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REPORT

Comparative phylogeography of reef fishes indicates seamounts as stepping stones for dispersal and diversification

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Abstract Studies on oceanic island biodiversity have been the foundation for much theoretical work. However, seamounts are mostly underexplored, and little information is available about their potential as stepping stones for oceanic dispersal and their role in diversification. Here we used a genetic approach to test different models of marine dispersal between the continental coast and a volcanic ridge composed of seamounts and oceanic islands. We observed that the stepping stone model best fits our results, with one reef fish species displaying ongoing gene flow and another showing endemic lineages restricted to the islands and most isolated seamounts. The data also suggest that connectivity among remote regions could be influenced by Pleistocene sea level fluctuations and that a widespread genetic lineage was originated from an island endemic. Recent findings on island endemic species showed a similar pattern of both origin and export of genetic lineages, indicating that this process occurred multiple times in the Pleistocene. This study highlights the role of seamounts in supporting subpopulations that, in turn, allow island colonization, diversification, and a biodiversity feedback process that nourishes source populations with evolutionary novelty from peripheral regions.

Keywords Biodiversity feedback process · Connectivity · Evolution · Pleistocene sea level fluctuations · Reef fishes · Volcanic island

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Introduction

Remote oceanic islands often have high levels of endemism, representing iconic systems for evolutionary studies. In marine systems, due to the high dispersal ability of most species, speciation and diversification in isolated localities occur as a result of a combination of oceanographic, glacial-eustatic, geographic, and ecological drivers (Rocha et al. 2005; Pinheiro et al. 2017). Studies suggest that peripheral provinces, including isolated oceanic islands, are not just a receiving sink for marine propagules, but also export newly evolved taxa and lineages back toward biodiversity hotspots, a process called "biodiversity feedback" (Bowen et al. 2013). According to Bowen et al. (2013), this biodiversity feedback model is based on rare dispersal events in which marine species sometimes escape the potential evolutionary dead end of peripheral isolation. Thus, dispersal capacity and isolation seem to influence

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colonization, speciation, and consequently the biodiversity feedback process.

In this context, colonization rate of islands and peripheral provinces is predicted to decrease with time, as species that are better dispersers arrive first and are followed by weak dispersers that stochastically and slowly colonize the islands (MacArthur and Wilson 1967; Pinheiro et al. 2017). Dispersal efficiency influences gene flow between populations, and the gradient of dispersal among discrete habitats has direct effects on evolutionary processes (Garant et al. 2007), likely regulating speciation. Two classic models of dispersal and gene flow have been proposed for oceanic islands, the island model (Wright 1943) and the stepping stone model (Kimura 1953). In the island model, a population is divided into subpopulations occupying distinct islands as discrete habitats, where mating is random among resident individuals, but with the possibility of random gene flow with migrants from other subpopulations. In the stepping stones model, which assumes a scenario of isolation by distance, migration is not random but is constrained by the distance, and the gene flow occurs mainly between adjacent subpopulations, and consequently, neighboring populations tend to be more genetically similar to one another (Hutchison and Templeton 1999).

Since a small island connected to the mainland by a chain of islands has higher biodiversity than a single island with the same total area and distance from the coast, the stepping stones dispersal has a relevant role in island biogeography (Gilpin 1980). In addition to oceanic islands, there are hundreds of thousands of seamounts scattered throughout the world's ocean basins, with at least 8000 of them considered large—taller than one km above the seafloor (Kim and Wessel 2011). Seamounts, defined as extinct or active submerged volcanoes, collectively occupy an area greater than Europe (Wessel et al. 2010; Kvile et al. 2014), being considered a biome distinct from other marine environments (Etnoyer et al. 2010). Moreover, like emerged islands, seamounts represent discrete, island-like habitats in the deep ocean, possibly facilitating the dispersal of bottom-associated species over extensive areas (Hubbs 1959; Wilson and Kaufmann 1987; Pinheiro et al. 2014; Dawson 2016). Since only 0.4–4% of seamounts have been surveyed for scientific purposes (Kvile et al. 2014), few studies have adequately tested the functioning of seamounts as stepping stones for dispersal (Cho and Shank 2010; Pinheiro et al. 2017), and none has evaluated their role in the biodiversity feedback process. While some studies revealed ongoing gene flow between populations from seamounts and continental slopes (Samadi et al. 2006; Clague et al. 2012), others found cryptic genetic lineages and species when comparing populations from different seamount chains (Tunnicliffe et al. 2010; Castelin et al. 2012; Zeng et al. 2017).

