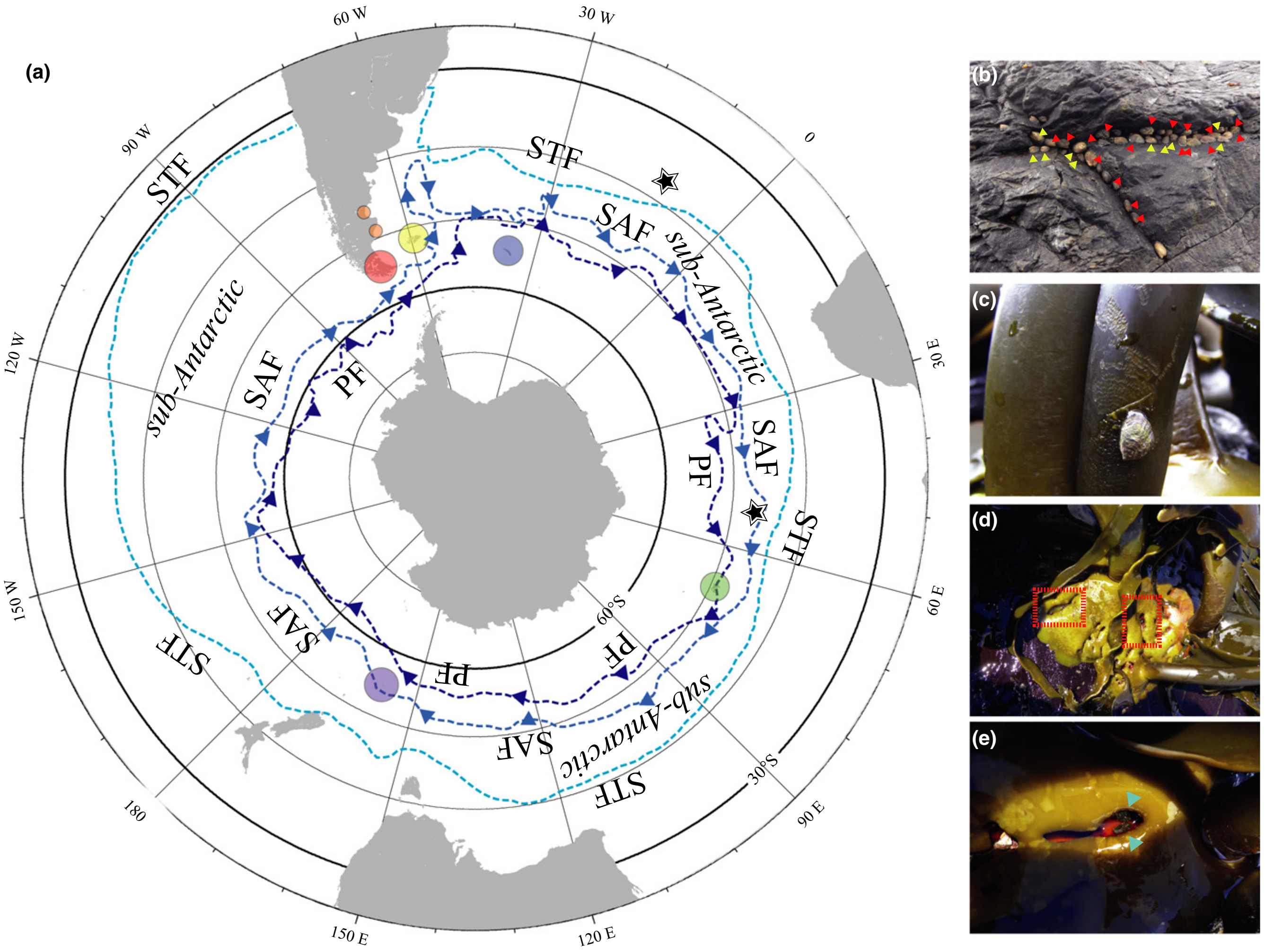

FIGURE 1 (a) Distribution of *Siphonaria lateralis* around the Southern Ocean showing major oceanographic currents and subdivisions where STF, subtropical front, SAF, sub-Antarctic front, PF, polar front. Stars indicate records of the species (Griffiths & Waller, 2016) and coloured areas show sampling sites in different provinces of the Southern Ocean (red, Pacific Patagonia; orange, Atlantic Patagonia; blue, South Georgia; yellow, Falkland/Malvinas Islands; green, Kerguelen archipelago; purple, Macquarie Island). (b) Syntopic individuals of *S. lateralis* (red) and *S. fuegiensis* (yellow) recorded at Kerguelen Islands. (c) Individuals of *Siphonaria* living closely associated with the bull-kelp *Durvillaea antartica*. (d–e) *Siphonaria* individuals living encased in kelp holdfasts at Kerguelen archipelago [Colour figure can be viewed at wileyonlinelibrary.com]

permitting a broad distribution of its representatives across the sub-Antarctic.

