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Does rafting promote contemporary gene flow? Global and regional patterns of population genetic diversity and structure on the false limpet *Siphonaria lateralis* in the Southern Ocean

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Rafting has been proposed as an effective mechanism for species without free-living pelagic larvae to achieve long-distance dispersal, theoretically preventing population differentiation over wide distributional ranges. Moreover, rafting has been advocated as a main dispersal mechanism for marine invertebrates with sub-Antarctic distributions, because of abundant buoyant kelps, driven by the Antarctic Circumpolar Current. Nonetheless, little attention has been given to the role of rafting to establish regular gene flow across the sub-Antarctic, and the geographic and temporal scales at which it occurs. Aiming to unravel these major questions about the extent of genetic connectivity across the Southern Ocean (SO), we studied the pulmonate limpet *Siphonaria lateralis*, a benthic species with encapsulated larvae, found on the rocky intertidal of sub-Antarctic islands and southern South America. Since *S. lateralis* is closely associated with *D. antarctica*, dispersal by rafting is plausible, as revealed by the absence of phylogeographic structure across the sub-Antarctic. We sampled 116 individuals from eight localities across the SO, and used 5,515 SNPs obtained through Genotyping-by-Sequencing, to determine contemporary genetic diversity, structure, and gene flow at two spatial scales; global, across the SO, and regional, within Kerguelen. Results identified substantial genetic structure, differentiating Patagonia, Falklands/Malvinas Islands, South Georgia and the Kerguelen archipelago, and low levels of contemporary gene flow. The most notable genetic differentiation was found between Patagonia/Falklands and South Georgia/Kerguelen. Structure was also significant between Patagonia and the

Falkland/Malvinas Islands. Conversely, South Georgia and Kerguelen exhibited closer genetic affinity, and indications of recent but limited gene flow. Moreover, historical gene flow estimates between the four populations were low. At regional scale, noteworthy genetic structure persisted, and gene flow was insufficient to prevent genetic differentiation within Kerguelen. Consequently, rafting's potential may be overestimated as a contemporary mechanism promoting gene flow across the SO, as these events may be sporadic, irregular, and unpredictable for marine invertebrates lacking a larval dispersal stage, since contemporary dispersal events don't seem to facilitate high gene flow at both scales. Accordingly, other oceanographic factors or processes may hinder the establishment of species associated with macroalgae, and as consequence, contemporary genetic connectivity in the sub-Antarctic.

KEYWORDS

long distance dispersal, sub-Antarctic, rafting, Antarctic Circumpolar Current, benthic protected development, Genotyping-by-Sequencing, gene flow

1 Introduction

Dispersal is a key trait for species from ecological and evolutionary perspectives, as movement plays a role in population dynamics, the extent of a species' geographic range, the degree of gene flow, and the potential for local adaptation (Slatkin, 1985; Palumbi, 1994; Cowen and Sponaugle, 2009; Manel et al., 2023). In marine ecosystems, fish and invertebrates have complex life cycles where at least one stage may be mobile and promotes a species' dispersal, either by active or passive movement, as dictated by life histories (Gaines et al., 2007). Because some of these earlier stages are often small sized, it's difficult to directly measure dispersal (Weersing and Toonen, 2009). However, genetic data has been used to study the exchange of individuals and their genes between populations, by estimating a direct consequence of effective dispersal: population connectivity (henceforth 'connectivity'), defined as the degree to which gene flow affects a species' evolutionary processes (Lowe and Allendorf, 2010).

For most benthic invertebrate species with complex life cycles, connectivity is usually associated with pelagic larval stages, which, aided by interactions with oceanic currents and processes, can travel and settle up to tens to thousands of kilometers away from their spawning populations (Cowen and Sponaugle, 2009; White et al., 2019). While numerous larval traits influence dispersal and connectivity (Blanco et al., 2019), pelagic larval duration (PLD) is key, as the longer larvae spend in the water column, the higher the chances to traverse longer distances, increasing dispersal potential, gene flow and limiting genetic structure (*i.e.* F_{ST}) (Waples, 1987; Haye et al., 2014; Pinsky et al., 2017; Álvarez-Noriega et al., 2020; Hernawan et al., 2021). On the contrary, restricted or null dispersal, low gene flow and marked genetic structure is to be expected from species with short PLD (*i.e.* lecithotrophic larvae) or without pelagic larval stages (*i.e.* brooders or direct developers). While this paradigm

is widely accepted, there are plenty of exceptions to both these assumptions, as some species with high dispersal potential display unexpectedly high levels of genetic structure (Selkoe et al., 2016; Larsson et al., 2017; Gaeta et al., 2020), and on the other end of the spectrum, species with low or null dispersal potential report low genetic structure spanning great geographic distances (Selkoe et al., 2016; Fleming et al., 2018; Gélin et al., 2018; Bertola et al., 2020). These 'exceptions' further illustrate that dispersal in the marine ecosystem is complex and multidimensional and is subjected to intrinsic and extrinsic mechanisms and processes that influence its extent and consequences. As such, while larvae are undoubtedly important and PLD can guarantee a minimum dispersal distance, these traits may be a poor predictor of gene flow (D'Aloia et al., 2015; Hilário et al., 2015; Esser et al., 2023), because other factors such as ecology, physiology, oceanography or habitat selectivity limit dispersal and/or settlement rates (Waters et al., 2013; Sjöqvist et al., 2015; Pascual et al., 2017; Gaeta et al., 2020). Moreover, regardless of development mode, other life stages can play an important role in a species dispersal, such as adult migrations (Frisk et al., 2014), or other mechanisms or processes of natural or anthropogenic origin that may facilitate dispersal (Carlton et al., 2017).

One of such mechanisms is rafting, defined as marine dispersal mediated by buoyant elements of organic or inorganic origin, often described for organisms that live in close association with macroalgae (Highsmith, 1985; Thiel and Gutow, 2005; Winston, 2012). Numerous studies provide global evidence supporting the hypothesis that direct developers and brooders can disperse through rafting (Haye et al., 2012; Haye et al., 2014; Trickey et al., 2016; Bertola et al., 2020), arguing that this mechanism may be as relevant for dispersal and connectivity as having a pelagic larvae dispersal phase (Carlton et al., 2017; Simkanin et al., 2019; Pfaller et al., 2019). The Southern Ocean (SO) is a vast mass of open ocean encircling Antarctica and tens of relatively small islands, and

