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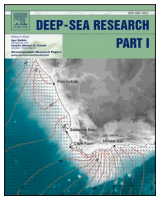

High genetic connectivity of the two main cold-water scleractinian framework engineers from the Southwestern Atlantic

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ABSTRACT

Cold-water coral reefs (>150 m) are highly biodiverse ecosystems mainly engineered by few scleractinian and Porifera species. Due to the low number of framework building scleractinian species combined with their low growth rates, cold-water reefs are considered vulnerable marine ecosystems susceptible to human impacts such as demersal fisheries. Apart from their occurrence, a seminal information that subsidizes best practices for their conservation is related to gene flow/population genetics. However, research on the latter is hampered by the expensive sampling logistics and, to date, most studies have focused on the North Atlantic. Here we use microsatellite markers to understand the genetic diversity and population structure of the most important cold-water framework builders in the Southwestern Atlantic, *Desmophyllum pertusum* and *Solenosmilia variabilis*. The genotyping of 285 specimens belonging to both species showed low clonality rates, high levels of genetic diversity with no evidence of inbreeding, and no population structure along a latitudinal gradient of nearly 700 km, similar to what has been previously observed for the sympatric species *Madrepora oculata* and *M. piresae*. The recurrent absence of population structure for cold-water corals in the Southwestern Atlantic along latitudinal and depth ranges, suggests that oceanographic factors, such as the direction and speed of the Western South Atlantic Central Water and of the Antarctic Intermediate Water, combined with the spawning "window" and the pelagic larval duration (PLD) of these species play crucial roles in their dispersion and connectivity patterns.

1. Introduction

Cold-water coral reefs (>150 m) have been known since the 18th century, but their distribution and overall biodiversity only began to be more thoroughly documented after the intensification of fishing and oil and gas exploration in deep waters (Roberts et al., 2006). Although cold-water reefs are primarily engineered by a limited number of framework scleractinians (e.g., *Madrepora oculata*, *Solenosmilia variabilis*, *Desmophyllum pertusum*, *Enallopsammia rostrata*, and *Dendrophyllia alternata*) (Roberts and Hirshfield, 2004), these ecosystems harbor biodiversity comparable to shallow-water tropical reefs (Dower and Perry, 2001; Reed, 2002; Roberts et al., 2006; Rogers, 1999), and are as susceptible to a range of human-based activities (Hall-Spencer et al., 2002; Kitahara, 2009). Among the main threats to these ecosystems, demersal fisheries (including trawl, bottom longline, bottom gillnet, and trap) can rapidly extinguish extensive reef areas (Kitahara, 2009; Ragnarsson et al., 2015; Roberts and Hirshfield, 2004). Due to the slow growth rate of cold-water corals (Williams et al., 2020), their recovery can take decades, if it happens. Apart from those direct human activities, the increase in ocean temperature and acidification, as a consequence of global climate changes, also pose major threats to cold-water coral environments (Desbruyères et al., 2016; Perez et al., 2018; Yasuhara and Danovaro, 2016). Given the importance of this sensitive ecosystem, there is a need to expand the knowledge on cold-water coral reefs and mounds and its associated fauna, with particular emphasis on research that can underpin the development of effective management and conservation strategies, such as population genetic studies.

Maintenance of high levels of genetic diversity in natural populations is essential for species persistence and resilience, as well as preserving the evolutionary potential of a species (Fisher, 1930; Hughes et al.,

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2008; Neel and Cummings, 2003). Thus, incorporating genetic data on conservation planning can increase its effectiveness (see Riginos and Beger, 2022). Gene flow between populations plays a crucial role in maintaining genetic diversity, as interconnected populations tend to preserve greater genetic diversity compared to more isolated ones, which are, in general, less resilient to environmental changes. Depending on the level of gene flow and population structure, different conservation strategies, such as protecting genetically divergent populations and/or populations that most contribute to migrants to adjacent areas, may be necessary to ensure that genetic diversity is maintained. To date, most studies involving cold-water corals focused on *D. pertusum*, one of the most commonly found cold-water reef framework engineer species in the Atlantic (e.g., Le Goff-Vitry et al., 2004; Morrison et al., 2008, 2011; Weinnig et al., 2024). Although the number of population genetic studies involving cold-water species has been increasing in recent years, few have focused on local scales of meters to tens of kilometers, primarily due to the logistics of obtaining samples (Miller and Gunasekera, 2017). However, population structuring has been observed in cold-water species on scales ranging from a few hundreds to thousands of meters, highlighting the importance of studies at different scales (Baco et al., 2016). In general, life history traits (including mode of reproduction and larval dispersal capabilities) and local hydrodynamics appear to be the main factors driving connectivity in the ocean (i.e., Addamo et al., 2021; Baco et al., 2016; Gary et al., 2020; Miller and Gunasekera, 2017; Strömberg and Larsson, 2017).