2 | MATERIAL AND METHODS

2.1 | Sample collection, DNA preparation and sequence editing

Siphonaria individuals were sampled from around the Southern Ocean (Figure 1; Figure S1 in Appendix S1) including Pacific Patagonia (PP), Atlantic Patagonia (AP), the Falkland/Malvinas Islands (FI), South Georgia (SG), Kerguelen Islands (KI) and Macquarie Island (MI) (Table S1 in Appendix S2). All individuals were identified following Dayrat et al. (2014) and Güller et al. (2015). Whole specimens were fixed in ethanol (95%) and DNA was extracted from the mantle using standard salting-out methodologies (Aljanabi & Martinez, 1997). Universal primers were used to amplify partial fragments of the mitochondrial gene cytochrome c oxidase subunit I (COI) (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994), the nuclear 28S rRNA (Littlewood, Curini-Galletti, & Herniou, 2000) and the internal transcribed spacer region (ITS1 & ITS2) (Oliverio & Mariottini, 2001). Sequences for each of the analysed fragments were assembled independently and edited using GENEIOUS 5.1.7 (Kearse et al., 2012). Similarly, alignments and base composition of nucleotide sequences were analysed for each marker separately in MEGA 6.0 (Tamura, Strecher, Peterson, Filipski, & Kumar, 2013) using MUSCLE (Edgar, 2004) with standard settings. Mitochondrial codon usage was determined using the Effective Number of Codons value (ENC; Wright, 1990) using DNASP v5 (Librado & Rozas, 2009). New high latitude *Siphonaria* sequences are available at Genbank under the following Accession Numbers: COI (MF651995–MF652021), ITSs (MF652022–MF652042) and 28S rRNA (MF652043–MF652059).

2.2 | Phylogenetic reconstructions and divergence time estimates

Mitochondrial (COI) DNA reconstructions used new and previously published (Dayrat et al., 2014) *Siphonaria* haplotypes from the sub-Antarctic. For comparative purposes, we also performed multi-locus phylogenetic reconstructions using mtDNA (COI) and nucDNA (ITS1 & ITS2) sequences. For this we amplified each marker from at least eight individuals of *S. lateralis*, *S. fuegiensis* and *S. lessonii*, and we analysed them together with available sequences from *S. japonica* (Wang, Tsang, & Dong, 2015). Maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses (BA) were used to estimate phylogenetic relationships. MP analyses were performed using PAUP * (Swofford, 2002) following González-Wevar et al. (2010). The program JMODELTEST 2 (Darriba, Taboada, Doallo, & Posada, 2012) was used to select the GTR+I+G (COI) and GTR+G (ITS1 & ITS2) substitution models for the ML and BA. ML and BA reconstructions based on mtDNA (COI) and multi-locus data sets were carried out using PHYML (Guindon & Gascuel, 2003) and MRBAYES v.3.1.2 (Huelsenbeck & Ronquist, 2001) respectively. Nodal support for MP and ML analyses was inferred from non-parametric bootstrap (BS) using 1,000 pseudo-replicates (Felsenstein, 1981). Bayesian-inference posterior probabilities were estimated using the Metropolis coupled Markov chain Monte Carlo algorithm (MCMC) running four chains for 100 $\times$ 10^6 generations, with trees sampled every 1,000 generations. Stationarity was inferred when the average standard deviation of split frequencies was less than 0.01 (Huelsenbeck & Ronquist, 2001). The initial 10% of the trees were discarded (burn-in) and posterior probabilities were estimated as the fraction of trees showing a particular node. Posterior probability density was summarized as a maximum clade credibility tree using TREEANNOTATOR v.1.6.1 (http://beast.bio.ed.ac.uk/TreeAnnotator) and visualized with FIGTREE v.1.4 (http://tree.bio.ed.ac.uk/software/figtree).