influencing a portion of the Australian and South American continents (Koubbi et al., 2014; Chapman et al., 2020). Within this area, the past two decades of phylogenetic and phylogeographic research have pointed out that rafting may be the leading hypothesis to explain the current distribution and high levels of genetic connectivity that some sub-Antarctic benthic species display (Nikula et al., 2010; Cumming et al., 2014; Moon et al., 2017; González-Wevar et al., 2018; Waters et al., 2018b; Fraser et al., 2020a; Güller et al., 2020; Macaya et al., 2020), as buoyant macroalgae may help achieve long-distance dispersal (LDD), a highly relevant evolutionary and ecological process (Jokiel, 1990; Gillespie et al., 2012; Waters et al., 2018a; Macaya et al., 2020). This hypothesis is not only supported by genetic data, as even considering the extension of the SO, as many coastal and benthic taxa are shared within the sub-Antarctic biogeographical region (Griffiths et al., 2009; De Broyer et al., 2014; Koubbi et al., 2014). Since most of these land masses are of heterogeneous origins and ages (continental or volcanic, ranging from ~95Ma to ~500Ka) and are geographically isolated (Quilty, 2007; Hodgson et al., 2014), the most plausible mechanism by which these shared taxa could have colonized their coasts is via transoceanic LDD, largely associated to kelp rafts of *Durvillaea antarctica* and *Macrocystis pyrifera* (Waters et al., 2018a; Fraser et al., 2020a). These macroalgae not only dominate near-shore, hard-substrate ecosystems, but are frequently observed floating in open waters, and around 20 million of viable rafts have been estimated to be adrift in the Southern Ocean (Smith, 2002; Stevens et al., 2002). Moreover, phylogeographic studies illustrate common haplotypes between sub-Antarctic islands and southern South America (Patagonia and Falklands/Malvinas Islands), suggesting that *D. antarctica* (Fraser et al., 2009; Fraser et al., 2010; Bussolini and Waters, 2015) and *M. pyrifera* (Macaya and Zuccarello, 2010; Assis et al., 2023) have great ability to disperse across the Southern Ocean. Coupled with the fact that live, viable benthic invertebrates have been registered on beached rafts (Fraser et al., 2010; Layton et al., 2022), it is to be expected that species associated with rafting macroalgae are able to withstand floating adrift, settle into new populations, and achieve contemporary gene flow unrelated to their developmental mode, hinted by the scarce studies with SNPs (Single Nucleotide Polymorphisms) in the Southern Ocean (Leiva et al., 2019; Zbawicka et al., 2019; Lau et al., 2023).

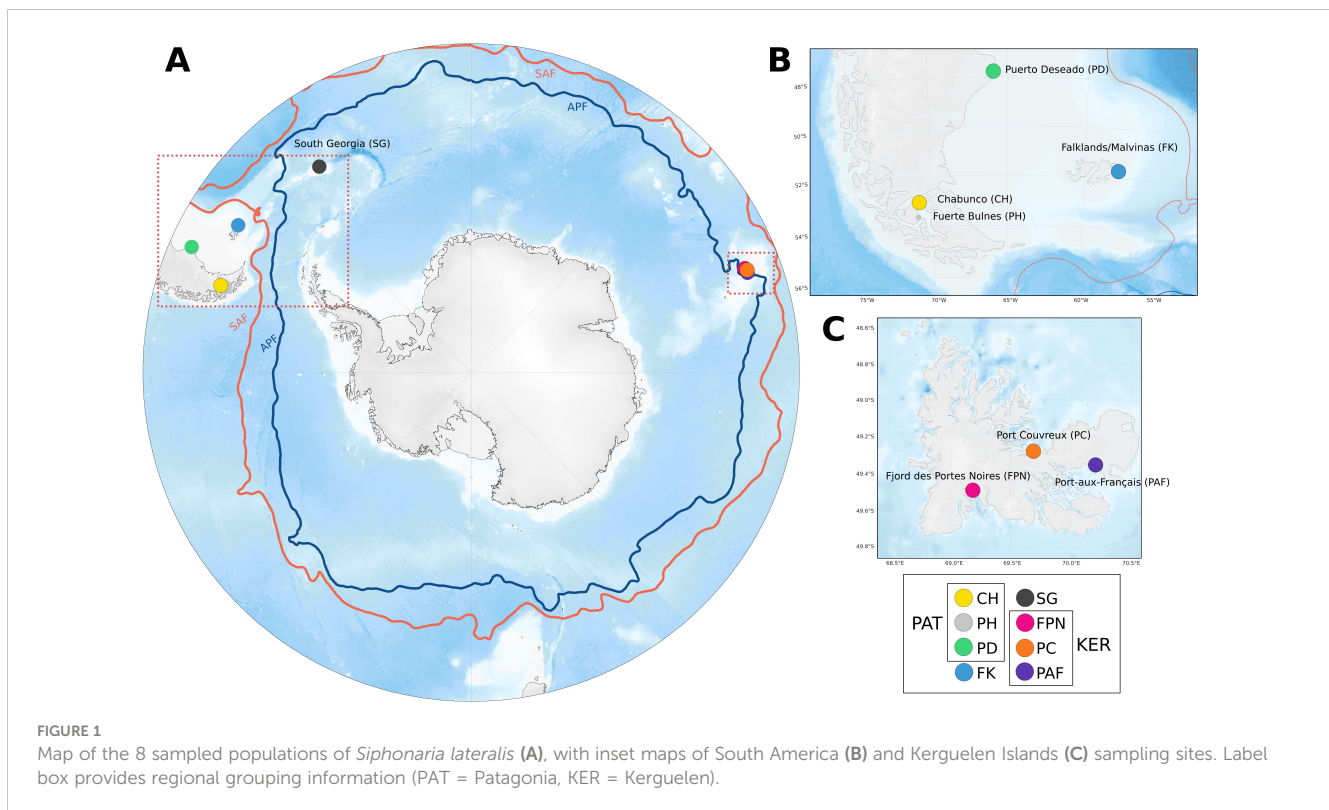
However, knowledge of this mechanism is still lacking, and less attention has been given to the frequency of these events and its consequences on contemporary patterns of connectivity (Gillespie et al., 2012; Waters et al., 2018a). Are rafting events rare enough that there's only sporadic gene flow, to be able to sustain a species' integrity? Or are they frequent enough to establish a regular, contemporary gene flow amongst isolated, distant coasts? To address this issue, we studied the pulmonate false limpet *Siphonaria lateralis* (Gastropoda: Heterobranchia) as a model to re-evaluate connectivity and rafting in the Southern Ocean. Despite its benthic protected development with encapsulated larvae in egg masses (Zabala et al., 2020), this species is widely distributed across the rocky intertidal of Patagonia, Falkland/Malvinas Islands, South Georgia, Kerguelen and Macquarie (Dayrat et al., 2014; Güller et al.,

2015; González-Wevar et al., 2018), a paradoxical distribution for a species with low dispersal potential. Nevertheless, as discussed above, such extended distribution is not considered rare for species that live in close association with *D. antarctica*, and rafting has been proposed as the main mechanism explaining such a broad distribution of *S. lateralis* (Morton and Miller, 1973; Simpson, 1976; González-Wevar et al., 2018). Moreover, phylogeographic studies with mtDNA and nucDNA markers evidenced shallow genetic differentiation across the sub-Antarctic region (>8,000 Km) suggesting that dispersal through rafting may preserve the genetic integrity of the species over large geographic distances (González-Wevar et al., 2018). However, recent studies aiming to explore connectivity with multilocus genetic markers such as SNPs (Single Nucleotide Polymorphisms) have demonstrated that, even in light of absent or low phylogeographic structure, marine species exhibit significant genetic subdivision and restricted gene flow across populations (Pazmiño et al., 2017; Teske et al., 2018; Green et al., 2022). Moreover, while *D. antarctica* across the Southern Ocean consists of a single broader, sub-Antarctic clade, this macroalgae is sub-structured and there is substantial differentiation between islands according to SNP data (Fraser et al., 2018), that nevertheless seem to be sporadically connected, as supported by distributional modeling and beached kelp rafts, which provide evidence of LDD events across the Southern Ocean (Fraser et al., 2018; Fraser et al., 2022). Considering this information, we expect that associated species such as *S. lateralis* will display moderate levels of genetic structure and low levels of recent gene flow, enough to maintain contemporary connectivity. Furthermore, our objective is twofold. Firstly, to evaluate whether the long-debated mechanism of rafting maintains substantial contemporary levels of connectivity throughout the distribution range of *S. lateralis*. Secondly, to ascertain whether this mechanism is effective at a regional scale, facilitating connectivity among disjoint yet geographically proximate coastal populations, particularly within the Kerguelen Islands. Clarifying these two aspects will help towards drawing robust conclusions about the extent and implications of rafting on the Southern Ocean, and its effects on evolutionary history, biogeographic patterns, and eventual conservation strategies.

