



Mechanisms of dispersal and establishment drive a stepping stone community assembly on seamounts and oceanic islands

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Abstract

The mechanisms driving the ecology and biodiversity of seamount communities are still unclear. Here we analyzed the distribution and species traits of reef fish species recorded over seamounts, oceanic islands, and the continental shelf of the southwestern Atlantic Ocean to understand the influence of mechanisms of dispersal and establishment in these ecosystems. Species richness did not decrease with distance from the mainland, and community composition was not related to geographic position and geological history of seamounts and oceanic islands. Similarity among sites was explained by habitat heterogeneity, shallowest depth, and distance from mainland. Inter-site isolation had a significant influence on the spatial turnover of species. All species traits related to dispersal and establishment worked as ecological filters driving the composition of communities and distribution of species along seamounts and oceanic islands. We conclude that seamount communities are closely related to those of oceanic islands, with the stepping-stones (inter-site isolation) process being the most important one shaping species composition and distribution. Establishment and dispersal mechanisms, in combination with historical sea-level fluctuations, regulate the persistence of species and the similarity of communities among adjacent and environmentally similar sites.

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Introduction

Hundreds of thousands of seamounts exist in the oceans (Wessel et al. 2010). Together, they constitute one of Earth's most common biomes (Etnoyer et al. 2010). However, they are among the least scientifically known ecosystems (Clark et al. 2012). Less than 600 seamounts have been biologically surveyed (Kvile et al. 2014), and the poor sampling of these environments prevents the

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evaluation of important paradigms, such as the role of seamounts as stepping stones for dispersal and hotspots of species richness (Rowden et al. 2010). Seamounts are volcanic mountains in development, or the result of erosion and subsidence of old islands and atolls (Stuessy et al. 2012). These volcanic buildings contribute to oceanographic processes that regulate local primary production (Genin 2004; Meirelles et al. 2015), and can hence be considered as functional islands (FIs), or isolated marine oases of suitable habitat for a number of species (Hart and Pearson 2011; Pinheiro et al. 2014). The ecological and evolutionary mechanisms that regulate their communities are suggested to match those observed in islands (Pinheiro et al. 2015a; 2017). Similarities between seamounts and oceanic islands include the balance between immigration and extinction (Losos and Ricklefs 2009; Pinheiro et al. 2017), habitat area (Heaney 2007; Losos and Ricklefs 2009), geological history and oceanographic features (Hobbs et al. 2012; Keith et al. 2013; Pinheiro et al. 2017).

Seamounts might also work as stepping-stones for reef-associated species (Hubbs 1959; Rowden et al. 2010), connecting meta-populations and creating avenues for dispersal (Macieira et al. 2015; Pinheiro et al. 2017). Ecological characteristics (i.e., species traits), such as body size, depth range, use of rafting might contribute to meta-population connectivity and geographical range sizes (Luiz et al. 2013). Besides, these traits can determine species ability to inhabit oceanic islands (Pinheiro et al. 2018) or to cross biogeographic barriers (Luiz et al. 2012). In addition to the importance of species dispersal capabilities for ecological and evolutionary processes (Pinheiro et al. 2017), mechanisms responsible for the establishment of species have also been highlighted as critical in determining the composition of reef communities (Keith et al. 2015).

Here, we explore the ecological factors that drive the distribution and composition of fish communities on the seamounts and oceanic islands of the Vitória-Trindade Chain (VTC), in the Southwestern Atlantic. The VTC seamounts have been proposed as stepping-stones that support the marine biodiversity found in the insular complex situated at the end of the chain (Floeter and Gasparini 2000; Joyeux et al. 2001; Coimbra and Carreño 2012; Pinheiro et al. 2015a). Reef fish endemism level at the islands is high (9.6%) (Simon et al. 2013a) and similar to that of other remote oceanic islands in the Atlantic such as St. Paul's Archipelago and Cape Verde (Floeter et al. 2008; Hachich et al. 2015). This high endemism has been explained by vicariant events caused by sea level fluctuations which exposed seamounts and created shallow habitats, thus contributing to the dispersal and subsequent isolation of weak colonizers (Macieira et al. 2015; Pinheiro et al. 2017). Other studies investigated the effect of geographical isolation on invertebrates and algae, highlighting the continental shelf

as an important source of propagules (Leal and Bouchet 1991; O'Hara et al. 2010).