The best fit model for the mtDNA COI data set, a relaxed molecular-clock analysis with an uncorrelated lognormal (ucln) model of evolutionary rate heterogeneity, was implemented using the GTR+I+G substitution model in BEAST v.1.6.2 (Drummond, Suchard, Xie, & Rambaut, 2012). A birth-death speciation prior was used for branching rates in the phylogeny, four chains were run twice for 100 $\times$ 10^6 generations, and trees were sampled every 1,000 generations. Because of the absence of a clear fossil record in *Siphonaria* we used a conservative mutation rate (1%), following previous studies in siphonariids (Teske et al., 2011; Wang et al., 2015). Convergence of model parameters was estimated by plotting the marginal posterior probabilities versus the generations in TRACER v.1.5 (http://beast.bio.ed.ac.uk/Tracer). Effective sample-size values were estimated for each parameter to ensure adequate mixing of the MCMC (ESSs > 1,000).

2.3 | Estimating levels of genetic diversity and structuring

Levels of mtDNA genetic polymorphism were determined using standard diversity indices including number of haplotypes (k), number of segregating sites (S), haplotype diversity (H), average number of pairwise differences (Π) and nucleotide diversity (π) for each locality and species with DNASP. Genealogical relationships in sub-Antarctic *Siphonaria* populations were reconstructed using maximum parsimony networks in HAPVIEW (http://www.cibiv.at/~greg/haploviewer). For comparative purposes, we also reconstructed haplotype networks based on 28S rRNA (n = 60) and ITS1 & ITS2 (n = 40) sequences, independently. We estimated the levels of mtDNA differentiation following Pons and Petit (1996) through mean pairwise differences (N_{ST}) and haplotype frequencies (G_{ST}) with ARLEQUIN v. 3.5 (Excoffier, Laval, & Schneider, 2005). The statistical significance of these analyses was assessed using permutation tests (20,000 iterations). We estimated the levels of mtDNA phylogeographical differentiation between subpopulations using the nearest-neighbor statistic (S_{nn}) (Hudson, 2000) and its statistical significance was estimated through a permutation test (10,000 iterations). We inferred the spatial pattern of COI genetic structure in each species by estimating the number and the composition of groups that were the most differentiated based on sequence data with SAMOVA (Spatial Analysis of Molecular Variance) following Dupanloup, Schneider, and Excoffier (2002).

3 | RESULTS

Mitochondrial DNA alignment within the clearly resolved *Siphonaria* Clade A (Dayrat et al., 2014) included 268 variable positions (40.79%) of which 259 (96.64%) were parsimony informative. Mitochondrial sequences were A-T rich (65.7%). In contrast, nuclear 28S rRNAs (n = 36) and ITSs sequences (n = 40) were C-G rich (55.5% and 60.7% respectively). Mitochondrial and nuclear sequences were not saturated at any position. No evidence for mtDNA codon bias was detected (ENC = 39.70).

3.1 | Phylogenetic reconstructions

Mitochondrial reconstructions corroborated previous molecular studies in *Siphonaria* and discriminated major taxonomic lineages within Clade A of Dayrat et al. (2014), with high bootstrap values and posterior probabilities (Figure 2). All the reconstruction methods (MP, ML and BA) and markers showed *S. lateralis* and *S. fuegiensis* as sister species (Figure 2 and Figure S2 in Appendix S1). Uncorrected *p*-values between these species are 6.4% and 3.0% for COI and ITS (Figure 3a & b) respectively. In contrast, *S. lateralis* and *S. fuegiensis* differed by just a single base pair for 28S rRNA (Figure 3c), highlighting the low resolution of this marker in siphonariids. Even while COI and ITS registered high levels of genetic divergence (>12%), the 28S rRNA recorded only three substitutions between *S. lessonii* and *S. fuegiensis*/*S. lateralis*. Divergence time estimates based on mtDNA (COI) sequences, under a 95% Bayesian confidence credible interval for BCI for relative divergence times (Figure S3 in Appendix S1), suggest that the separation between *S. lateralis* and *S. fuegiensis* occurred during the Pliocene, ~4 Ma (3–8 Ma).