2 Materials and methods

2.1 Sampling, sequencing and SNP filtering

Between the years 2013 and 2017, 190 adult *Siphonaria lateralis* individuals were sampled from eight locations, spanning most of the species' range (Figure 1). Specimens were stored in 96% ethanol for posterior genomic DNA extraction with Qiagen's DNeasy Blood & Tissue™ Kit, following the manufacturer's instructions, and DNA concentration was assessed with Qubit™ 3.0 fluorometer (Lifetechnologies). Samples were sent to the Biotechnology Center of the University of Wisconsin, USA. Sequencing and construction of genomic libraries was done by Genotyping by Sequencing (GBS) using



Illumina NovaSeq 6000 platform, following a Reduced Representation Sequencing (RRS) approach, which is a reliable and affordable method to study population structure of non-model species without a reference genome, and produce a large number of Single Nucleotide Polymorphisms (SNPs) (Rovelli et al., 2019; Kunvar et al., 2021). Under this approach, library preparation used two restriction enzymes to reduce the complexity of the genome (NsiI-MspI), and barcode adaptors for each individual. Single end reads were visualized in FastQC for quality checks. To generate our SNP dataset, our data was prepared and analyzed following the UNEAK pipeline (Universal Network-Enabled Analysis Kit) implemented in TASSEL v.5, which is useful for *de novo* locus identification for non-model organisms (Lu et al., 2013). With the UNEAK pipeline, the dataset was demultiplexed, barcodes were removed and reads were trimmed from ~100 bp to 64 bp. Identical tags were aligned with an error tolerance rate of 0.03, to minimize considering real tags as sequencing errors, and we kept only biallelic loci. Following this, we assembled two SNPs datasets according to our research objectives, one global, encompassing *S. lateralis* individuals sampled across different Southern Ocean sub-Antarctic provinces, and a regional dataset, considering three populations from Kerguelen Islands. We used a 80% mnC (minimum call rate), 5% MAF (minimum allele frequency) to filter the SNPs from each dataset (global and regional), and we allowed a maximum of 40% missing data per individual in TASSEL v.5. Then, we excluded those SNPs that failed the Hardy-Weinberg equilibrium (HWE) test implemented in Arlequin v3.5 (Excoffier and Lischer, 2010) at

$p < 0.05$, and we used a False Discovery Rate (FDR) correction to avoid false positives (incorrectly considering as a SNP as out of HWE), in at least 60% of each of the dataset populations. Since the interest of the study was to focus on neutral evolutionary processes, we identified potential outlier SNPs with BAYESCAN 2.1 (Foll and Gaggiotti, 2008). For this, 500,000 MCMC iterations were run with a 10% burnin', a thinning interval of 10, and a prior odd of 1,000 (100 for the regional dataset), to minimize potential false positives, according to the large number of SNPs to test. Subsequently, we removed all SNPs after FDR q-value correction that had strong or very strong evidence to be under selection according to Jeffrey's criterion, to obtain a global and a regional neutral SNPs dataset for downstream analyses.

2.2 Genetic diversity

Analyses were performed for the global and regional datasets to evaluate the differences in genetic diversity at both spatial scales. For each population, expected heterozygosity (H_e), observed heterozygosity (H_o), average number of alleles per locus (allelic richness, A), the proportion of polymorphic loci (%Po), and the inbreeding coefficient (F_{IS}) were computed in GENETIX (Belkhir et al., 2004). Additionally, genetic diversity parameters were estimated for the four major geographic areas within the global dataset, and private alleles for each area, and within Kerguelen populations, were quantified in HP-RARE 1.0 (Kalinowski, 2005). Within Kerguelen populations, we estimated the effective

population size (N_e) based on the linkage disequilibrium (LD) method using NeEstimator v2.1 (Do et al., 2014), and jackknife 95% confidence intervals (CIs) (Waples and Do, 2008).

2.3 Population structure

We used multiple approaches to assess population genetic structure at global and regional scale. First, pairwise population F_{ST} and their significance was estimated using a test of 10,000 permutations in Genodive v 3.0 (Meirmans, 2020). Corresponding F_{ST} p-values of multiple testing were adjusted through FDR (Narum, 2006). Secondly, we performed three individual-based population assignment tests to estimate genetic structure; 1) IBS analysis, which clusters together unrelated individuals based on similarities between genotypes at each locus, implemented in the R package *SNPRelate* (Zheng et al., 2012), 2) Principal Component Analysis (PCA), to determine the percentage of variation in allele frequencies explained by the major axes, implemented in *adeigenet* (Jombart, 2008), and 3), STRUCTURE (Pritchard et al., 2000), a bayesian clustering method that assigns individuals to populations based on allele frequencies. Our aim with STRUCTURE was to discover the main genetic groups across the species' distribution across the Southern Ocean, and secondly, to determine substructure within each main group. Due to the large number of SNPs in our datasets, we used StrAuto, a Python script that reduces analysis time by allowing for parallel computing of STRUCTURE runs (Chhatre and Emerson, 2017). Number of estimated ancestral populations (K) varied from one to six. Ten replicate runs were performed for each estimated K under the admixture model, with 600,000 MCMC, a 10% burnin'. The most probable K value was inferred based on the ΔK method (Evanno et al., 2005), utilizing Structure Harvester online (Earl and vonHoldt, 2012). Post processing of STRUCTURE results and cluster graphs were drawn in CLUMPAK (Kopelman et al., 2015). Finally, we implemented an Analysis of Molecular Variance (AMOVA) in Arlequin (Excoffier and Lischer, 2010) to evaluate three grouping scenarios/hypothesis of *a priori* partitioning, to determine which grouping hypothesis maximized the difference between groups.

2.4 Gene flow

Two methods were used to estimate migration rates between the four major geographical areas, and at regional scale; 1) a multilocus approach based on the number of rare alleles, assuming that populations are under migration–drift equilibrium, to estimate the historical effective number of migrants (N_m) (Barton and Slatkin, 1986) in GENEPOP v.4.5 (Rousset, 2008), and 2) BayesAss V3, a bayesian approach that uses individual information to estimate recent migration events, asymmetric patterns of gene flow and directionality. At the same time, this analysis allows to identify first, second or third generation migrants between populations (Wilson and Rannala, 2003). A total of 100,000,000 MCMC iterations were run with a 25% burnin',

sampling every 1,000 chains, to ensure chain independency, and convergence was confirmed in Tracer (Rambaut et al., 2018).

3 Results

3.1 Global and regional datasets

Raw data for each plate consisted of 260,135,231 and 263,506,046 reads, with 249,396,409 and 253,244,524 high-quality reads respectively. Using the UNEAK pipeline, 69,412 candidate SNP sites were detected across 140 individuals of *Siphonaria lateralis* from eight sampled populations. Out of the 140 individuals, only 116 had sufficient information to be included in the dataset after the bioinformatic filters, resulting in 6,277 SNPs. A total of 351 loci were removed due to being out of HWE in 60% or more of the populations after FDR correction, and another 411 loci were removed after Bayescan analysis identified these loci as outliers, with strong evidence of being under diversifying selection. The final global dataset was made up of 5,515 SNPs putatively neutral loci, for downstream diversity, structure, and gene flow analyses.