In the southwestern Atlantic, a marine volcanic ridge named Vitória-Trindade Seamount Chain (VTC) is composed of several seamounts and extends 1200 km perpendicularly from the mainland, ending at the peripheral Trindade-Martin Vaz insular complex. The seamounts, situated between the islands and the mainland, are separated by relatively short distances ($\sim$ 30–190 km), and at least nine of them have summits reaching shallow depths ($\sim$ 20–90 m). The oldest seamounts ($\sim$ 60–40 My) are those closer to the continental shelf, while the islands are the youngest structures, emerging between 3 and 0.5 Mya (Motoki et al. 2012). Surface circulation in the VTC is dominated by the Brazil Current, which flows southwards near and parallel to the coast, perpendicularly to the chain (Evans and Signorini 1985), and has been suggested as a biogeographic barrier between the mainland and seamounts (Pinheiro et al. 2015; Mazzei et al. 2021). However, other oceanographic processes such as eddies and rings moving northward from the continental shelf often reach the VTC (Schmid et al. 1995; Mill et al. 2015; Costa et al. 2017). The VTC has recently been highlighted as a natural laboratory for evolutionary and biogeography studies, which suggest that sea-level fluctuations played an important role for island colonization, establishment, and speciation through vicariance (Macieira et al. 2015; Pinheiro et al. 2017; Mazzei et al. 2021).

Here we use a comparative phylogeographic approach along the VTC to assess whether seamounts work as stepping stones for the dispersal of reef fishes between peripheral oceanic islands and biodiversity centers. Two reef fish species differing in reproductive strategy and biological traits were chosen to test the influence of the stepping stones and island models in the VTC system: one with pelagic eggs and larva, and a larger body size and bathymetric range (the Coney *Cephalopholis fulva*), and another with benthic eggs, a shorter pelagic larval stage and shallower bathymetric distribution (the Brazilian Damselfish *Stegastes pictus*).

Methods

Sampling

The present work was carried out on five seamounts and two oceanic islands of the VTC and at two coastal regions in mainland, one northern (Abrolhos Shelf) and other southern (southern coast of the state of Espírito Santo) of the VTC (Table 1). Sampling was done by SCUBA diving (mixed gas in depths greater than 45 m) using spear and hand nets, and fishing using hook and line. Fishes on

Table 1 Main characteristics of sampling sites (total area, distance from continental shelf and isolation from nearby reef environment, measured from the 120 m isobath, and diving depth range) and number of sampled individuals of each species (*Cephalopholis fulva* and S*tegastes pictus*) in each site

Sampling site	Area (km^2)	Distance from shelf (km)	Isolation (km)	Depth (m)	N *C. fulva*	N *S. pictus*
Abrolhos Shelf	–	–	–	10–100	30	26
Espírito Santo southern shelf	–	–	–	5–70	27	39
Vitória Seamount	1184	120	50	35–55	37	31
East-Jaseur Seamount	99	300	40	55	10	30
Davis Seamount	1002	350	45	17–57	28	22
Dogaressa Seamount	81	480	100	65	6	10
Columbia Seamount	36.5	660	175	84	2	2
Trindade Island	85	910	50	5–40	46	40
Martin Vaz Archipelago	24	960	50	10–30	27	14

seamounts were caught during an expedition carried out in April 2011, in Trindade between July and August 2011, and in Martin Vaz during one dive performed in January 2012. The coastal populations were sampled during scattered dives between 2010 and 2013. Immediately after collection, fishes received a lethal dose of quinaldine sulphate (Ross and Ross 2008) and muscle tissues were preserved in 93% alcohol and kept on ice.

Model species

Two reef fish species, the Coney, *Cephalopholis fulva* (Linnaeus 1758) (Perciformes: Epinephelidae) and the Brazilian damselfish, *Stegastes pictus* (Castelnau 1855) (Perciformes: Pomacentridae), were used as models to represent potentially divergent scenarios of gene flow along the VTC. These species differ in many characteristics that can influence their dispersal potential, such as body size and pelagic larval duration (Luiz et al. 2013). While *C. fulva* has pelagic eggs, a pelagic larval duration of 40 days (B.C. Victor, unpubl. data) is widespread in the western Atlantic (Heemstra and Randall 1993) and has a maximum body size greater than 40 cm (Araujo and Martins 2006), *S. pictus* has benthic eggs, a pelagic larval duration of 30 days (B.C. Victor, unpubl. data), is endemic to the Brazilian Province, and has a maximum body size of about 10 cm. In addition, *C. fulva has* a much wider bathymetric range, occurring between 1 and 350 m depth, while *S. pictus* has only been found between 5 and 85 m (Robertson and Van Tassell 2019). Both species have been recorded at all VTC surveyed sites (Pinheiro et al. 2015), but their biological characteristics suggest that *C. fulva* might present higher dispersal potential compared to *S. pictus*.