In this study, we assessed the composition and richness of fish communities along the Vitória-Trindade Chain. Specifically, we focused on seamounts, islands and continental shelf adjacent to the VTC. We evaluated predictions from the contemporary island biogeography theory (MacArthur and Wilson 1967; Hachich et al. 2019) in seamounts, namely: (1) species richness and similarity decrease from mainland to oceanic sites and (2) geographic position and geological history of sites affect the similarity between species communities. We further analyzed the role of the continental shelf as a potential source of propagules, and its influence on the assembly of fish communities along the seamount chain and oceanic islands. Specifically, we used the beta diversity among sites to test three hypotheses about community assembly: (1) The "target-area-distance effect" (or propagule rain) hypothesis whereby available shallow area of seamounts and oceanic islands (FIs), as well as their distance from the purported source (continental shelf), determine the community composition at each site. In this model, a positive correlation between beta diversity and the inter-FI dissimilarity (built from Z scores composed by FI area and distance from the mainland) is expected (Fattorini 2010). (2) The "stepping stones" hypothesis, in which beta diversity results from the amount of faunal exchange between FIs and a positive correlation between dissimilarity and inter-FI isolation (geographic distance) is expected (Fattorini 2010). (3) The "island age" hypothesis predicts a correlation between beta diversity and site age, as a result of the balance between colonization and extinction, and a higher similarity in composition among sites of similar age is expected (as proposed by Fattorini 2010).

Finally, we assessed major ecological drivers of dispersal and the ecological filters of establishment that may regulate the distribution of reef fishes on seamounts and oceanic islands, by analyzing key species traits related to dispersal (body size, mobility, and rafting behavior) and establishment (habitat use, brackish water requirements and depth range). We hypothesize that species with larger body size, greater mobility and ability to use rafting would have higher dispersal potential (Luiz et al. 2013; Pinheiro et al. 2018) and, therefore, a wider geographical distribution along the seamounts and oceanic islands. In addition, we hypothesize that species geographical distribution would be constrained by ecological filtering associated with habitat specialization and dependency to brackish or shallow waters (Pinheiro et al. 2018).

Methods

Study area

The study was carried out in the Southwestern Atlantic, in a region that encompasses the VTC and the continental shelf from the north of the Abrolhos Bank to the south of the Espírito Santo state (Fig. 1). The VTC is composed of approximately 30 seamounts and the Trindade-Martin Vaz insular complex (TMVIC). The VTC was formed by the activity of a stationary hotspot (Ferrari and Riccomini 1999), beginning its activity during the Cenozoic (60–40 Mya; Mohriak 2020). The age of the seamounts and islands decreases from west to east (Table 1), with more recent activity forming the TMVIC around 5 million years ago (Mohriak 2020). The seamounts are separated from the continental shelf and from each other by deep water (1000–4500 m deep) and moderate distances (50–250 km

away), forming a 1000 km west–east chain that ends in the TMVIC (Fig. 1).

Surface circulation is dominated by the Brazil Current (BC) which follows three different paths perpendicular to the VTC (Evans and Signorini 1985). The main flow is between Besnard and Vitória seamounts, followed by a second and more offshore flux between Vitória and Jaseur seamounts. The third and weakest path occurs between the Abrolhos Bank and Besnard seamount (Ghisolfi et al. 2015; Lemos et al. 2018). The BC becomes unstable after crossing the VTC and reorganizes itself as a single jet just south of 21°S. Within the Tubarão Bight (Fig. 1), the hydrodynamics is complex, with the presence of offshore eddies and coastal upwelling (Schmid et al. 1995; Gaeta et al. 1999; Mill et al. 2015). Because of the strong southward flow, the BC may constrain dispersal of organisms between the mainland and the VTC (Pinheiro et al. 2015a). Northward-moving cyclonic eddies, generated along the shelf break, reach the seamounts of the VTC (Costa et al. 2017).

Fig. 1 The studied region, showing mainland continental shelf (state of Espírito Santo and Abrolhos Bank) and the Vitória-Trindade Chain (VTC). The eight sampled seamounts and islands of the VTC are shown. Areas above water are in black, while shades of white to gray indicates depth range. Bathymetric data from Amante & Eakins (2009)