For the regional dataset, after implementing bioinformatic filters on 69,412 candidate SNPs from 53 individuals collected at Kerguelen Islands, 52 individuals showed sufficient data across a total of 1,646 SNPs. However, after HWE and FDR filters, we kept 1,298 SNPs, where a further 34 loci were removed for showing significant signals of being under selection. Accordingly, our putatively neutral working dataset consisted of 1,264 SNPs for diversity, structure and gene flow analyses on a smaller regional scale.

3.2 Population genetics across the Southern Ocean

3.2.1 Genetic diversity

All genetic diversity statistics were similar and low in each of the eight sampled populations of *S. lateralis*, except from Falklands/Malvinas Islands (for values and population codes hereinafter used, Table 1). Proportion of polymorphic loci ranged from 2.99% to 69.23%, where Falklands/Malvinas had the highest polymorphic loci, and contrarily, populations from South America (PH and PD) exhibited the lowest levels of genetic diversity. Observed heterozygosity (H_o) ranged from 0.0153 (FPN) to 0.2148 (FK), yet most values ranged from 0.0153 to 0.0288 (PAF), except from the FK population, which showed the highest H_o by more than an order of magnitude compared to all other populations. Expected heterozygosity (H_e) ranged from 0.0131 (PH) to 0.2406 (FK), and was slightly lower than H_o in half the populations (Table 1, values indicated in bold letters), and slightly higher than H_o in the other half. Allelic richness (A) ranged from 1.0299 (PH) to 1.6923 (FK), and was similar between all populations except for FK. Finally, F_{IS} ranged from -0.25854 (PH) to 0.39936 (SG), with negative values found only in continental sites (CH, PH, PD) and PAF.

TABLE 1 Genetic diversity of *Siphonaria lateralis* across the Southern Ocean.

Population	Coordinates	Code	N	%Po	H _o	H _e	A	F _{IS}
Chabunco	53°01'12.7S, 70°49'26.2W	CH	9	10.01	0.0217	0.0177	1.1001	-0.23809
Fuerte Bulnes	53°36'51.1S, 70°55'37.2W	PH	3	2.99*	0.0157	0.0131	1.0299	-0.25854
Puerto Deseado	47°45'06.9S, 65°51'53.1W	PD	4	5.33*	0.0215	0.0182	1.0533	-0.21810
Falklands/Malvinas	51°42'00.8S, 57°46'55.7W	FK	22	69.23	0.2148	0.2406	1.6923	0.10981
South Georgia	54°17'01.4S, 36°29'18.5W	SG	25	20.96	0.0197	0.0325	1.2096	0.39936
Fjord des Portes Noires	49°29'32.4S, 69°11'12.4E	FPN	16	10.61	0.0153	0.0162	1.1061	0.05779
Port Couvreur	49°16'49.6S, 69°41'31.1E	PC	17	11.66	0.0166	0.0180	1.1166	0.07914
Port-aux-Français	49°21'12.2"S, 70°13'0.1"E	PAF	20	21.12	0.0288	0.0262	1.2112	-0.10142

Table shows sampling populations, coordinates, codes (population abbreviation), sampling size (N), proportion of polymorphic loci (%Po), observed heterozygosity (H_o), expected heterozygosity (H_e), allelic richness (A), and inbreeding coefficient (F_{IS}).

Grouping all populations by geographical area (Patagonia = PAT, Falklands/Malvinas = FK, South Georgia = SG, and Kerguelen = KER, [Supplementary Table 1](#)) illustrates similar diversity patterns, as FK remains the most diverse across all statistics. Polymorphism ranged from 14.84% (PAT) to 69.23% (FK), where at least 818 of the 5,515 loci were polymorphic. The H_e index ranged between 0.0193 (PAT) to 0.2350 (FK), and H_o ranged from 0.0197 (SG) to 0.2148 (FK), where H_e was lower than H_o only in PAT. F_{IS} ranged from -0.02749 (PAT) to 0.39936 (SG), with PAT being the only negative value and SG more than doubled the value of other areas. The number of alleles per area ranged from 6334 (PAT) to 9333 (FK), with 1% (SG) to 36% (FK) of them being private. The number of private alleles from FK were three times higher than those recorded in other areas.

3.2.2 Population structure

All pairwise F_{ST} comparisons were significant amongst the eight sampled populations, with high and extremely high values across the studied distribution of *Siphonaria lateralis* ([Table 2](#)). The lowest F_{ST} value between sampled populations was found between CH-PH (F_{ST} = 0.236), the closest populations. In a general pattern, populations within the same geographical areas (within Patagonia and within Kerguelen islands) exhibited the lowest levels of

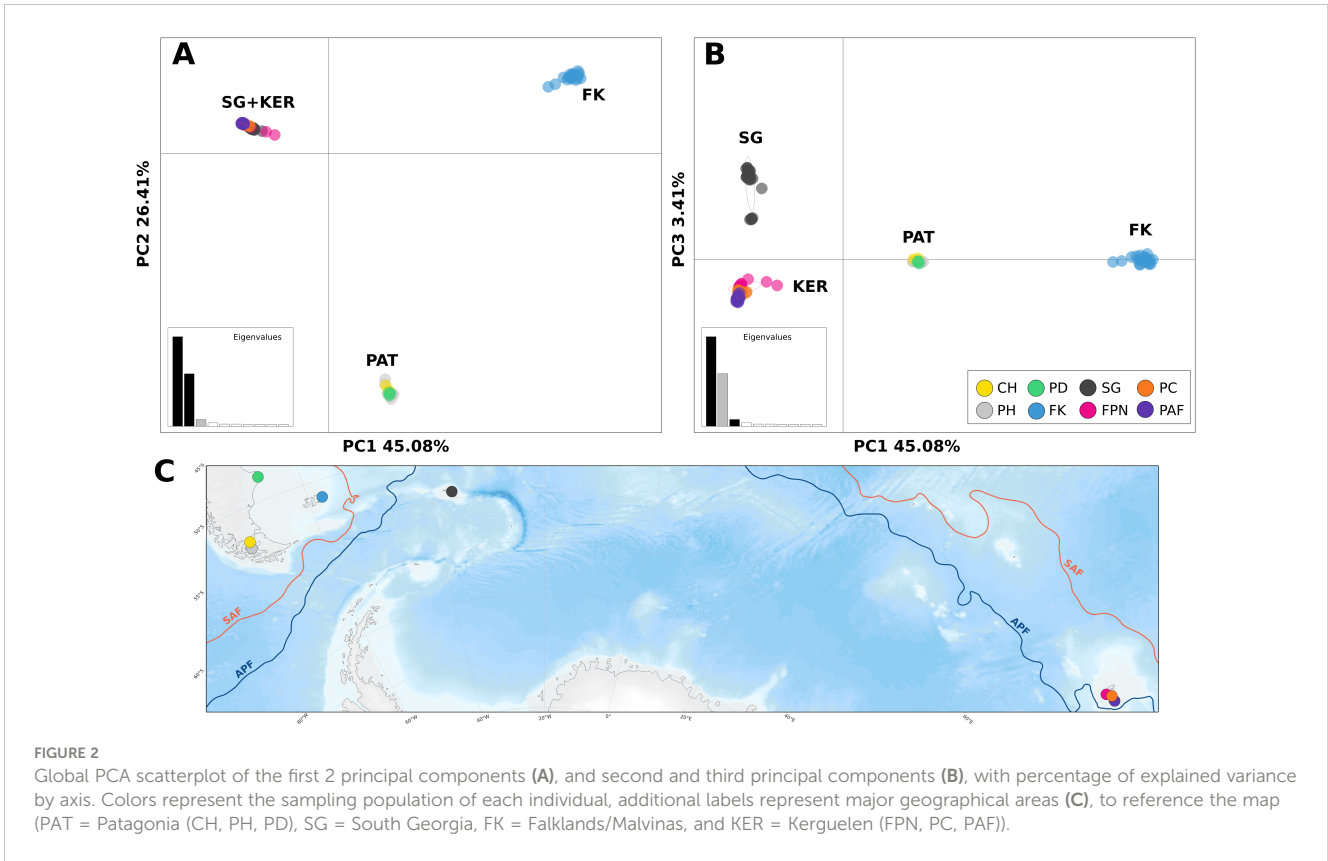
differentiation amongst themselves (F_{ST} < 0.3). The highest F_{ST} value was found between FPN-PC (F_{ST} = 0.962), some of the most distant populations (8,000 Km). In fact, the highest comparisons (F_{ST} > 0.9) were found comparing Kerguelen populations (FPN, PC, PAF) with Patagonia populations (CH, PH, PD), and South Georgia with Patagonia populations. Genetic differentiation was slightly lower between South Georgia and Falkland/Malvinas (F_{ST} = 0.752), which are separated by approximately 1,500-2,200 Km of open ocean. South Georgia and Kerguelen populations displayed lower levels of genetic differentiation (F_{ST} = 0.579 - 0.604), despite being geographically more distant (>6,500 Km). Falklands/Malvinas Islands, on the other hand, was moderately-highly differentiated with all sampled populations (F_{ST} = 0.655 - 0.752).