Samples used in this study include 213 adult individuals of *C. fulva* and 214 of *S. pictus*, with each site being represented by an average 24 individuals (range 2–46, Table 1). For both species, sites with few samples include Dogaressa and Columbia seamounts, due to technical constraints associated with deep diving logistics (the shallower reefs were found at 65 m and 83 m, respectively) and remote locations ($\sim$ 600 km and $\sim$ 800 km from the coast, respectively). Few specimens were obtained at the East Jaseur Seamount and the Martin Vaz Archipelago due to logistical issues.

Genetic analyses and dataset preparation

DNA was isolated using the Wizard Genomic Purification Kit (Promega Corp., Madison, WI, USA), following the manufacturer's protocol. Two mtDNA markers (used on adult individuals only), the Cytochrome B (CytB) and the Control Region (CR), and 12 microsatellite loci (used both on adults and recruits) were analyzed. The CytB was amplified using FishCytB and TrucCytB primers (Sevilla et al. 2007), and the CR was amplified using primers A (Lee et al. 1995) and H1 (Santa Brígida et al. 2007). For microsatellite genotyping, six dinucleotide (Cfu21, Cfu23, Cfu52, Cfu57, RH_CA_002, RH_CA_004), two trinucleotide (Cfu69, Cfu70), and four tetranucleotide markers (Cfu72, Cfu75, Cfu92, RH_GATA_034) previously developed for (those starting with the initials Cfu) or characterized in (those starting with the initials RH) *C. fulva* were used (Renshaw et al. 2010). For *S. pictus,* we developed eight specific dinucleotide markers (Spi03, Spi29, Spi43, Spi45, Spi49, Spi50, Spi53, and Spi60) and characterized three trinucleotide (SpGGA7, SpAAC33, SpAAC42) and one tetranucleotide markers that were originally developed for *S. partitus* (Williams et al. 2003; Thiessen and Heath 2007).

For the mtDNA markers, PCRs were performed in a 12.5 µl volume containing 10–100 ng of template DNA, 1.25 µl of 10X PCR buffer, 2.5 pmols of each dNTP, 25

pmols of $MgCl_2$, 2.5 pmols of each primer, 1 unit of Taq polymerase (Invitrogen, Carlsbad, CA, USA) and ultrapure water to reach the final reaction volume. PCRs were performed with the following cycling parameters: initial denaturation at 94 °C for 5 min, 35 cycles of 30 s at 94 °C, 1 min at the annealing temperature (60 °C and 51 °C for CytB, and 52 °C and 55 °C for RC; *C. fulva* and *S. pictus*, respectively), and 2 min at 72 °C, with a final extension of 7 min at 72 °C. PCR products were purified using ExoSAP-IT (USB, Cleveland, OH, USA). Sanger sequencing was performed using BigDye Terminator v3.1 kit in a 3500 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). All samples were sequenced in the forward direction and those with ambiguous peaks were also sequenced in the reverse direction. The chromatograms were visually inspected in Geneious R6 (Kearse et al. 2012), where sequences were trimmed and aligned using MAFFT algorithm (Katoh and Standley 2013).

For the microsatellite markers, PCRs were performed in a 10 µl volume containing 1–10 ng of template DNA, 1 µl of 10X PCR buffer, 2 pmols of each dNTP, 10–20 pmols of $MgCl_2$, 2 pmols of each primer (forward primers labeled with 6-FAM, VIC, NED or PET fluorescent dyes), 1 unit of Taq polymerase (Invitrogen, Carlsbad, CA, USA) and ultrapure water to reach the final reaction volume. PCRs were performed with the following cycling parameters: initial denaturation at 95 °C for 4 min, 35 cycles of 1 min at 95 °C, 30 s at the annealing temperature {48–60 °C for *C. fulva* [see (Renshaw et al. 2010)] and 60 °C for *S. pictus*}, and 1 min at 72 °C, with a final extension of 20 min at 72 °C. For each species, markers labeled with different dyes (three sets of four loci) were pooled with GeneScan 600 LIZ size standard and Hi-Di formamide to volume and genotyped in a 3500 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). Alleles were identified manually in the software GeneMapper v4.1 (Applied Biosystems). To make allele scoring more precise, the raw size data were transformed using a power function and then rounded in the software TANDEM (Matschiner and Salzburger 2009). Bin sets generated by TANDEM were imported into GeneMapper, and data were reanalyzed using an automated routine. Finally, each genotype was inspected visually twice in order to ensure that alleles were identified correctly.

Genotyping errors caused by the presence of null alleles, large allele dropout, or stuttering were investigated at the population level (only the Columbia population was left out due to low sample size) with MICRO-CHECKER (Van Oosterhout et al. 2004). Markers were analyzed for Hardy–Weinberg Equilibrium (HWE) and Linkage Disequilibrium (LD) using the software Arlequin 3.5 (Excoffier and Lischer 2010), considering a significance level of 0.05. For the HWE test, 1,000,000 steps in the Markov Chain were run and 100,000 steps were sampled. For the LD test, 10,000 permutations were done. Both analyses were performed for each population in separated.