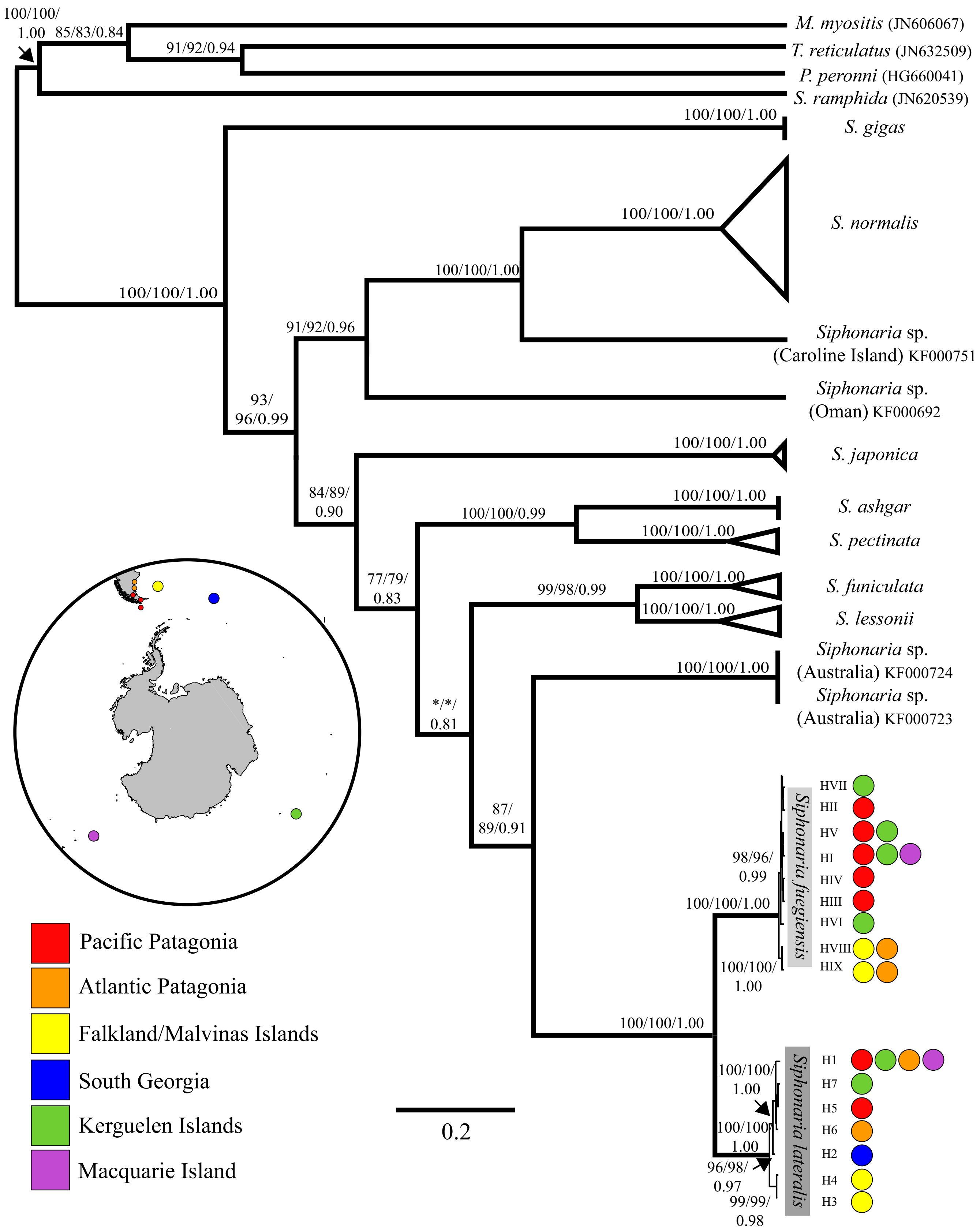

FIGURE 2 Bayesian maximum clade credibility tree of *Siphonaria* relationships based on mtDNA (COI) sequences with special emphasis on sub-Antarctic individuals collected from around the Southern Ocean. Bootstrap support values (MP and ML) and BPP are shown above the nodes (in that order). Map and colours indicate major sampled areas [Colour figure can be viewed at wileyonlinelibrary.com]