Individual-based analyses of global genetic structure suggest the existence of at least three, if not four genetic groups. Based on the number of shared alleles between individuals, the IBS analysis ([Supplementary Figure 1](#)) recognized four groups, two clearly defined and separate, and two relatively closer, similar to the PCA ([Figure 2](#)). The first two Principal Components explain most of the genetic variance (>70%): the first axis clearly differentiates FK from all other populations, and the second axis segregates CH, PH, PD (PAT) from a FPN, PC, PAF and SG (KER + SG) ([Figure 2A](#)). When considering a third axis, while it explains little of the genetic variance (3.41%), the PCA was able to distinguish South Georgia as a slightly differentiated group compared to Kerguelen Islands ([Figure 2B](#)). STRUCTURE's bayesian clustering and Evanno's ΔK indicate that two genetic clusters make up the first hierarchical level of genetic structure ([Figure 3B](#), [Supplementary Figure 2](#)), highlighting the stark divergence between southern South America (CH, PH, PD and FK) and sub-Antarctic Islands (SG, FPN, PC and PAF). While further exploration into K = 3 distinguishes Falklands/Malvinas from the rest of South America ([Figure 3C](#)), matching results from the first two principal components of the PCA and the IBS, the second hierarchical level of genetic structure is accounted for when observing K = 4, which reveals significant substructure within the 2 main genetic clusters, southern South America and sub-Antarctic islands, providing a visual representation of what pairwise F_{ST} and PC3 suggest ([Table 2](#), [Figure 2B](#)): South Georgia is a genetically distinct group, that, however, has a significant presence of a genetic component from

TABLE 2 Pairwise F_{ST} values (below diagonal) for all Southern Ocean populations, and their statistical significance (above diagonal).

	CH	PH	PD	FK	SG	FPN	PC	PAF
CH	-	0.04	0.001	<0.001	<0.001	<0.001	<0.001	<0.001
PH	0.236	-	0.03*	<0.001	<0.001	0.001	0.001	0.001
PD	0.265	0.112	-	<0.001	<0.001	<0.001	<0.001	<0.001
FK	0.706	0.655	0.666	-	<0.001	<0.001	<0.001	<0.001
SG	0.933	0.927	0.928	0.752	-	<0.001	<0.001	<0.001
FPN	0.961	0.962	0.961	0.731	0.588	-	<0.001	<0.001
PC	0.958	0.959	0.958	0.739	0.604	0.286	-	<0.001
PAF	0.946	0.943	0.943	0.748	0.579	0.243	0.293	-

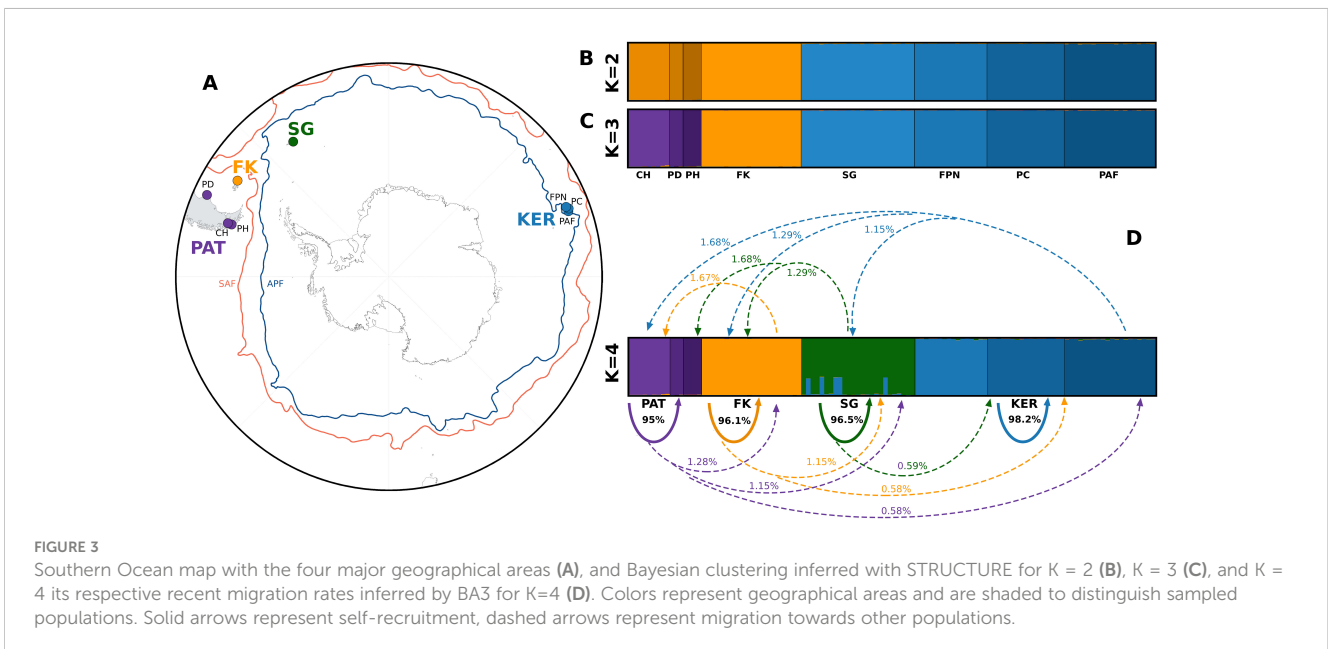
Cell shading delimit sampled geographical areas.