Studies on the genetic diversity and connectivity of cold-water corals remain incipient compared to those from their shallow-water counterparts, with only a few available to date (Dahl et al., 2012; Flot et al., 2013; Miller and Gunasekera, 2017; Le Goff-Vitry et al., 2004; Le Goff-Vitry and Rogers, 2005; Miller et al., 2010; Weinnig et al., 2024). Additionally, most of these studies have been conducted in the North Atlantic, with only one in the Southwestern Atlantic (SWA) (Capel et al., 2024). In Brazil, within the 59 reported azooxanthellate corals, six actively participate in the construction of cold-water reefs: *M. oculata*, *M. piresae*, *Dendrophyllia alternata, Enallopsammia rostrata, D. pertusum*, and *S. variabilis*, particularly in Campos, Santos, and Pelotas sedimentary basins (Capel et al., 2024; Cavalcanti et al., 2017; Kitahara, 2007; Kitahara et al., 2009). While there is little information on species abundance, a recent study showed that *S. variabilis* and *D. pertusum* are within the most common species in the Santos basin (Carvalho et al., 2023), but the genetic diversity and connectivity remain unknown for both species along the SWA. Here we use microsatellite markers to provide the seminal investigation of the genetic diversity and population structure of two cold-water framework-building corals, *D. pertusum* and *S. variabilis* in the SWA. Based on previous population genetic results for *M. oculata* (Capel et al., 2024), we expect to find no genetic structure for both species analyzed herein within the studied localities. Results presented herein increase the knowledge of evolutionary processes and might assist future conservation planning that focuses on preserving the adaptive potential of cold-water corals within the understudied SWA.

2. Methods

2.1. Sampling

Between 2016 and 2019, 96 fragments of *Solenosmilia variabilis* and 189 of *Desmophyllum pertusum* were sampled from three sedimentary basins in the SWA (Santos, Campos, and Espirito Santo basins; Fig. 1) at different depths, within the scope of the SENSIMAR Project–Sensitive Marine Environments coordinated by the Research, Development & Innovation Center (CENPES) of PETROBRAS (Brazilian Energy Company) (sampling permit n°731/2016 from the Brazilian Institute for the Environment and Renewable Natural Resources - IBAMA) (Table 1; Supplementary File 1). Sampling was performed opportunistically, depending on the species occurrence. Colony fragments were sampled between 206 and 1,128 m deep, using a remotely operated vehicle (ROV). Most samples were taken from colonies at least 50 m apart from each other, except for 58 samples of *D. pertusum* (39 from Santos Basin and 19 from Campos Basin) that were collected close to one another (i.e., <50 m) for clonal analysis. For each colony, a fragment of ~1 cm^2 was preserved in CHAOS buffer (Fukami et al., 2004) for DNA extraction.

2.2. DNA extraction and microsatellite amplification

Total genomic DNA was extracted using the Phenol:Chloroform method described by Fukami et al. (2004). DNA quality and quantity/purity were assessed by 1 % agarose gel electrophoresis and spectrophotometry (Nanodrop, Thermo Fisher Scientific), respectively. For *S. variabilis,* a total of 27 pairs of microsatellite primers previously designed by Miller and Gunasekera (2017) and Zeng (2016) were tested but did not work. Therefore, 13 pairs of primers designed for *D. pertusum* (Morrison et al., 2008) were also tested. For *D. pertusum*, the 23 pairs of primers previously designed for the species (Le Goff and Rogers, 2002; Morrison et al., 2008) were tested. Of those, only seven and eight *loci* were successfully amplified by Polymerase Chain Reactions (PCRs) for most individuals of *S. variabilis* and *D. pertusum*, respectively (Supplementary Table 1). PCRs were performed in 15 µl reactions including: 0.2 µM of the forward primer with a M13 tail at its 5′ end (TGT