Genetic diversity analyses

For the mtDNA markers, the total number of haplotypes and the haplotype and nucleotide diversities, analyzed in the software DnaSP v5 (Librado and Rozas 2009), and the number of private haplotypes (those observed in only one population) were used to assess the genetic diversity of populations. For microsatellites the total, the effective, and the private number of alleles, the Shannon information index and the expected and observed heterozygosity were calculated in GenAlEx 6.5 (Peakall and Smouse 2012).

Genealogy of mtDNA haplotypes

The genealogies of mtDNA haplotypes were estimated using the topology of maximum-likelihood trees generated by PhyML 3.1 (Guindon et al. 2010) using the method proposed by Salzburger et al. (Salzburger et al. 2011), as implemented in the software Haploviewer. The model of nucleotide substitution that best fits each dataset was inferred in the software jModelTest 2 (Darriba et al. 2012) under the Akaike information criterion. The time of divergence between distinct lineages was estimated using the Bayesian coalescence approach implemented in Beast v1.7 (Drummond et al. 2012). For the CytB, a strict molecular clock of 2% per million years was used, which is the common value used for fishes (Bowen et al. 2001, 2006b, 2006a; Lessios 2008; Reece et al. 2010; Gaither et al. 2011). The age of cladogenetic events observed in CytB was used to calibrate the molecular clock of the CR, assuming clonal inheritance, and then to estimate the age of cladogenetic events observed in the CR but not in the CytB. Simulations were run for 100 million generations with sampling at every 1000 generations and the first 10% being discarded as burn-in. The convergence of the posterior probabilities was checked using Tracer v1.5 (available at http://tree.bio.ed.ac.uk/software/tracer/).

Demographic history

Only sites where more than 20 individuals were sampled were included in population analyses. The Bonferroni correction for multiple comparisons was applied in all tests, considering a significance level (α) of 0.05. The demographic history of each population and haplogroup observed in the mtDNA genealogies was inferred through mismatch distribution analysis performed in Arlequin 3.5. The observed distributions were compared with distributions simulated under pure demographic expansion

(Schneider and Excoffier 1999) and range expansion (Excoffier 2004) models. The sum of square deviations [SSD; (Schneider and Excoffier 1999)] between observed and simulated values and the raggedness statistic [ragged-stat; (Harpending 1994)] were used to test the null hypothesis of recent population expansion. Statistical significances were calculated through the parametric bootstrap method (Schneider and Excoffier 1999) with 10,000 simulations. The parameters θ_0, θ_1, and τ (time since expansion in mutational units) and its 95% confidence interval were estimated using a nonlinear least-square approach (Schneider and Excoffier 1999). The equation $\tau = 2\mu t$, where μ is the mutation rate per site per generation and t is the time in number of generations, was used to calculate the age of the expansion event. The generation time (age at which half of the individuals reproduce for the first time) in *C. fulva* is estimated at two years (Araujo and Martins 2006; Freitas et al. 2011) and in *S. pictus* at one year (based on the generation time of its sister species *Stegastes partitus*; Wilson and Meekan 2002). The same mutation rates used to calibrate the molecular clock were used to calculate the age of expansion. Tajima's D-test (Tajima 1989) and Fu's Fs (Fu 1997) were used to test for departures from mutation-drift equilibrium. Their significance was assessed with 10,000 permutations, using a coalescent simulation algorithm adapted from Hudson (Hudson 1990). All analyses were performed in Arlequin 3.5.

Population structure

Pairwise F_{ST} comparisons and the distribution of genetic variation with analyses of molecular variance (AMOVA) were performed in Arlequin 3.5. In the AMOVA, different scenarios were tested, where populations were clustered in two or three groups. In the first scenario, three populations were tested: continental coast, seamounts, and islands. The second scenario tested the partitioning in two groups, one containing continental coast populations and the other grouping island and seamount populations. From the third scenario on, seamounts were clustered sequentially from the continental coast sites, beginning with the closest (Vitória Seamount), while the other seamounts remained clustered with the islands, thus ending with a last partition, where the continental coast and seamounts composed one group and the islands (the easternmost Trindade and Martin Vaz), the other.

Correlation analyses between the geographic and genetic distance (F_{ST}) among sites were performed using Mantel test and Pearson's correlation using the *mantel* function of the Vegan package in the R-statistical language (Oksanen et al. 2020). Negative F_{ST} values were considered equal to zero. The genetic structure of microsatellite data was assessed using STRUCTURE 2.3.4 (Pritchard et al. 2000), assuming a no admixture model and correlated allele frequencies, and included no prior information on taxon identity. We used a burn-in of 100 K steps followed by another 1000 K MCMC steps. The method of Evanno et al. (Evanno et al. 2005) was used to find the most likely value of K (1–5), as implemented in Structure Harvester (Earl and vonHoldt 2012). The origin and gene flow of the recruits sampled in Trindade Island during two seasons (summer and winter) were also evaluated by the methods described above.