Kerguelen, which may correspond to third-generation migrants (Figure 3D).

Additionally, to further clarify the global genetic structure, we performed an AMOVA analysis considering the three alternative grouping hypotheses provided by the genetic structuring analyses as follows: H1 = two groups South America - Sub-Antarctic Islands (SA-IS), H2 = three groups Patagonia - Falklands/Malvinas - sub-Antarctic Islands (PAT-FK-IS), and H3 = four groups Patagonia -

Falklands/Malvinas - South Georgia - Kerguelen (PAT-FK-SG-KER) (Supplementary Table 3). H1 was discarded, given that variation among groups ($V_a = 57.56$, $F_{CT} = 0.5755$) was comparatively lower than for the other two hypotheses. While F_{CT} was slightly higher for H2 than H3 (0.81269 versus 0.80529), we took into consideration the significant substructure within sub-Antarctic islands, illustrated by the percentage of variance among populations within groups in H2 ($V_b = 4.69$) and pairwise F_{ST} with



$K = 4$ (KER-PAT $F_{ST} = 0.572$, p -value <0.001 , [Supplementary Table 2](#)). Therefore, we computed how much variation was truly just because of grouping choice, controlling for variation amongst populations within groups (V_a/V_a+V_b), which supported the four groups hypothesis over other grouping hypotheses ($H_3 = 98.33\%$ versus $H_2 = 94.84\%$), considering South Georgia as a fourth group on its own.

3.2.3 Gene flow estimates

Two approaches were used to estimate gene flow between the four genetic groups, across $>8,500$ Km in the Southern Ocean ([Figure 3A](#)). Historical gene flow inferred by GENEPOP was low ($N_m < 1$), and ranged from 0.0135 (between Patagonia and Kerguelen) to 0.305 (between South Georgia and Kerguelen) ([Table 3](#)). However, migration between South Georgia and Kerguelen Islands, albeit still low, was an order of magnitude higher than between the other genetic groups. On the other hand, recent migration rates between groups, as indicated by the BA3 results ([Figure 3D](#)), illustrate two scenarios; pairwise population migration rates range from 0.58% to 1.68%, whereas the highest rates consist on self-recruitment, ranging from 95% to 98.2%, meaning that $>95\%$ of individuals were genetically assigned to their population of origin. However, pairwise population migration rates were not symmetrical; inferred gene flow from Patagonia, Falklands/Malvinas and South Georgia towards Kerguelen is an order of magnitude lower than inferred gene flow from Kerguelen to the other three areas (*i.e.* KER towards PAT = 1.68%, PAT towards KER = 0.58%). Finally, BA3 did not identify migrants of first, second, or third generations, with all individuals being assigned as $\sim 100\%$ belonging to their population of origin, unlike the five individuals visually identified as possible third-generation migrants in STRUCTURE ([Figure 3D](#)).

3.3 Regional population genetics

3.3.1 Kerguelen genetic diversity

For the regional scale, which encompasses the Kerguelen Archipelago, genetic diversity was similar across populations, yet slightly higher in PAF across all statistics ([Table 4](#)). Proportion of polymorphic loci ranged from 75.16% to 91.07%, expected heterozygosity (H_e) ranged from 0.271 to 0.345, and observed heterozygosity (H_o) ranged from 0.280 to 0.449, where H_e was lower than H_o for FPN and PAF. Allelic richness (A) within populations ranged from 1.75518 to 1.9107. F_{IS} ranged from -0.278 to 0.055, negative only within PAF, suggesting a slight excess of heterozygotes and departure from HWE. Effective

population size (N_e) was higher in PAF (224.4), and lowest in FPN (91.8). As for private alleles, FPN had the lowest value with 13 alleles, followed by PC with 64, and the highest value was observed in PAF with 155 alleles, representing between 1% and $\sim 12\%$ of the 1,264 loci in the regional dataset.

3.3.2 Kerguelen structure and gene flow

The pairwise F_{ST} analyzes all resulted in significance ($p < 0.05$), with values ranging from 0.124 to 0.154 ([Supplementary Table 4](#)). The presence of three genetic groups corresponding to the sampled locations observed is suggested by IBS ([Supplementary Figure 3](#)), and the PCA, where the first two principal components (PC1 and PC2) explain $>40\%$ of the genetic variance results ([Figure 4A](#)). Likewise, STRUCTURE analyses determined an optimal $K = 3$, with three genetic groups clearly defined, each corresponding to the different sampled locations across Kerguelen, with only a slight signal of mixed genetic component of other groups, and without visual evidence of first, second or third generation migrants ([Figure 4C](#)).

Both historical and contemporary gene flow between these three groups is very low. According to GENEPOP, historical N_m between groups ranges from 0.06 to 0.077, the lowest genetic exchange being between PC and PAF ([Supplementary Table 5](#)). At contemporary scale, migration rates between the described populations ranged from 1.44% to 1.86%, were migration from FPN towards PAF (1.44%) was slightly lower than from PC to PAF (1.46%), providing evidence of low regional migration rates among the analyzed populations, which are mostly sustained by self-recruitment ($>96\%$) ([Figure 4B](#)). Furthermore, BA3 did not provide any evidence for first, second, or third generation migrants.

4 Discussion

Through the analysis of genomic data (SNPs), we found that distant populations of *Siphonaria lateralis* distributed across the Southern Ocean are not sufficiently connected to prevent significant genetic differentiation. Buoyant kelp such as *Durvillaea antarctica* have probably played a crucial role in favoring transoceanic, long distance dispersal by rafting, and genetic homogeneity, of various coastal marine invertebrates, which largely match this macroalgae distribution ([Fraser et al., 2010](#); [Nikula et al., 2010](#); [González-Wevar et al., 2018](#); [Halanych and Mahon, 2018](#); [Fraser et al., 2020a](#)). This has allowed the colonization and re-colonization of sub-Antarctic coasts by different species ([Leese et al., 2010](#); [Nikula et al., 2010](#); [Cumming et al., 2014](#); [González-Wevar et al., 2018](#)). Nonetheless, this dispersal mechanism would not necessarily prevent population differentiation. In light of our estimations of genetic structure and gene flow among populations at different geographical scales across the SO, based on more than 5,000 SNPs, we found that contemporary rafting does not promote sufficient ongoing gene flow in the pulmonate limpet *S. lateralis*, a species with benthic protected development, to homogenize distant populations. Furthermore, our results serve as evidence that connectivity is a process more complex than just accounting for dispersal potential, as [Moon et al. \(2017\)](#) argue, in which local dynamics, past and contemporary climate and physical barriers to dispersal, among other factors, may determine the extent of connectivity.

TABLE 3 Global pairwise estimates of the effective number of migrants (N_m) as determined with GENEPOP.

	PAT	FK	SG
PAT	-		
FK	0.0297	-	
SG	0.0209	0.0258	-
KER	0.0135	0.0162	0.305

TABLE 4 Genetic diversity within Kerguelen Islands.

	N	%Po	H _o	H _e	A	F _{IS}	N _e (95% CI)	Private alleles	% of private alleles
FPN	15	75.16	0.296	0.271	1.7518	0.055	91.8 (12.9 - ∞)	13	1.03
PC	17	79.50	0.280	0.285	1.7950	0.055	130.2 (36.5 - ∞)	64	5.06
PAF	20	91.07	0.449	0.345	1.9107	-0.278	223.4 (65.0 - ∞)	155	12.26

Table shows population codes, sampling size (N), proportion of polymorphic loci (%Po), observed heterozygosity (H_o), expected heterozygosity (H_e), allelic richness (A), inbreeding coefficient (F_{IS}), effective population size (N_e) with 95% confidence intervals (CI), number of private alleles and percentage of private alleles.