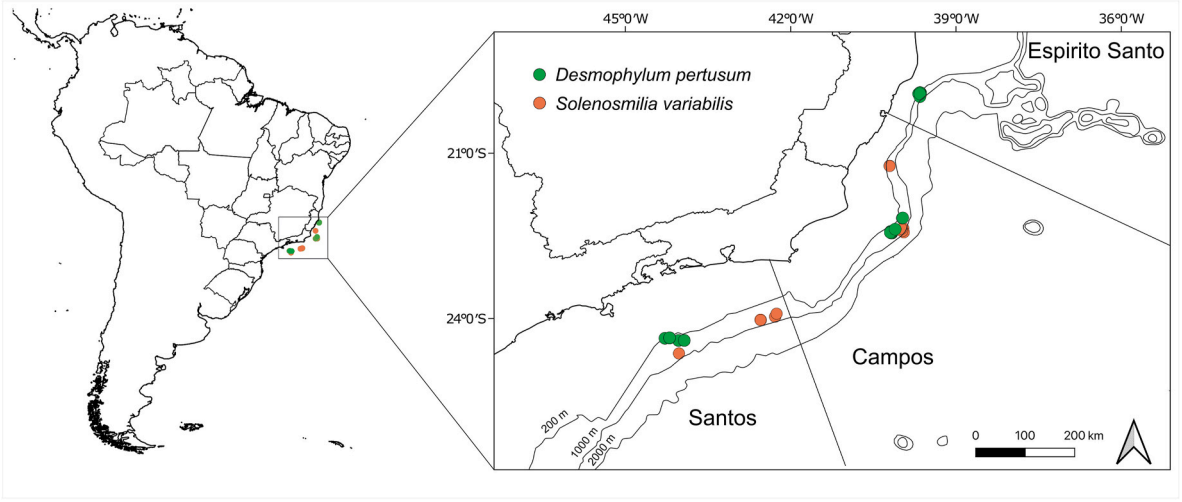

Fig. 1. Map of the Southwestern Atlantic sampling sites for *Desmophyllum pertusum* (green circles) and *Solenosmilia variabilis* (orange circles) at the three sedimentary basins: Santos, Campos, and Espirito Santo.

Table 1
Summary of statistics per sampling site for *Desmophyllum pertusum* (eight *loci* analyzed) and *Solenosmilia variabilis* (seven *loci* analyzed) containing the number of successfully genotyped individuals for each locality and depth range (N), number of unique multilocus genotypes (MLG), allele richness (Ar), number of effective alleles (Aeff), number of alleles unique to each locality (Ae), observed (Ho) and expected (He) heterozygosity and inbreeding index (F_{IS}). Asterisk (*) indicates significant deviations from the Hardy-Weinberg equilibrium. Values in parentheses represent the results obtained for five *loci* for each species, after removing *loci* with evidence of null alleles at all locations (three for *D. pertusum* and two for *S. variabilis*).

Species	Depth	N	MLG	Ar	Aeff	Ae	Ho	He	F_{IS}
Desmophyllum pertusum									
Espírito Santo Basin (ESB)	400–700	21	21	6.4 (6.8)	5 (4.8)	3 (2)	0.583 (0.620)	0.770 (0.752)	0.243* (0.174*)
Campos Basin (CB)	300–700	58	58	7.4 (7.9)	4.6 (4.9)	10 (8)	0.520 (0.693)	0.765 (0.745)	0.320* (0.070)
Santos Basin (SB)	200–550	97	97	7.3 (7.6)	5,2 (5.3)	17 (9)	0.553 (0.690)	0.756 (0.750)	0.268* (0.080*)
Overall		**176**	**176**	-	**5.3**	-	**0.559**	**0.765**	**0.277**
Solenosmilia variabilis									
Espírito Santo Basin (ESB)	650–950	29	28	6.0 (4.7)	6.0 (3.9)	6 (4)	0.559 (0.564)	0.653 (0.542)	0.143* (−0.042)
Campos Basin (CB)	550-1150	43	43	6.0 (5.1)	6.8 (4.1)	16 (8)	0.556 (0.553)	0.676 (0.571)	0.177* (0.031)
Santos Basin (SB)	750–900	10	10	5.0 (4.9)	4.7 (4.2)	4 (2)	0.596 (0.660)	0.689 (0.601)	0.134 (−0.098)
Overall		**82**	**81**	-	**5.5**	-	**0.570**	**0.674**	**0.151**

AAA ACG ACG GCC AGT); 0.4 μM of the labeled primer (M13 with 6-FAM fluorescent dye) (Schuelke, 2000); 0.8 μM of the reverse primer; 1U GoTaq G2 Flexi (Promega); 5X PCR Buffer (Promega); 0.20 mM dNTPs (Invitrogen); 2.5 mM MgCl2; 10 μg BSA (Invitrogen); and 5–10 ng of DNA. PCR cycling conditions were: 95 °C for 3 min followed by 5 cycles at 95 °C for 30s; 50 °C for 30s; 72 °C for 45s; and 30 cycles at 92 °C for 30s; 50 °C, 30s; 72 °C for 55 s; with a final extension at 72 °C for 30 min. Amplicons were pooled with GS600-LIZ size standard (Applied Biosystems) and genotyped in an ABI 3500 genetic Analyzer (Applied Biosystems). Genotypes were determined using the program Geneious 11 (Kearse et al., 2012) (https://www.geneious.com).