Gene flow

Gene flow between populations along the VTC and continental coast was assessed using the program Migrate (Beerli and Felsenstein 2001; Beerli 2006), to evaluate directionality and what populations significantly contribute to the connectivity between the continental coast and islands. Six coalescent gene flow models were compared based in Bayesian inference, following protocol of Beerli & Palczewski (Beerli and Palczewski 2010). Models were based on two classic gene flow models: Islands (Wright 1943) and stepping stones (Kimura 1953). In the Island model, bidirectional gene flow among all subpopulations was allowed. In the second model, bidirectional flow between adjacent subpopulations was allowed. In this scenario, since Abrolhos, Espírito Santo, and Vitória Seamount are distributed in a triangle, migration among all three locations was equally allowed. From the Vitória Seamount toward the oceanic islands, the subpopulations are linearly distributed and each subpopulation was only allowed to export and import recruits from adjacent subpopulations. The third model (unidimensional stepping stones) was a modification of the second model by not allowing gene flow between Abrolhos and Vitória Seamount—testing whether the Brazil Current could be a barrier for gene flow and suggesting northward eddies and rings as main drivers of connectivity. The fourth model accounts for source and sink subpopulations by modifying the previous model in order to only allow unidirectional gene flow between adjacent populations. The fifth model combines the possibility of gene flow within the island and within the seamounts and the mainland but does not allow for gene flow to occur between the islands and the seamounts/mainland. The last model considers panmixia, where all subpopulations may freely interchange propagules, and random mating among all individuals from all subpopulations is allowed. The log-probability number used for this calculation was obtained by using a Bezier curve and thermodynamic integration [provided in the Migrate outfile (Beerli and Palczewski 2010)].

Results

Our results, based on mitochondrial DNA and microsatellite analyses, show a lack of genetic population structure in Coney, indicating ongoing gene flow along the seamount chain and high connectivity between mainland and islands (Fig. 1a, b, c). Genetic diversity was generally high, especially at the islands (Table S1, S2), and levels of observed heterozygosity matched the expected in all sampled populations (Table S2). Mismatch distribution analyses and Fu's (*Fs*) tests indicated recent population expansion for all Coney populations, which began between 20 and 42 thousand years ago (Table S3, S4).

The Brazilian damselfish, conversely, showed strong genetic structure, with some haplotype groups shared between seamounts and mainland populations, and other haplotypes endemic to the islands and most-distant seamounts (Fig. 1d, e, f). Moreover, in one of the markers, we found support for a widespread genetic lineage originating from an endemic lineage (Fig. 1e II.I). Unexpectedly, genetic diversity of mitochondrial markers was higher at the islands, while microsatellite diversity was similar among populations (Table S1, S2). In general, genetic diversity was lower in Brazilian damselfish compared to Coney (Table S1, S2). Indeed, for the Brazilian damselfish, divergence time of the endemic haplotype group from the coastal lineage was estimated to lay between 149 and 262 kyrs (CytB confidence interval = 95%: 49–261 kyrs, control region, confidence interval = 95%: 90–450 kyrs). Harpending's raggedness (r) and SSD indices did not