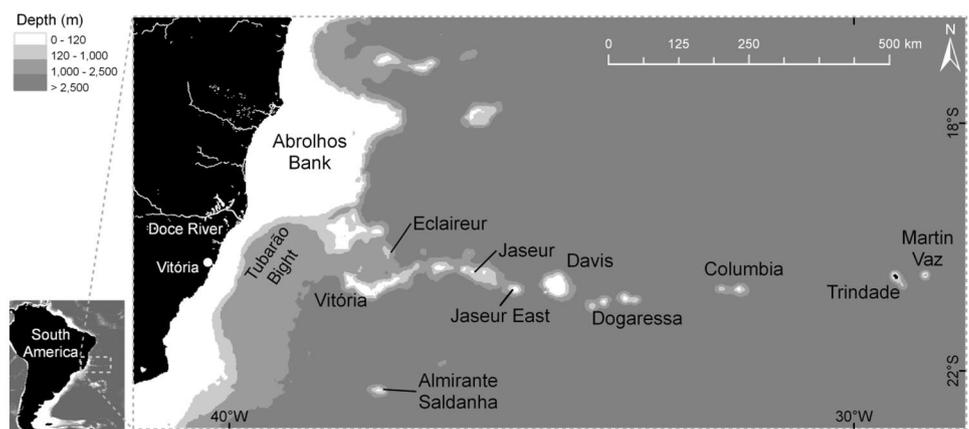


Table 1 Summary of the environmental characteristics of the sampling sites

| Site | Summit area (km ²) | Distance (km) | Inter-FI isolation (km) | Substrate type | Age (Ma) | Depth studied (m) |
|--------------------|--------------------------------|---------------|-------------------------|----------------|----------|-------------------|
| Vitoria | 1184 | 170 | 37 | RH/RS/PR/SD | 41.28 | 35–120 |
| Almirante Saldanha | 37 | 235 | * | RH/SD | * | 66 |
| Eclairer | 6.4 | 107 | 37 | RH/SD | 38.22 | 71 |
| Jaseur | 89 | 272 | 40 | RH/RS/SD | 32.05 | 62 |
| Jaseur East | 99 | 316 | 40 | RS/RH/PR/SD | 29.25 | 62 |
| Davis | 1002 | 386 | 48 | RS/RH/PR/SD | 26.94 | 17–57 |
| Dogaressa | 80.5 | 500 | 102 | RH/SD | 20.49 | 65 |
| Columbia | 36.5 | 670 | 168 | RH/SD | 12.79 | 84 |
| Trindade | 85 | 915 | 40 | RS/RR/PR/RH/SD | 3.69 | 0–85 |
| Martin Vaz | 24 | 960 | 40 | RR/PR/SD | 1.2 | 0–30 |

Distance distance from the nearest continental shelf, *Inter-FI isolation* geographical distance between the closer functional island. Substrate type, *RS* reef structure (carbonate), *RR* Rocky reef, *PR* patch reef, *RH* Rhodolith bed, *SD* Sand and unconsolidated substrate

*Not estimated

Rhodolith beds composed of free-living calcareous nodules of coralline algae are the dominant habitat on the summits of the seamounts and the adjacent continental shelf between 40 and 120 m (Pereira-Filho et al. 2011; Amado-Filho et al. 2012). Such habitats are covered by dense macroalgae canopies (Pereira-Filho et al. 2011; Amado-Filho et al. 2012; Dias and Villaça 2012), mainly on the westernmost seamounts (e.g., Vitória, Eclairer, and Almirante Saldanha; Lavrado and Ignacio 2006; O'Hara et al. 2010). The Abrolhos Bank also harbors the most developed coral reefs in the Southwestern Atlantic (Leão et al. 2003; Mazzei et al. 2016) and extensive rhodolith beds (Amado-Filho et al. 2012). Biogenic complex reefs are found in low density on the seamount summits (Pinheiro et al. 2014), whereas rocky reefs sparsely covered with reef building corals are the main habitat of the TMVIC (Pinheiro et al. 2015a).

Fish database

A comprehensive presence/absence reef fish database (Appendix S1: Table S1, Supplementary file) was built based on literature data and primary observations from underwater visual censuses, images from remote operated vehicles (ROV), and commercial fishing records. To ensure that most species present at each site were reported, this database contains only species belonging to the 40 fish families that are typically associated with reef habitats (Thresher 1991; Floeter and Gasparini 2000), and considered both the euphotic and mesophotic zones (0–150 m) (Pinheiro et al. 2015a; Fig. 1). The continental shelf dataset encompasses the fish composition from the Abrolhos Bank (Moura and Francini-Filho 2005; Simon et al. 2016) and the continental shelf of the Espírito Santo State, south of the Doce River mouth (Floeter et al. 2007; Simon et al. 2013b; Pinheiro et al. 2015b), a region that shelters the highest fish diversity in the southwestern Atlantic (Pinheiro et al. 2018).

Species were classified according to traits associated with dispersal and establishment in seamounts and oceanic islands. These traits were compiled from the literature (Böhlke and Chaplin 1993; Carvalho-Filho 1999; Luiz et al. 2012; 2013; Froese and Pauly 2018; Quimbayo et al. 2021) and complemented with primary data obtained here. The dispersal traits considered were: maximum body size (total length in cm); mobility, organized in three order categories: sedentary (species that don't usually move more than a few meters), roving (species that move within reefs and between adjacent reefs) and highly mobile (species that are able to cross large oceanic extents and move between seamounts and islands); and the ability to raft with floating objects, which is an important mechanism of dispersal in reef fishes (Luiz et al. 2012; 2013), and was considered a binomial variable (i.e., presence or absence). We considered as establishment traits the maximum depth (*m*), as compiled from the

literature and primary records; the multi-habitat use, based on whether a species inhabits multiple habitats or not; and brackish-water dependency, another binomial variable, which indicates whether a species requires coastal or estuarine habitats to complete its life cycle.