The eight sampled populations represent four major geographical areas; Patagonia, Falkland/Malvinas Islands, South Georgia, and Kerguelen. Genetic diversity was remarkably low across populations and geographical areas, in comparison to other genomic (SNPs) studies on gastropods across the world (*i.e.* H_o = 0.35-0.06) (Cortez et al., 2021; Maes et al., 2022; Morrissey et al., 2022; Quintero-Galvis et al., 2023). Moreover, values were low, regardless of whether populations were under-sampled or well-sampled. Falkland/Malvinas Islands was the only exception to this pattern, displaying genetic diversity values more than an order of magnitude higher than the rest of the populations, but falling in line with diversity from other gastropods. At global scale, patterns of low genetic diversity most likely reflect a founder takes all effect (Waters et al., 2013), where LDD rafting allow few founder alleles to colonize new populations, and genetic diversity remains low after demographic growth due to density dependent processes, with new alleles having little success in arriving and establishing in high-density populations. During Quaternary glaciations, the majority of the Pacific coast of southern South America was covered by the Patagonian Ice Sheet (Rabassa et al., 2005, Rabassa et al., 2011), extinguishing most of the benthic taxa (Clarke and

Crame, 2010; Post et al., 2014), yet some taxa survived in pockets of glacial refugia (Montecinos et al., 2012; Trovant et al., 2015). On the contrary, the Atlantic coastline receded and exposed the continental shelf (Glasser and Jansson, 2008), causing local extinctions and/or range contractions, with refugium at lower latitudes for cold-temperate taxa. Moreover, SO islands had different glaciation scenarios; Falklands/Malvinas Islands had little to no ice during the Last Glacial Maximum (LGM), while South Georgia and Kerguelen Islands had terrestrial and marine glaciers (Fraser et al., 2009; Hodgson et al., 2014). While these scenarios offer different paths for recolonization events, phylogeographic patterns of *S. lateralis* support the hypothesis of two independent glacial refugia for the species (González-Wevar et al., 2018). One in Falklands/Malvinas, refugium illustrated by other benthic taxa (Leese et al., 2010; González-Wevar et al., 2012), which has thrived in isolation to this day, as illustrated by the rich genetic diversity found in our results (heterozygosity, polymorphism and number of private alleles). And a second refugium, in southern South America, with a reduced genetic diversity that recolonized both Patagonian coasts and distant populations across the SO such as South Georgia and Kerguelen Islands, which are less diverse in

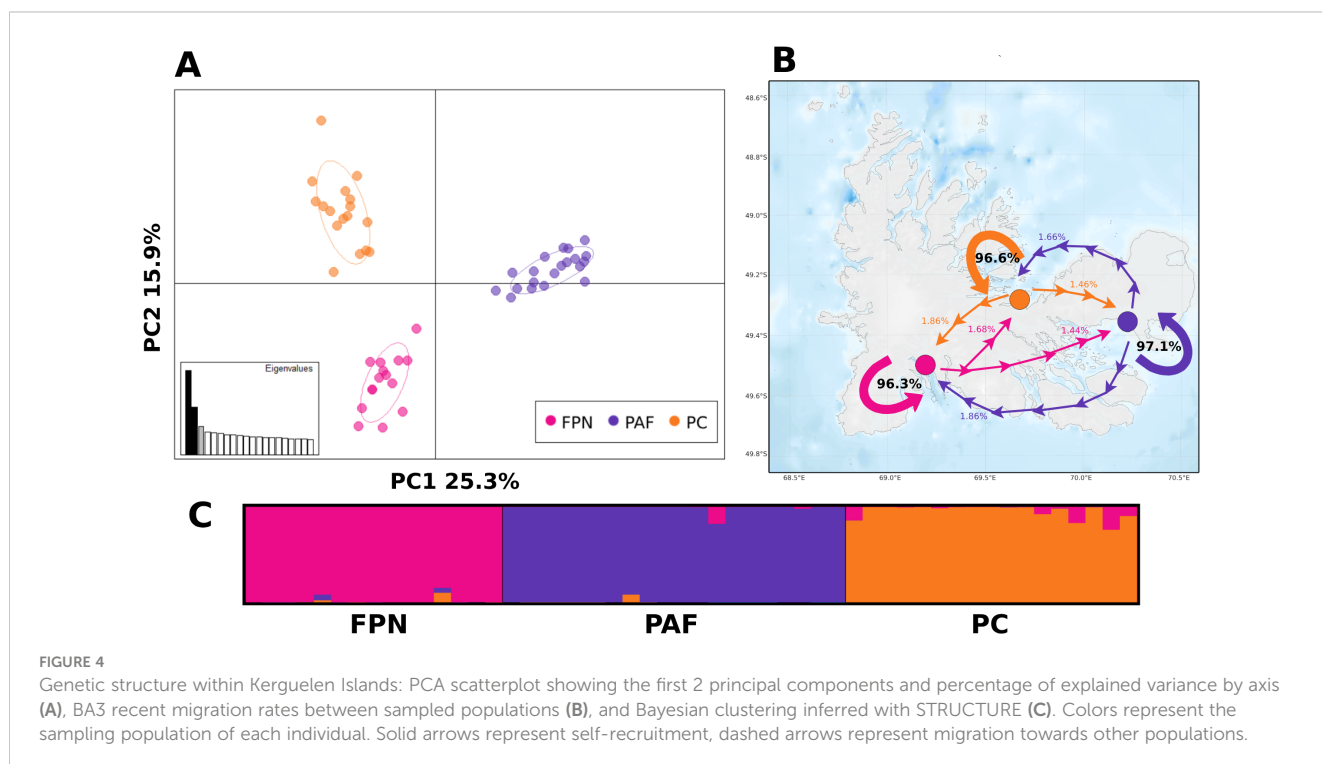


FIGURE 4 Genetic structure within Kerguelen Islands: PCA scatterplot showing the first 2 principal components and percentage of explained variance by axis (A), BA3 recent migration rates between sampled populations (B), and Bayesian clustering inferred with STRUCTURE (C). Colors represent the sampling population of each individual. Solid arrows represent self-recruitment, dashed arrows represent migration towards other populations.

comparison to Falklands/Malvinas Islands, that have evolved separately with little to no allele surfing from other populations.