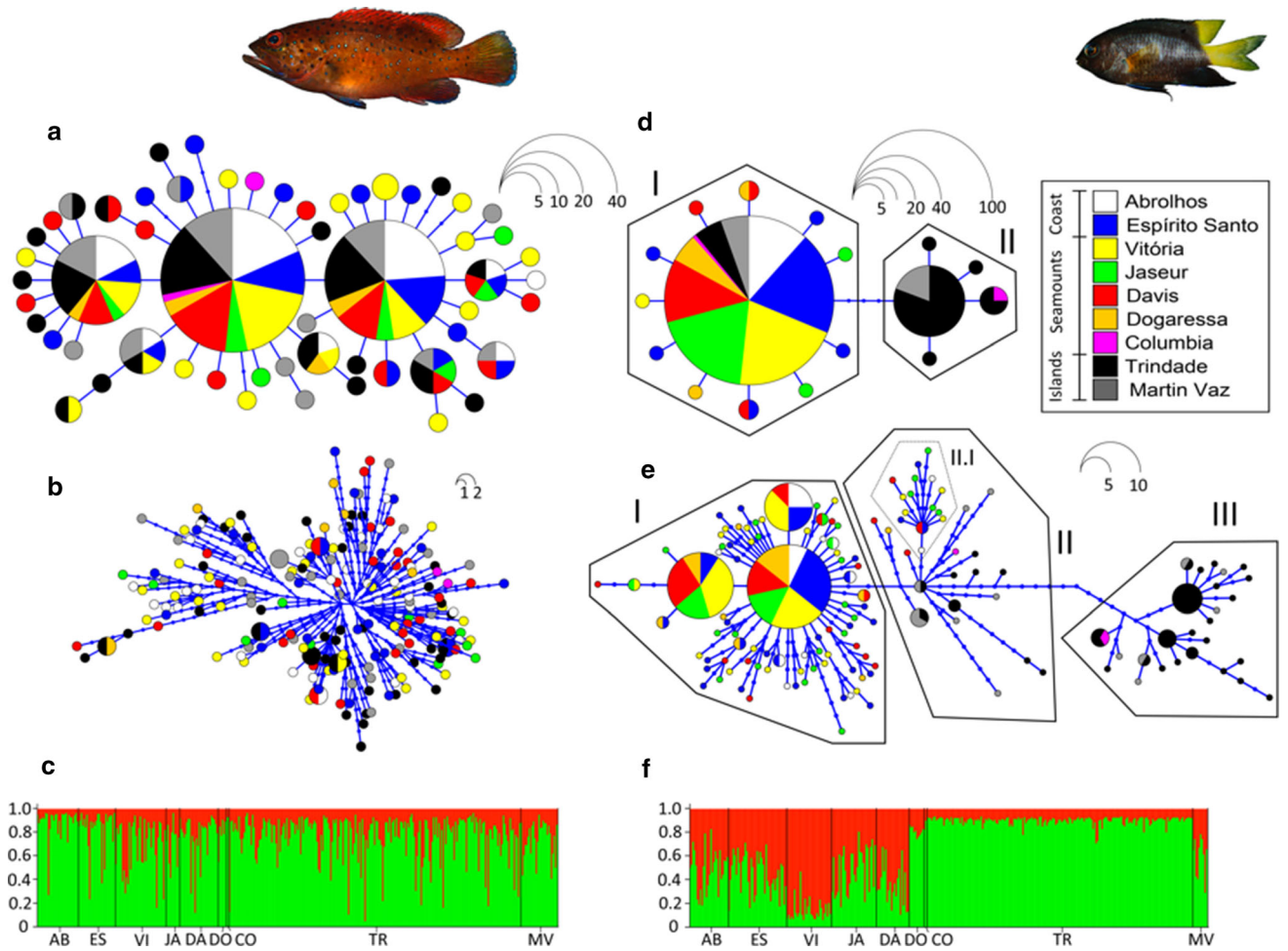

Fig. 1 Haplotype network of CytB (above, **a** and **d**) and D-loop (center, **b** and **e**) and results of the STRUCTURE analysis for the number of clusters $k = 2$ on microsatellites (below **c** and **f**) of *Cephalopholis fulva* (left **a**, **b,** and **c**) and *Stegastes pictus* (right **d**, **e,** and **f**) sampled along the Vitória-Trindade Chain. In the networks, each circle represents a distinct haplotype, the diameter its frequency, and the colors the sampling region. The line between haplotypes represents a mutation and each dot on the line an additional mutation. *Stegastes pictus* genealogies are divided in different haplogroups (I, II, II.I, and III). In the results of the STRUCTURE analysis, each bar represents an individual sample and the probability of belonging to one or other group is indicated by the color. Black bars separate subpopulations: AB = Abrolhos, ES = Espírito Santo, VI = Vitória, JA = East-Jaseur, DA = Davis, DO = Dogaressa, CO = Columbia, TR = Trindade and MV = Martin Vaz

deviate from the growth decline model, showing two modes (Table S5), and neutrality tests (*D* and *Fs*) suggested recent population expansion for all haplotype groups (Table S4), between 4 and 115 kyrs for the ancestral group and between 18 and 40 kyrs for the seamounts islands group (Table S5).

Structure analyses based on microsatellites showed that, for both species, the most likely number of population groups is two (Fig. 1c, f). However, all Coney populations present ≥ 0.69 probability of belonging to the same population, whereas for the Brazilian damselfish, some seamounts and islands presented ≥ 0.80 probability of belonging to a different population (Fig. 1c). Pairwise genetic divergence analyses (F_{ST}) for both mtDNA and microsatellites did not show any significant values for the Coney (Table S6). AMOVA tests showed that nearly 100% of the genetic variation is found within populations (Table S7), and no isolation by distance was found (CytB: $R^2 = 0.3819$, $p = 0.1333$; control region: $R^2 = 0.4605$, $p = 0.0611$; microsatellites: $R^2 = 0.2013$, $p = 0.2097$; Figure S1).