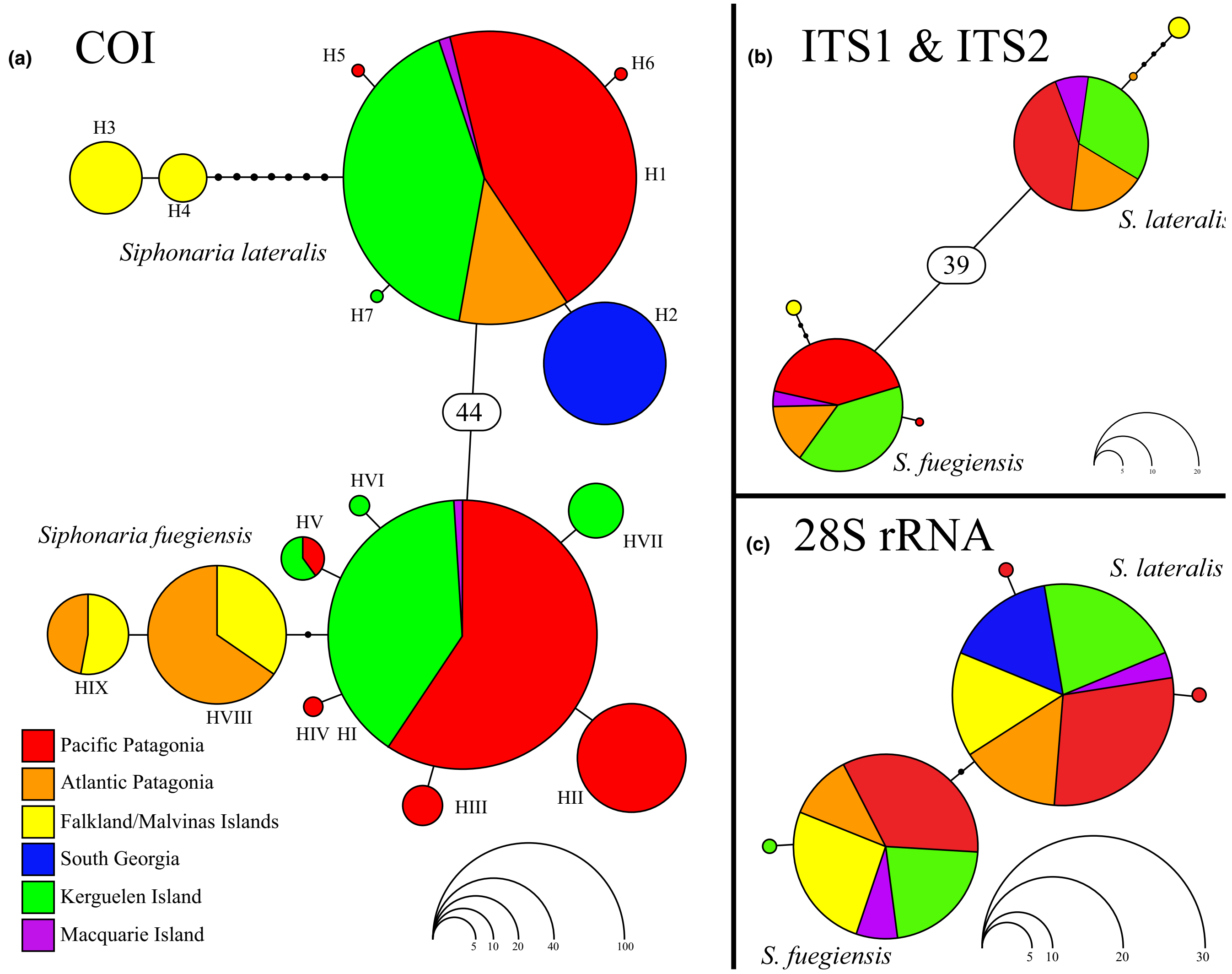

FIGURE 3 (a) mtDNA (COI) Maximum parsimony network including 714 sub-Antarctic individuals of *Siphonaria* (*S. lateralis* and *S. fuegiensis*) collected at different localities in the Southern Ocean. (b) & (c) nucDNA Maximum parsimony networks based on ITS and 28S rRNA sequences respectively. Each haplotype is represented by a coloured circle indicating the main area where it was collected. The size of the circle is proportional to its frequency in the whole sampling effort [Colour figure can be viewed at wileyonlinelibrary.com]

Within *S. lateralis*, mtDNA reconstructions showed three subclades: (1) Pacific Patagonia (PP) + Atlantic Patagonia (AP) + Kerguelen Islands (KI) + Macquarie Island (MI), (2) South Georgia (SG) and (3) the Falkland/Malvinas Islands (FI) (Figure 2). Within *S. fuegiensis*, the COI phylogeny showed two subclades: (1) PP+KI+MI and (2) FI+AP (Figure 2), being this species absent in SG. Multi-locus reconstructions recovered similar subdivisions within *S. lateralis* and *S. fuegiensis* (Figure S2 in Appendix S1). Considering the low resolution of the 28S rRNAs, this marker failed to resolve any grouping within high latitude *Siphonaria*.