According to what we expected, we found significant genetic structure in *S. lateralis* across the SO. Results indicated that a substantial differentiation coincided with areas North and South of the Antarctic Convergence, an oceanographic feature that according to recent genomic studies, both represents a genetic barrier for gene flow on some species (Moore et al., 2018) or has no influence whatsoever (Galaska et al., 2017). However, we found strong evidence of four genetic clusters, matching the four major geographical areas sampled; Patagonia, Falklands/Malvinas Islands, South Georgia, and Kerguelen. The highest differentiation occurred between the two most distant populations, Patagonia and Kerguelen, however, Patagonia and South Georgia were also markedly differentiated, which is interesting to note, because it may hint at a deeper or older differentiation between these sub-Antarctic islands and the continent. On the other hand, the marked differentiation of Falklands/Malvinas Islands from the rest of the SO is most likely due to a historical differentiation (Quaternary glaciations) from the rest of southern South America, also evidenced in other studies that evaluate the phylogeographic structure of marine invertebrates without free-living larvae, which display significant phylogeographic structure between Falklands/Malvinas Islands and Patagonia (Leese et al., 2008; González-Wevar et al., 2018; González-Wevar et al., 2021). However, there are some exceptions, as some benthic brooders lack genetic structure between both populations (Cumming et al., 2014; Segovia et al., 2022), and few benthic broadcasters display significant differentiation (González-Wevar et al., 2021). Therefore, in addition to historical patterns, other factors must be sustaining and/or promoting this differentiation, as either environmental discontinuities arising from oceanographic characteristics, or species traits that could limit dispersal and act as gene flow barriers (Gillespie and Roderick, 2014; Moon et al., 2017), as seen in studies compending the notothenioid fish *Harpacifer*, which has reduced phylogeographic structure between Falklands/Malvinas Islands and Patagonia, yet its population discrimination analyses using SNPs clearly differentiate both populations (Segovia et al., 2022).

On the other hand, similar to what was found with traditional markers, multilocus markers exhibit significant, but lesser genetic structuring between South Georgia and Kerguelen. Our data provide scarce evidence of historical long-distance dispersal (LDD) on *S. lateralis* across sub-Antarctic islands approximately 7,000 Km apart, potentially via rafting, as previously hypothesized by González-Wevar et al. (2018). Despite noteworthy estimated historical migration rates between South Georgia and Kerguelen, in comparison to other pairwise estimates, these values are low ($Nm < 1$) and insufficient to prevent polymorphism loss and population differentiation (Wright, 1931; Vucetich and Waite, 2000). Moreover, self-recruitment dominates *S. lateralis* population dynamics, where 95% of individuals remain in their population of origin, and <2% migrate to other populations, insufficient gene flow to prevent genetic structuring across the SO. Interestingly, estimated contemporary migration rates, albeit marginal, evidence double the gene flow from Kerguelen to South Georgia, spanning ~16,000 Km, than from South Georgia towards Kerguelen, the shortest route, by

~10,000 Km less. This is plausible because the Antarctic Circumpolar Current flows eastward, connecting all SO land masses and remote islands by oceanic circulation and drifting macroalgae (Leese et al., 2010; Hunt et al., 2016), and simulated trajectories by Fraser et al. (2018) illustrate multiple pathways within ecologically viable timeframes for *D. antarctica* and the lifespan of associated hitchhiking invertebrates to reach Antarctica and sub-Antarctic islands (Fraser et al., 2010; López et al., 2017). However, as Moon et al. (2017) argue, and even in light of documented rafting events, these events may be insufficient to sustain levels of contemporary gene flow capable of preventing population structuring, as illustrated by *D. antarctica*, which displays significant genetic structure across the SO (Fraser et al., 2018; Fraser et al., 2022). Moreover, the current location and movement of the Antarctic Polar Front (APF) may limit dispersal between South Georgia and Kerguelen through different abiotic factors, such as temperature, which may affect survivorship or development and is a significant driver of genetic structure (Boulanger et al., 2022; Mendes et al., 2022), as rafting also depends on species traits and physiological tolerances (Simkanin et al., 2019). Therefore, while LDD through rafting remains a relevant dispersal mechanism at evolutionary timescales, our SNP data offer little support to the hypothesis that it promotes high levels of gene flow to sustain significant levels of contemporary connectivity, and population genetic structure may arise, as illustrated by our results.

Finally, at a regional scale within Kerguelen, genetic diversity was higher in PAF. Genetic structuring analyses within Kerguelen Islands reveal three similarly differentiated groups. Additionally, contemporary gene flow analyses failed to detect recent dispersal events by first, second or third generation migrants between the studied locations, with historical genetic flow being marginal at best. Few studies have evaluated contemporary genetic structure and gene flow within Kerguelen Islands, and yet both brooders and broadcasters exhibit marked genetic structure between North, South and East (Ledoux et al., 2012; Fraïsse et al., 2021). This is an even more interesting finding than the genetic structure of *S. lateralis* across the sub-Antarctic region, as rafting events across hundreds to thousands of kilometers have proven to be historically relevant, yet may be unpredictable and irregular at present day (Moon et al., 2017). But if macroalgae such as *D. antarctica* and *M. pyrifera* are as abundant as they are within Kerguelen Islands (Féral et al., 2021), surely, rafting at regional scale could be more frequent and/or less stochastic than at larger scales, as gene flow would offset genetic structuring. Studies within and around New Zealand provide evidence of sporadic rafting of direct developers across >500 Km (Fraser et al., 2020b; Donald et al., 2020). However, local upwelling processes, environmental discontinuities or habitat specificity are some of the potential drivers of genetic divergence regardless of developmental mode, leading to significant genetic fragmentation over short geographical distances (Johansson et al., 2008; Ayre et al., 2009; Gonzalez et al., 2016; Donald et al., 2020). Within Kerguelen, the intertidal zone has abundant and subdivided kelp forests forming defined patches of habitat, all of which are differently exposed to the diverse influences of both open sea and land water (rivers and melting glaciers) (Koubbi et al., 2016). On the other hand, the Kerguelen coast is heterogeneous, as it has both jagged and linear coastlines, and exposed or sheltered bays,

which in turn determine the spatial distribution of benthic species (Poulin and Féral, 1995; Améziane et al., 2011). Therefore, this oceanographic and environmental patchiness, even under the assumption that *S. lateralis* disperses by rafting within Kerguelen, could lead to the levels of genetic structure found in our study. On the other hand, currents around the Kerguelen Islands either transport waters coastward, eastward or northward of the Kerguelen Plateau (Park et al., 2008; Zhou et al., 2014), providing little means for kelp rafts to move within Kerguelen, which could explain the low levels of gene flow and high estimates of self-recruitment among sampled populations of *S. lateralis*. Furthermore, Fraïsse et al. (2021) tested for the role of habitat heterogeneity in explaining the North-South differentiation of *Mytilus* in Kerguelen, and found that the presence of *Macrocystis* kelps, substrate type and coastal slope had a low but significant role in genetic differentiation.

Therefore, considering the observed patterns at global and regional scale, multilocus markers such as SNPs provide further tools to comprehend the extent and reach of dispersal and connectivity paradigms in the SO. Rafting has been an important Quaternary dispersal mechanism for benthic fauna, which provided the means to colonize/recolonize the sub-Antarctic region, yet its present relevance in promoting high levels of gene flow is disputed by our data, which, albeit limited to a single species, demonstrates that rafting sustains low levels of gene flow, evidenced in significant contemporary genetic structure across SO populations. Nevertheless, further research is needed to clarify contemporary dispersal patterns across the SO, which need to consider studying SNPs or whole genome sequencing in other species with different dispersal potential as study models, as well as environmental/oceanographical characteristics as potential barriers to present-day dispersal and genetic connectivity in the SO, where seascape genomic studies could help clarify these patterns.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://figshare.com/>, <https://doi.org/10.6084/m9.figshare.25939687.v2>.

Ethics statement

The animal study was approved by Comité de Ética, Facultad de Ciencias, Universidad Austral de Chile. The study was conducted in accordance with the local legislation and institutional requirements. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

CM-M: Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft.

ML: Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft. TS: Funding acquisition, Project administration, Resources, Writing – review & editing. EP: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. NS: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing. CG-W: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2024.1441397/full#supplementary-material>

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