2.3. Clonal contribution analysis, genetic diversity, and population structure

A total of 14 and 13 samples failed to amplify for more than two *loci* for *S. variabilis* and *D. pertusum*, respectively, and were excluded from the analyses. The package RClone (Bailleul et al., 2016) in the software R 4.2.1 was used to assess each species' clonal contribution at all sites. Individuals with identical alleles at all *loci* were assigned to the same multilocus genotype (MLG). Linkage disequilibrium among all pairs of *loci*, inbreeding coefficient (F_{IS}), and deviations from Hardy-Weinberg equilibrium were calculated with the software FSTAT (Goudet, 1995). The software microchecker (Van Oosterhout et al., 2004) was used to evaluate the occurrence of null alleles. Genetic diversity of each species was evaluated by allelic richness (Ar), effective number of alleles (Aeff), alleles unique to each locality (Ae), and observed (Ho) and expected heterozygosity (He), all using the package 'diveRsity' (Keenan et al., 2013) in R 4.2.1 and the software GenoDive 3.06 (Meirmans, 2020). Overall F_{ST} (using AMOVA with Infinite Allele Model and 999 permutations) (Excoffier et al., 1992) and F_{ST} pairwise population differentiation (with 999 permutations) were calculated on GenoDive 3.06 (Meirmans, 2020). Isolation by distance (IBD) using the Mantel test was calculated in the software R 4.2.1 using the packages hierfstat (Goudet, 2005), vegan (Oksanen et al., 2025), geosphere (Hijmans, 2024), and poppr (Kamvar et al., 2014).

To visualize possible genetic groupings, for each species, a Principal Component Analysis (PCA), using sampling sites as a grouping factor, was performed with the package Adegenet (Jombart, 2008) in R 4.2.1. Bayesian analysis was performed to estimate the likely number of genetic clusters using the software STRUCTURE v.2.3.4 (Pritchard et al., 2000) with the admixture ancestry model, correlated allele frequency, and no sampling locations as prior. Bayesian analysis was performed with an initial burn-in of 250,000 cycles, followed by 1,000,000 additional cycles. The number of clusters (K) tested varied from 1 to 5, with 10 iterations for each K-value. The most likely K-value was calculated by estimating the "log probability of data" for each value of K (mean LnP (K)) and ΔK criterion (Evanno et al., 2005) using STRUCTURE Harvester (Earl and VonHoldt, 2012).

3. Results

After several amplification tests, only seven heterologous primers, originally designed for *Desmophyllum pertusum* (Morrison et al., 2008), were successfully amplified and genotyped for *Solenosmilia variabilis*. A total of 176 and 82 specimens were successfully genotyped for *D. pertusum* and *S. variabilis*, respectively (Supplementary File 2). For *S. variabilis*, two samples from the Espírito Santo Basin had the same multilocus genotype (MLG) (Sva111 and Sva160, both collected at 681 m depth, approximately 1 km away from each other). No clones were identified for *D. pertusum*. Both species showed evidence of null alleles at all three basins for two (*Lpe*D5 and SvD213) and three (*Lpe*C44, *Lpe*C142, and *Lpe*D5) *loci*, respectively. Evidence of linkage disequilibrium was observed for *D. pertusum* between four pairs of *loci* (*Lpe*C120 x *Lpe*C91, p-value = 0.002; C44 x C91, p-value = 0.002; *Lpe*C91 x *Lpe*D5, p-value = 0.002; *Lpe*C151 x Lp355, p-value = 0.002 - Bonferroni adjusted p-value = 0.002) and for *S. variabilis* between one pair of loci (*Lpe*C142 x *Lpe*D5, p-value = 0.002 - Bonferroni adjusted p-value = 0.002). Genetic diversity and connectivity analyses were performed with all *loci* (seven *loci* for *S. variabilis* and eight for *D. pertusum*) and removing *loci* with evidence of null alleles (five for each species). Genetic diversity analysis showed similar levels among basins for both species (Table 1), with the highest estimates of genetic diversity being found in *D. pertusum* (Table 1). Additionally, for both species, significant heterozygote deficiencies were observed when each basin was analyzed separately. When all samples were analyzed as a single population, no deviations from the Hardy-Weinberg equilibrium were observed.

The most likely number of clusters (K) recovered for *S. variabilis* based on the "log probability of data" (mean L(K)) was one when using all *loci* or after removing *loci* with evidence of null alleles (it is important to note that the ΔK criterion does not test for $K = 1$) (Fig. 2; Supplementary Fig. S1–2). For *D. pertusum*, the most likely number of clusters (K) was three when using all *loci*, and one after removing *loci* with evidence of null alleles (Fig. 2; Supplementary Fig. S1–2). The recovery of $K = 3$ for *D. pertusum* is probably an artifact due to the presence of null alleles, as $K = 1$ was recovered in the dataset where *loci* with evidence of null alleles were removed (Supplementary Figs. S1–2). For the PCA, the first two axes explained 3.2 % and 3.0 % of the variation for *D. pertusum*, and 4.7 % and 4.0 % for *S. variabilis* (Fig. 3; Supplementary Fig. S3). Overall, F_{ST} for *D. pertusum* was significantly different from zero when all *loci* were included (F_{ST} = 0.008; p-value = 0.003), but not after removing *loci* with evidence of null alleles (F_{ST} = 0.001; p-value = 0.318), suggesting low differentiation among sites. Either when all *loci* were included or after removing *loci* with evidence of null alleles, nearly all genetic variation was observed within individuals (72.8 % and 91.1 %) or within basins (26.4 % and 8.4 %), with a practically null fraction