3.2 | Population-based analyses

The complete COI data set for *S. lateralis* and *S. fuegiensis* included 395 and 319 individuals, respectively, and consisted of 687 nucleotide positions coding for 229 amino acids. Neither indels or stop codons, nor any amino acid change were recorded in the COI data matrix, even when *S. lateralis* and *S. fuegiensis* were separated by a total of 44 substitutions (Figure 3a). ITS sequences for siphonariids ($n = 40$) consisted of 1,282 nucleotide positions. Several indels were recorded in the ITS data matrix and *S. lateralis* and *S. fuegiensis* were separated by 39 substitutions. Finally, 28S rRNA sequences included a total of 60 individuals and consisted of 698 nucleotide positions.

Across their respective distributions, very low levels of mtDNA genetic variation characterized the standard diversity indices (S, H, k, Π and π) in both *S. lateralis* and *S. fuegiensis* (Tables S2 and S3 in Appendix S2). In fact, 10 out of 14 *S. lateralis* localities showed no genetic diversity ($H = 0$). Similarly, H indices in *S. fuegiensis* were relatively low and fluctuated between 0.171 (Baie du Prince de Monaco) and 0.605 (Diego Ramírez Island).

Haplotype networks for *S. lateralis* and *S. fuegiensis* showed similar topologies with short genealogies and the presence of specific dominant haplotypes and several endemic ones (Figure 3). In the case of *S. lateralis*, PP, AP, KI and MI shared a highly dominant haplotype (H1). Individuals from SG showed a single private haplotype (H2) separated by a single substitution from H1. Finally, in the FI, we recorded two closely related private haplotypes (H3 and H4) that are separated by seven substitutional steps from H1 (Figure 3). Similarly, in the case of *S. fuegiensis*, PP, KI and MI shared a dominant COI haplotype (HI; Figure 3a). A less common haplotype (HV) was recorded in both PP and KI. In addition, PP and KI exhibited private medium-frequency haplotypes (HII and HVII respectively). In contrast to *S. lateralis*, the dominant haplotype was not found in AP localities. In fact, AP and FI shared two medium-frequency haplotypes (HVIII and HIX) separated by one and two substitutions from HI respectively (Figure 3a).

In spite of the low number of individuals analysed, ITS sequences in *S. lateralis* showed the presence of a dominant shared haplotype across PP, AP, KI and MI. Again, individuals from FI showed a different haplotype ($n = 3$) separated by four substitutional steps from the dominant one. Similarly, in the case of *S. fuegiensis* ITS sequences recorded a dominant haplotype broadly distributed in PP, AP, KI and MI, whereas FI individuals ($n = 2$) carried a single haplotype separated by two mutational steps from the dominant one (Figure 3b).

3.3 | Genetic structure in *Siphonaria* species across the sub-Antarctic

Mean general values of COI differentiation measured over 14 populations of *S. lateralis* were high, especially average G_{ST} (0.239) and N_{ST} (0.259) (Table S4 in Appendix S2). Nevertheless, these results must be regarded with caution because of the presence of endemic haplotypes at SG and FI that strongly separated these localities from the rest. In fact, pairwise N_{ST} and G_{ST} comparisons, S_{nn} and SAMOVA all clearly discriminated three groups in this species: (1) PP/AP/KI, (2) FI and (3) SG. SAMOVA analyses of *S. lateralis* showed that among-group variation accounts for 95.01% of the total variance (Table S6 in Appendix S2). Similarly, the nearest-neighbour statistic algorithm recorded high levels of phylogeographical signal ($S_{nn} = 1.000$ $p < .0001$) among these SAMOVA's recognized groups.

Within *S. fuegiensis*, average G_{ST} (0.229) and N_{ST} (0.300) values for COI were also high as a consequence of the marked differentiation of FI/AP from the remaining populations (Table S5 in Appendix S2). Pairwise N_{ST} and G_{ST} comparisons, S_{nn} and SAMOVA in *S. fuegiensis* showed two clearly differentiated groups: (1) PP/KI and (2) FI/AP. SAMOVA analyses indicated that variation among these groups accounted for 64.41% of the total variance (Table S7 in Appendix S2). Similarly, the S_{nn} statistic recorded high levels of phylogeographical signal ($S_{nn} = 1.000$ $p > .0001$) among the recognized SAMOVA groups.