In the Brazilian damselfish, mtDNA F_{ST} analyses showed that the Trindade Island population significantly differed from all others (Table S8). Microsatellite F_{ST} analyses showed that the Trindade population differed only from populations from the mainland and the furthest seamount from the island (Table S8), a scenario corroborated by significant AMOVA results (Table S9). AMOVA tests also showed that most of the genetic variation was found within populations (Table S9). Mantel tests showed isolation by distance for all genetic markers (CytB: $R^2 = 0.7726$, $p = 0.0583$; control region: $R^2 = 0.7706$, $p = 0.0333$; microsatellites: $R^2 = 0.6861$, $p = 0.0166$), but only the microsatellites data seem to follow a pattern of isolation by distance as expected for a stepping stones model (Hutchison and Templeton 1999) (Figure S1).

STRUCTURE did not show an apparent gradient of genetic structure (as predicted by an isolation by distance or stepping stones model), thus favoring an island model of dispersal. However, among all tested gene flow models, the best fit for both species was the "unidimensional stepping stones," where the mainland populations disperse southward and northward on the Brazilian coast, and from the southern population toward the seamounts and oceanic islands and vice-versa (Fig. 2; Table S10). The haplotype networks of both species corroborate this result, showing that the southern coastal population shares more haplotypes with the VTC than the northern population (Fig. 1).

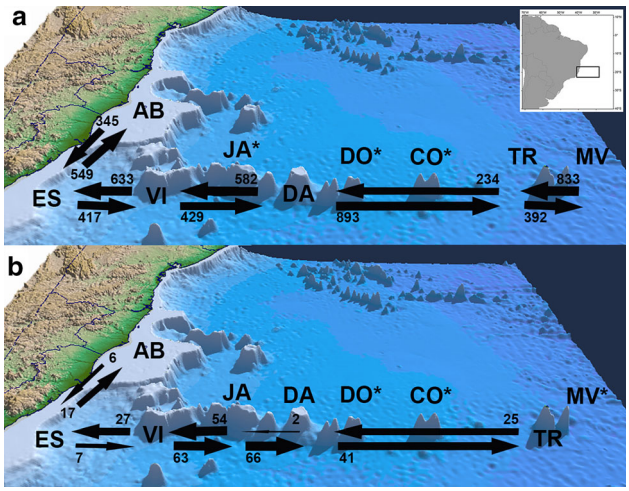

Fig. 2 Unidimensional stepping stones model (the best-fitting gene flow model) and Migrate values for microsatellites data for **a** *Cephalopholis fulva* and **b** *Stegastes pictus* in the Vitória-Trindade Chain. Arrows' width is calibrated following migrate data. (AB) Abrolhos Shelf, (ES) Espírito Santo southern shelf, (VI) Vitória Seamount, (JA) East-Jaseur Seamount, (DA) Davis Seamount, (DO) Dogaressa Seamount, (CO) Columbia Seamount, (TR) Trindade Island, and (MV) Martin Vaz Archipelago. *Site not included in the analysis due low sampling number

Discussion

Species with different biological traits have distinct levels of gene flow between seamounts and oceanic islands, a characteristic shared with deeper habitat invertebrate species such as gastropods and ophiuroids (Samadi et al. 2006; Cho and Shank 2010). Demography and dispersal characteristics often influence spatial sorting and drive evolution (Ochocki et al. 2020). However, in the dispersive aquatic medium, the relationship between specific biological traits and genetic structure or distribution range is uncertain (Selkoe et al. 2014; DiBattista et al. 2017). In this study, the Coney shows high connectivity along the entire chain, whereas the Brazilian damselfish subpopulations situated at the end of the chain are significantly different (despite low ongoing migration of individuals—Fig. 2). Further, similar to the Brazilian damselfish, most of the VTC endemic fishes inhabit shallow waters, lay demersal eggs, and are small and weak dispersers, but comprise populations that have been isolated within the volcanic chain for longer periods (Pinheiro et al. 2017). For instance, the youngest endemic, the Blenny *Entomacrodus* sp.n., shows an estimated age of 0.61 My (using CytB), or four times older than the Brazilian damselfish endemic lineage (Pinheiro et al. 2017). The evolutionary history of these weak dispersers seems to be influenced by vicariance events; they reach the most remote sites during sea level lowstands when at least nine seamounts of the VTC are exposed as islands, decreasing the distance between intertidal shallow

waters from 1200 to around 100 km, forming a dispersal corridor along the chain (Macieira et al. 2015). Then, these populations become isolated during high sea level stands, when seamounts sink to depths beyond their limit. However, the same intermittent avenue that allows colonization also supports the export of endemic lineages back to the coast through the biodiversity feedback process (Bowen et al. 2013). Like *S. pictus*, the VTC endemic lineage of the goby *Elacatinus pridisi*, found along the whole volcanic chain, also seems to have spread back toward the coastal population (see Fig. 3a in Pinheiro et al. 2017), indicating that biodiversity feedback occurred multiple times in the Pleistocene.