of the variation being observed among basins (0.8 % and 0.1 %). When comparing among basins, significant results were observed between Campos and Santos (F_{ST} = 0.011; p-value = 0.001) only when all *loci* were included (Table 2). For *S. variabilis*, overall F_{ST} was not significant using seven (F_{ST} = 0.001; p-value = 0.354) nor five *loci* (F_{ST} = −0.001; p-value = 0.491), and no significant results were observed between basins (Table 2). Either when all *loci* were included or after removing *loci* with evidence of null alleles, nearly all genetic variation was also observed within individuals (84 % and 100 %) or within basins (15.9 % and −0.1 %), with a practically null fraction of the variation being observed among basins (0.1 % and −0.1 %).

For both species, IBD among basins was not significant, either when all *loci* were considered (*D. pertusum*: r = 0.650, p = 0.333 and *S. variabilis*: r = 0.999, p = 0.167) or after removing those with evidence of null alleles (*D. pertusum*: r = 0.772, p = 0.333 and *S. variabilis*: r = 0.671, p = 0.333) (Supplementary Fig. S4). Nevertheless, the Mantel test can have low statistical power when there is a low number of sites for comparison (Legendre and Fortin, 2010), and the inclusion of additional sampling sites is recommended to further explore patterns of IBD. Overall, genetic connectivity recovered by PCA, STRUCTURE, and F_{ST} showed no genetic differentiation among the three analyzed basins, suggesting only one population for both species within the Espirito Santo, Campos, and Santos basins (Figs. 2–3; Table 2; Supplementary Figs. S1–3). The application of more refined methods, such as single-nucleotide polymorphism (SNPs), is recommended to test these results and check if there is/are undetected sub-population structure for *D. pertusum*.

4. Discussion

Cold-water reefs and mounds are increasingly threatened by global and local impacts (Desbruyères et al., 2016; Perez et al., 2018; Yasuhara and Danovaro, 2016). Studies focusing on their engineers are frequently hampered by the complex and expensive sampling logistics, limiting our understanding on several biological features, including population connectivity, which is a powerful tool to inform conservation efforts. Here, we found that two of the six main cold-water scleractinian framework engineers from three sedimentary basins of the Brazilian continental shelf and slope, *S. variabilis* and *D. pertusum*, form one single population each, with high levels of genetic diversity within a latitudinal gradient of nearly 700 km. Results indicate that both species have a high gene flow, connecting coral mounds and reefs across latitudes and depths, with a negligible proportion of asexual reproduction. Similar results showing low clonality and no population structure in the same geographic area were also found for *M. oculata* and *M. piresae* (Capel et al., 2024).

Table 2
Summary of F_{ST} statistics between sampling sites for *Desmophyllum pertusum* (eight *loci* analyzed) and *Solenosmilia variabilis* (seven *loci* analyzed). Values in parentheses represent the results obtained for five *loci* for each species, after removing *loci* with evidence of null alleles at all locations (three for *D. pertusum* and two for *S. variabilis*). Asterisk (*) indicates a significant difference.

Desmophyllum pertusum		
	Campos Basin (CB)	Santos Basin (SB)
Espírito Santo Basin (ESB)	−0.006; p = 0.880 (−0.005; p = 0.799)	0.006; p = 0.115 (0.002; p = 0.315)
Campos Basin (CB)	–	0.011; p = 0.001* (0.002; p = 0.173)
Solenosmilia variabilis		
	Campos Basin (CB)	Santos Basin (SB)
Espírito Santo Basin (ESB)	−0.000; p = 0.473 (0.001; p = 0.349)	0.008; p = 0.198 (0.006; p = 0.261)
Campos Basin (CB)	–	0.001; p = 0.417 (−0.009; p = 0.791)

Cold-water coral species usually have widespread latitudinal, longitudinal, and bathymetric distributions when compared to their shallow water counterparts. Together, these suggest that deep-water currents/water masses play an important role in maintaining gene flow in this environment (see Costello et al., 2017; Watling et al., 2013). However, it is important to note that molecular analysis of previously thought cosmopolitan and widely distributed species revealed the existence of cryptic species with limited distribution (Danovaro et al., 2017). Indeed, deep-water cryptic species have been described in the past decades for several taxa (e.g., Capel et al., 2024; Dautova, 2019; Kawauchi and Giribet, 2010; Mohrbeck et al., 2021; Periasamy et al., 2023), highlighting the need for more molecular studies focusing on these organisms.