4 | DISCUSSION

Our results show that two species of pulmonate limpet, *Siphonaria lateralis* and *S. fuegiensis*, occur across vast distances of the Southern Ocean, from the Pacific and Atlantic coasts of Patagonia eastward to the Falkland/Malvinas (FI), South Georgia (SG), Kerguelen (KI) and Macquarie Islands (MI). The presence of two such widespread direct-developing species is a surprise considering that several studies have revealed locally endemic cryptic species on different island groups in the Southern Ocean across different marine invertebrate groups (Gonzalez-Wevar et al., 2017; Janosik et al., 2011; Leese et al., 2008; Wilson et al., 2009), macroalgae (Billard, Reyes, Mansilla, Faugeron, & Guillemin, 2015; Fraser et al., 2013) and fishes (Dornburg, Federman, Eytan, & Near, 2016). In these latter cases, there appears to be a limited connectivity among benthic marine populations, regardless of dispersal capacity (Moon et al., 2017). For instance South American and South Georgia populations of the broadcast-spawning nemertean Parborlasia *corrugatus* are genetically distinct, despite the high dispersal capacity (evidenced by population panmixia within the sub-Antarctic and Antarctic regions) (Thornhill, Mahon, Norenburg, & Halanych, 2008). Similarly, populations of the sea spider *Pallenopsis* from the Falkland/Malvinas Islands, Antarctica and South America are genetically differentiated (Harder, Halanych, & Mahon, 2016; Weis et al., 2014).

The vast distributions recorded in both *S. fuegiensis* and *S. lateralis*, together with the extensive sharing of mitochondrial haplotypes among far-flung populations (Patagonia-Kerguelen-Macquarie) and the low levels of nucleotide polymorphism, imply that both species are good long-distance dispersers. It might seem unlikely that direct-developing pulmonates would be able to travel across several thousand kilometres of open ocean. Nevertheless, previous studies have demonstrated striking discrepancies between dispersal potential and the observed distribution of direct developers (Ayre et al., 2009). In fact, several direct developing species in the sub-Antarctic including molluscs (Cumming et al., 2014) and crustaceans (Leese, Agrawal, & Held, 2010; Nikula et al., 2010) exhibit a marked genetic homogeneity across geographically distant areas.

Sub-Antarctic *Siphonaria* often live closely associated with, and even encased in bull-kelp (*Durvillaea antarctica*) holdfasts (Morton & Miller, 1973; Simpson, 1976; E. Poulin & T. Saucède observations at Kerguelen Islands). Such observations strongly suggest that bull-kelp provides the mechanism for long-distance dispersal as has been inferred for other sub-Antarctic taxa (Cumming et al., 2014; Fraser, Nikula, & Waters, 2011; Moon et al., 2017; Nikula et al., 2010). As also noted by Griffiths and Waller (2016), the distribution of several sub-Antarctic molluscs (*Laevilitorina caliginosa*, *Nacella* and *Mytilus*) matches the distribution of the bull-kelp. Alternative mechanisms (e.g., rafting on other substrates and anthropogenic introductions) might explain our data, but they seem unlikely (Cumming et al., 2014). We conclude that for species with no dispersive larval stage, long-distance dispersal mediated by rafting is a key biogeographical mechanism explaining the low, or even the absence, of phylogeographical structure across geographically distant areas in the sub-

Antarctic connected by the flow of the Antarctic circumpolar current (ACC).

Divergence time estimates suggest that the separation of *S. lateralis* and *S. fuegiensis* took place during the Pliocene 4 Ma (3–8 Ma) and after that they followed different evolutionary trajectories in sympatry—and even in syntopy—across almost their whole range. At SG only a single species, *S. lateralis*, was recorded; the apparent absence of *S. fuegiensis* needs to be confirmed. If genuine, this distributional discrepancy could be due to different thermal tolerances between them. At the sampling locations where both species occurred, we noted that *S. fuegiensis* was more prevalent at lower latitudes on the Atlantic coast and in the FI than *S. lateralis*, which was more common at higher latitudes of PP and KI. Thus, the absence of *S. fuegiensis* in SG, the locality of our sampling area with the lowest winter sea-surface temperatures and that was heavily glaciated during the Last Glacial Maximum (LGM) (Hodgson et al., 2014), could be due to a restricted lower thermal tolerance. This hypothesis will be tested by future physiological experiments.