The biodiversity feedback process, nevertheless, is rarely considered in the origin of diversity when compared to other modes. Previous evidence for this process includes exchange in lineages and species between the Brazilian Province and the Caribbean (Rocha et al. 2008), and between Hawaii and the western Pacific (Bowen et al. 2013). Peripheral oceanic islands and marginal provinces are also a cradle of species (Hodge et al. 2012; Pinheiro et al. 2018), presenting endemism hotspots that work in synergy with diversity hotspots, enhancing ocean biodiversity (Bowen et al. 2016). In the VTC, endemic lineages and species are mostly found in the extreme east of the chain, which are the geologically youngest volcanic spots. According to the general dynamic model of island biogeography of marine organisms, speciation might occur during the whole evolutionary history of the island, reaching the highest rates when islands are in advanced erosion and sharply decreasing during the island subsidence (Pinheiro et al. 2017).

During lowstand sea levels in glacial periods, continental shelves and seamounts emerge and often have their shelf area considerably contracted (Ludt and Rocha 2015), consequently affecting the population size of shallow water species (Ludt et al. 2012; Liedke et al. 2020). Therefore, the wider bathymetric range of the Coney may have favored its stronger connectivity along the VTC. However, following our findings from the mismatch distributions (Table S3), the star-shaped haplotype networks from most studied populations (Fig. 1) indicate effects of bottlenecks followed by population expansion (Slatkin and Hudson 1991; Marjoram and Donnelly 1994; Galtier et al. 2000; Depaulis et al. 2003). Thus, our results show that the reduction in the reef area driven by lowstand sea levels is causing a bottleneck and subsequent highstand expansion on populations found on upper mesophotic reefs of the VTC's seamounts. This phenomenon might also explain the extinction events on seamounts that resulted in disjunct distributions, where many species are found in the islands and along the mainland but not on seamounts (Pinheiro et al. 2015; Mazzei et al. 2021).

The Brazilian damselfish population from the islands, on the other hand, showed no sign of a bottleneck. This result was unexpected because the islands present a much smaller reef area compared to many seamounts and the continental coast, what in a context of island biogeography could affect populations persistence. However, the subtidal reef area of these environments did not change as much as the continental shelf and seamounts, since their tops have remained emerged (even during sea-level highstands), allowing the persistence of a stable population. Similar results were observed for fishes that exclusively inhabit lagoon and slope environments in the Indo-Pacific (Fauvelot et al. 2003; Ludt et al. 2012). Thus, remote islands seem to represent refuges for extinctions caused by Pleistocene sea level fluctuations, and likely promote evolutionary changes in weak dispersers.

As direct connectivity between many reef fish populations is suggested to be limited to only 10–150 km (Palumbi 2003; Cowen et al. 2006), the stepping stones mode of dispersal seems to be one of the most important processes to maintain and expand geographic ranges (Cho and Shank 2010; Crandall et al. 2012). In fact, both species assessed in our study showed that the most probable model of dispersal was the unidimensional stepping stones. This dispersal strategy could benefit several marine species that maintain high levels of genetic connectivity over a distribution of tens of thousands kilometers (Eble et al. 2011). However, despite evidence that populations import and export migrants between adjacent oceanic populations, the unidimensionality of the model (low gene flow between Abrolhos Shelf and the VTC) suggests that the Brazil Current has historically (evolutionary time scale) acted as a barrier, instead of a driver, of genetic connectivity, setting current (ecological time scale) constraints for dispersal and establishments in the VTC (Mazzei et al. 2021). This result also suggests the importance of eddies and northward rings driving connectivity between the continental shelf and the seamounts (Gaeta et al. 1999; Mill et al. 2015; Costa et al. 2017). In the north Atlantic, similarly, the Gulf Stream is responsible for preventing gene flow between areas a few kilometers apart (Colin 2003, 2010; Dennis et al. 2005; Taylor and Hellberg 2005), as well as connecting the Florida mainland to remote Bermuda (Rocha et al. 2005). Studying ophiuroid populations from North Atlantic seamounts, Cho and Shank (2010) have found a similar result, where hydrographic dynamics drive stepping stones dispersal, isolation by distance, and genetic structure in different species.

Our results indicate that seamounts are important to the connectivity between the continental shelf and oceanic islands, in both ecological and evolutionary timescales, and that their role varies between species with distinct biological traits. In addition to creating opportunities for dispersal

and diversification, seamounts seem to also have a role in the biodiversity feedback processes, helping connect lineages originated in the periphery back toward higher biodiversity areas.

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