Gene flow and population structure depends on an intricate combination of biological (e.g., life history, reproductive strategy, maternal investment, larval type, larval duration, habitat preference, and behavior) and physicochemical aspects of the environment (e.g., currents, biogeographic barriers, habitat availability), both of which can vary by orders of magnitude between species (Palumbi, 1994; Selkoe and Toonen, 2011). Both scleractinians herein investigated are gonochoric (but hermaphroditism has been observed in *D. pertusum*, evidencing the potential for self-fertilization) and broadcast spawners (Pires et al., 2014). External fertilization can extend the pelagic larval duration (PLD), potentially enhancing dispersal capabilities, as has been observed for shallow-water corals (e.g., Nunes et al., 2011; Thomas et al., 2020). *Desmophyllum pertusum* is a widespread species, and its planula is known to have a high potential for dispersion, as they can survive up to eight weeks in the water column, are capable of swimming (Larsson et al., 2014; Strömberg and Larsson, 2017) and can migrate vertically (as observed in laboratory experiments) (Gary et al., 2020). Within a similar geographic scale along the Southeastern United States (~500 km), low values of pairwise F_{ST} (ranging from 0 to 0.004), PCA and STRUCTURE analysis indicate no evidence of genetic differentiation (Weinnig et al., 2024). Nevertheless, the occurrence of genetic structuring across oceanic regions with isolation by distance (Morrison et al., 2011) and within smaller spatial areas, as along the European margin and in Scandinavian fjords (Le Goff-Vitry et al., 2004) and the Eastern coast of the United States (Weinnig et al., 2024), has also been observed. In the Northeastern Atlantic, Le Goff-Vitry et al. (2004) found 12.93 % of the genetic variation among ten subpopulations distributed over more than 2,000 km, with a significant fixation index (F_{ST} = 0.1293). In this case, expanding the sampling area of *D. pertusum* is recommended to further investigate population structure in the Southwestern Atlantic. *Solenosmilia variabilis* is also widely distributed (Cairns, 1995; Davies and Guinotte, 2011; Freiwald et al., 2004) and generally found deeper than *D. pertusum* (Endress et al., 2022). While there is no evidence of population structure along the studied 700 km of the SWA, previous studies found evidence of five distinct genetic clusters structured by geographic provinces in New Zealand (Zeng, 2016), and at least two clusters in the Southern Ocean, suggesting limited gene flow at small scales in these localities, but with no clear geographic pattern (Miller and Gunasekera, 2017). For example, a significant F_{ST} of 0.111 was observed among *S. variabilis* populations from eight Tasmanian Seamounts distributed over less than 200 km (Miller and Gunasekera, 2017). Reproductive studies indicate that the SWA *S. variabilis* produces lecithotrophic (non-feeding) larvae with large oocytes (Pires et al., 2014), which might increase PLD and, therefore, dispersion, although reproductive mode alone cannot be used to predict dispersion potential.

As previously mentioned, cold-water coral populations can also be structured along their depth range (Miller et al., 2010; Miller and Gunasekera, 2017). In the New Zealand region, genetic differentiation by depth was observed for the solitary species *Desmophyllum dianthus* (Miller et al., 2010), but not for *S. variabilis* (Zeng et al., 2017). As in Zeng et al. (2017), herein we found no evidence of genetic differentiation in colonies collected between 206 m and 692 m for *D. pertusum,* and 588 m and 1,128 m for *S. variabilis*. The general absence of population