Quaternary glacial processes in the Southern Ocean severely affected the demography of shallow benthic populations as has been demonstrated in several population-based studies (e.g. Allcock & Strugnell, 2012; Fraser et al., 2009; González-Wevar, Saucède, Morley, Chown, & Poulin, 2013; González-Wevar et al., 2012, 2016; Nikula et al., 2010; Thornhill et al., 2008). Repeated ice advances and retreats would have generated massive reductions in population sizes (or even local extinctions) and consequent severe declines in genetic diversity. A key signature of populations formerly confined to ancient glacial refugia should be higher and older levels of genetic diversity compared to populations from recently recolonized areas (Allcock & Strugnell, 2012; González-Wevar et al., 2013; Provan & Bennett, 2008). Moreover, populations confined to geographically separate refugia are expected to show genetic differentiation due to genetic drift (Provan & Bennett, 2008). Accordingly, we hypothesize that both species of *Siphonaria* became extinct at KI and MI during the LGM, before they recolonized by rafting during the glacial-interglacial transition from geographically distant refugia, such as southern South America, where glacial impact is known to have been lower, particularly along the Atlantic coast (Rabassa, Coronato, & Salemme, 2005). Such a process could have occurred several times, during the Plio-Pleistocene, and generated a 'demographic reset' during glacial maxima on the sub-Antarctic islands followed by interglacial recolonization.

Unexpectedly, our results showed that haplotypes of *S. lateralis* from FI are clearly differentiated (≥8 steps away) from those of other localities, including adjacent areas such as Patagonia. Evidence of genetic differentiation between PP and FI populations has been recorded in crustaceans like *Parawaldeckia kidderi* (Nikula et al., 2010), and *Serolis paradoxa* (Leese et al., 2008) and limpets of the genus *Nacella* (González-Wevar et al., 2012, 2016). Due to their geographical position, the FI were less affected by Quaternary glaciations than other areas of the Southern Ocean (Hodgson et al., 2014). Hence, *Siphonaria* populations could have persisted and differentiated there during the LGM. In *S. fuegiensis*, populations from the FI and those of AP share two unique haplotypes, suggesting a closer connectivity between the two areas. There is, therefore, a contrast between the two *Siphonaria* species and their dispersal patterns between these areas. This is an unexpected finding considering the overall morphological and phylogeographical similarities recorded between the two taxa. In *S. lateralis*, the presence of a fixed SG haplotype indicates that this island may be currently isolated from other areas analysed with the Antarctic Polar Front acting as an oceanographic barrier between the Antarctic and the sub-Antarctic (Poulin et al., 2014). Such a barrier could also explain the absence of *S. fuegiensis* in SG. Alternatively, the stochasticity of rafting could also be used to explain the differences in phylogeographical structure recorded among Patagonia, FI and SG. Just by chance, *S. fuegiensis* may have rafted between FI and AP, but *S. lateralis* not. Similarly, by chance, just a single *S. lateralis* haplotype may have reached SG since the last deglaciation but no *S. fuegiensis* individuals successfully colonized this sub-Antarctic island during that period.

5 | CONCLUSIONS

New biogeographical studies in Southern Ocean near-shore marine benthic invertebrates help us understand the evolution of biota at higher latitudes (Allcock & Strugnell, 2012; Allcock et al., 2011; Fraser et al., 2009, 2011; Gonzalez-Wevar et al., 2017; Moon et al., 2017; Poulin et al., 2014; Saucède et al., 2014; Waters, 2008). Direct developing species like the pulmonates *S. lateralis* and *S. fuegiensis* show clear evidence of long-distance dispersal across the sub-Antarctic, whereas broadcast-spawning species like *Nacella* are clearly isolated and separated in the sub-Antarctic islands (Gonzalez-Wevar et al., 2017; González-Wevar et al., 2010). We argue that the geographical distribution of genetic lineages in the Southern Ocean depends on idiosyncratic life-history traits related to the ecology of the species, such as the association with buoyant kelps. In this context, our study suggests that species combining direct development and rafting may be more effective for long-distance dispersal than those species with free-living planktotrophic larval stages. Hence, biogeographical patterns in these organisms also depend on the stochasticity of long-distance dispersal that is mediated by particular vectors. Moreover, in intertidal and shallow water species, the processes of local extinction and recolonization driven by glacial cycles may have prevented speciation across the sub-Antarctic islands.

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BIOSKETCH

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Author contributions: C.A.G-W., E.P., T.S. and H.G.S. conceived the ideas; C.A.G-W., M.H., J.N., J.O., S.R., P.B., S.M., T.S. and E.P. collected *Siphonaria* material in different sub-Antarctic provinces. C.A.G-W., J.N., S.R., J.O. and M.H. performed laboratory work supervised by E.P. C.A.G-W., M.H. and N.I.S. performed phylogenetic reconstructions and analysed the data; C.A.G-W., E.P, T.S., S.R., J.N. and H.G.S. interpreted the data; and C.A.G-W, T.S., E.P. and H.G.S. led the writing of the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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