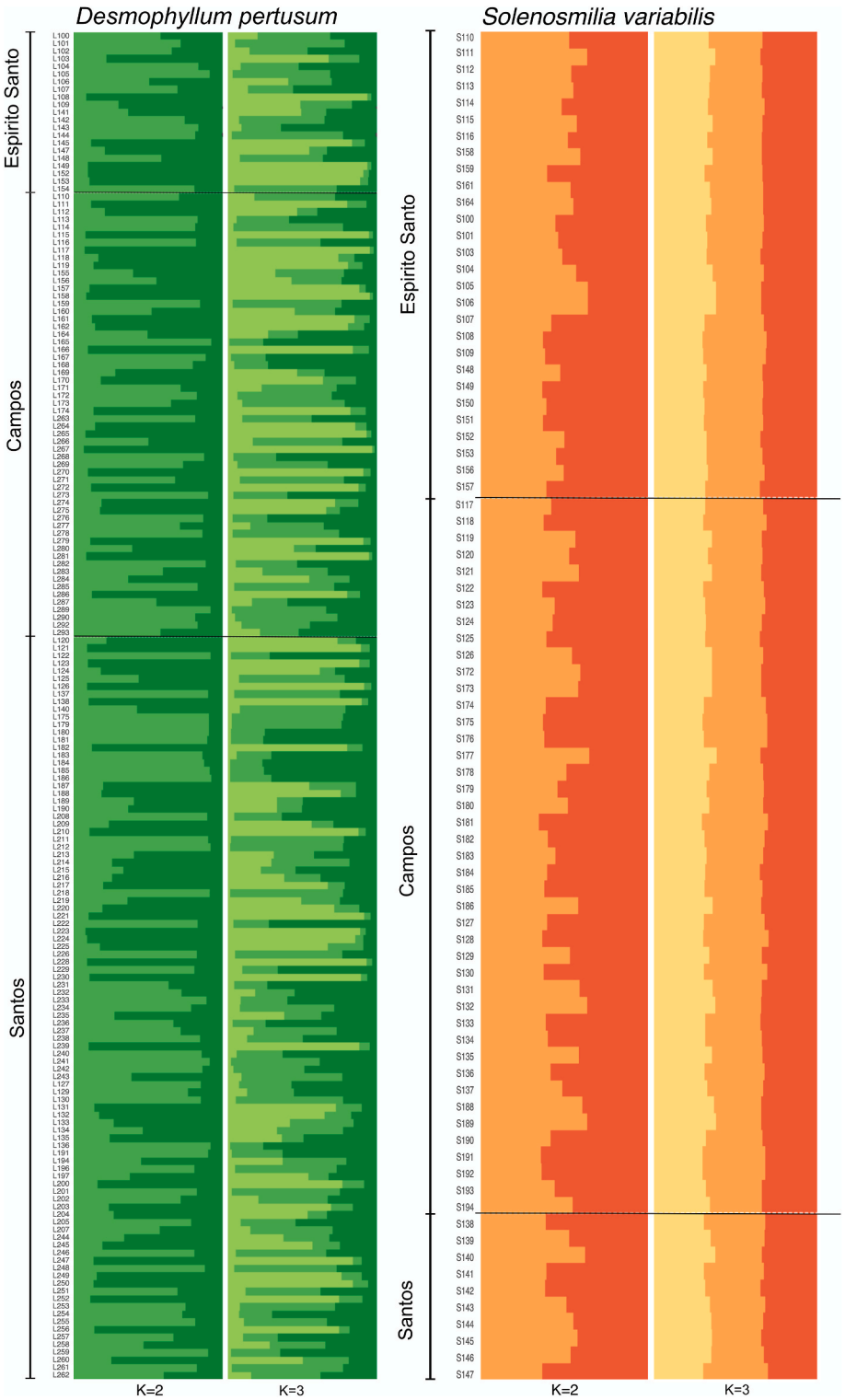

Fig. 2. STRUCTURE results of *Desmophyllum pertusum* (green shades) and *Solenosmilia variabilis* (orange shades) based on eight and seven *loci*, respectively. Bayesian clustering analyses for $K = 2$ and K = 3, where each individual is represented by a vertical bar with different colors indicating the relative proportion of each genetic cluster.

structure along latitudinal and depth ranges for the four main cold-water framework builders in Brazil (including results from *Madrepora oculata* and *M. piresae*; Capel et al., 2024) suggests that oceanographic factors play crucial roles in their dispersion and population connectivity. For example, the coral colonies studied herein are under the influence of the Western South Atlantic Central Water (down to around 500 m excluding the shallower mixed layer; Liu and Tanhua, 2021) and of the Antarctic Intermediate Water (between 500 m and 1,200 m; Talley, 1996), which, within the studied area, mainly flows southward and northward, respectively. It is well established that the velocity (Miller and Gunasekera, 2017) and direction of currents can change along the year, thus, hypothetically, it can be one of the triggers for the spawning period of *D. pertusum* and *S. variabilis,* ultimately influencing their dispersal capabilities. Overall, in promoting larval (Bracco et al., 2019) and gamete

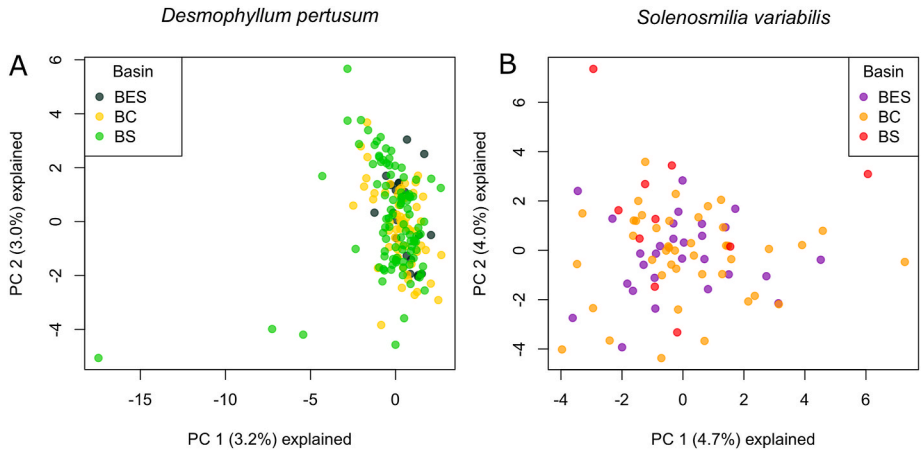

Fig. 3. PCA of *Desmophyllum pertusum* (on the left) and *Solenosmilia variabilis* (on the right) based on eight and seven *loci*, respectively.

dispersal, water masses increase gene flow and, consequently, population connectivity. Histological studies performed by Pires et al. (2014) using colonies from the Campos Basin (one of the localities also studied herein) indicate that *S. variabilis* reproduction peaks between April and September, while that of *D. pertusum* concentrates between May and July. Therefore, both water masses aforementioned direction and speed, spawning "window", and PLD are enabling high levels of gene flow among both coral species analyzed from the studied sedimentary basins.

High levels of genetic diversity increase the resistance, as well as the capacity of populations to recover after natural or anthropogenic disturbances (Vásquez et al., 2023). In this study, levels of genetic diversity were high for both studied species. Unexpectedly, the microsatellite markers developed for *S. variabilis* using colonies from the Pacific (Miller and Gunasekera, 2017; Zeng, 2016) did not work on *S. variabilis* from the Atlantic, despite several attempts to optimize amplification. Thus, we tested heterologous primers developed for *D. pertusum* (Morrison et al., 2008) that belong to the same family (Caryophylliidae – see Seiblitz et al., 2022), and they were successfully genotyped. The use of heterologous primers may lead to the presence of null alleles and lower levels of genetic diversity (Francisco et al., 2006), thereby leading to observations of higher levels of inbreeding. The presence of null alleles and low heterozygosity observed in *S. variabilis* was similar to the pattern observed for *D. pertusum,* which was examined using homologous primers. Consequently, these patterns most likely are not a function of using heterologous primers in *S. variabilis*. Additionally, although many studies have shown that the use of heterologous markers might show lower levels of genetic diversity compared with species-specific markers (e.g., Garner et al., 2005; Weber et al., 2020), in the present study, *S. variabilis* genetic diversity levels in the SWA were higher than those observed from Pacific samples, despite the lower number of *loci* (Miller and Gunasekera, 2017).

Conversely, the genetic diversity levels in the SWA *D. pertusum* population were similar to what has been observed in the North Atlantic, also using microsatellite markers (Skagerrad, North of Norway - Dahl et al., 2012). When all sampling sites are analyzed as a single population, both *S. variabilis* and *D. pertusum* show no evidence of Hardy-Weinberg disequilibrium. This is contrary to the high levels of inbreeding found by Weinnig et al. (2024) for *D. pertusum* populations along the Southeastern United States using SNPs. However, this result could be due to the lower sample size used after filtering sequencing data (Weinnig et al., 2024). Despite the linear scale sampling of ~700 km, only one colony was identified as clonal for *S. variabilis* and none for *D. pertusum*. This suggests that while they can form extensive mounds, asexual reproduction leading to "new colonies" is not relevant for these species in the SWA, even at small scales (<50 m). Contrasting results were observed for *S. variabilis* from the Southern Pacific Ocean, where nearly 76 % of the investigated samples (with a minimum distance among samples of ~100 m) were genetically identical and, therefore, considered the product of asexual reproduction (Miller and Gunasekera, 2017). Likewise, up to 50 % of clonal individuals were detected in Skagerrak (Dahl et al., 2012), and a variable proportion of clones within several reefs from the North Atlantic (Morrison et al., 2011) were detected for *D. pertusum*. High proportions of clones were also observed in other reefs along the European margin, where the fragmentation of the colonies into small pieces as a result of bottom trawling could have impaired sexual reproduction (Le Goff-Vitry et al., 2004; Waller and Tyler, 2005).

Without a doubt, *D. pertusum* and *S. variabilis* are the most important cold-water framework builders of the external continental shelf and slopes along the Brazilian coast, occurring from 17°S to 34°S and 9°S to 34°S, respectively (Pires, 2007; although large portions of the NE and N Brazilian deep waters have been poorly studied). The present study is the first assessment of the genetic structure of these important reef-building species in the SWA, rendering important implications for the conservation of the cold-water reefs and mounds. Nevertheless, while our results indicate no population structure along ~700 km for both species, a more extensive sampling covering the whole distribution of these species in the SWA, along with the use of more refined methods, such as single-nucleotide polymorphisms (SNPs), is recommended to better understand the connectivity patterns of these species. The application of more sensitive methodologies may indicate populational substructure(s) that were undetected by microsatellites, providing a more thorough picture to inform conservation strategies.

CRediT authorship contribution statement

Kátia Cristina Cruz Capel: Writing – review & editing, Writing – original draft, Validation, Formal analysis, Data curation, Conceptualization. **Pedro Leocorny:** Writing – review & editing, Formal analysis. **Raphael de Mello Carpes:** Writing – review & editing, Formal analysis. **Marcelo Visentini Kitahara:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Carla Zilberberg:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2025.104606.

Data availability

Data was submitted as supplementary file.

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