Data analysis

Spatial structure of communities

To summarize the relationship among sites based on fish community composition (presence/absence), a cluster analysis was run using a Jaccard similarity matrix and the unweighted pair group method with arithmetic mean (UPGMA; Clarke and Warwick 2001), which minimizes differences in sample size (Kreft and Jetz 2010; Fattorini 2010). To minimize the effects of FI habitat variability (Table 1) and to facilitate regional biogeographical inferences, analyses of similarity and richness were run for the entire region organized into five groups of sites: continental shelf (mainland), three seamount groups (SG) with increasing distance from mainland (SG I: Vitória, Eclairer and Almirante Saldanha; SG II: Jaseur and Jaseur-East; and SG III: Davis, Dogaressa and Columbia), and the two islands pooled (TMVIG).

Assembly of fish communities

To test the target-area-distance hypothesis, distances between mainland and studied sites were measured as the shortest linear geographic distance between the 120 m isobaths, and the surface area of summits was calculated based on the 120 m isobaths (Table 1). Because distance (km) and area (km²) are expressed in different units, they were standardized to Z scores [$Z = (\text{raw score} - \text{mean}) / \text{standard deviation}$], and an inter-FI distance matrix was computed using Euclidean distance over Z scores (Dapporto and Cini 2007; Fattorini 2010). To test the stepping stones hypothesis, we built a matrix of inter-site distances, where distances between sites were measured as the shortest linear geographic distance considering the 120 m isobaths. To test the island age hypotheses, age estimates for the studied sites were compiled from Ferrari and Riccomini (1999), and a matrix built using absolute values of age differences between sites (Fattorini 2010). Beta diversity was estimated as the difference (turnover) between species composition among sites (Koleff et al. 2003). Beta diversity matrices were generated using the Jaccard (J) coefficient, which minimizes the influence of differences in sample size and is considered the most appropriate to measure changes in taxonomic dissimilarity (Fattorini 2010; Villéger and Brosse 2012). Correlations between matrices (beta diversity and the three independent variables described for each hypothesis above) were

performed with a Mantel test using the PAST 2.17 software (Hammer et al. 2001). The Almirante Saldanha seamount was excluded from the FI analyses due to its long latitudinal distance from the seamounts of the VTC (~ 180 km to the south).

Ecological drivers of dispersal and establishment

To examine potential collinearity amongst the dispersal and establishment traits, we used Pearson correlation, considering a $r < 0.70$ as a cut-off value for keeping the traits in the model, since correlations below this threshold are not affected by multicollinearity (Dormann et al. 2013). In addition, we estimated the variance inflation factor (VIF) with the function “VIF” from the car package (Fox et al. 2020) to ensure that predictors were not correlated with each other, considering a value < 2 as a cut-off (Dormann et al. 2013). We did not observe any correlation or VIF values > 2 among the dispersal and establishment traits and therefore maintained all the traits in our model. To test the influence of dispersal and establishment traits (i.e., fixed factors) on the distance of each species from the continental shelf, we built a Generalized Linear Mixed Model (GLMM) with Poisson distribution and link-function (log), considering taxon (genus nested within family) as random factor. The model was built using the function “*glmmTMB*” from the *glmmTMB* package (Magnusson et al. 2020). We used the “*dredge*” function from the MuMIn R package to run a complete set of models with the possible combinations of the fixed effects and determined the subset of “best models”, which usually present $\Delta AIC < 2$. We then further evaluated the significance of all traits in the “best model” using likelihood ratio tests (LRTs), and calculated significant differences in model fit based on χ^2 distributions.

Results

Spatial patterns of biodiversity

A total of 247 species belonging to 40 reef fish families were recorded. Sixty-nine species (27 families, 28% of total species) are widely distributed across the studied region. Twenty-seven species (19 families, 11%) have a disjunct (~ 1,000 km gaps) regional distribution, occurring around the islands and on the continental shelf, but not on seamounts. Twenty-seven species occur exclusively on FIs (11 families, 11% of species), but not on the continental shelf. One hundred and thirty-two species (32 families, 53%) are absent from the islands and 88 (27 families, 35%) are restricted to the continental shelf (state of Espírito Santo and Abrolhos Bank). Eighteen species found across the region are endemic to the Brazilian Province (~ 7% of total species),

while 12 of them are found exclusively on FIs (~ 7% of the VTC, and 9.6% of the island biodiversity), with richness of endemics decreasing toward the continental shelf (Appendix S1: Fig. S1, Supplementary file).

Spatial structure and assembly of fish communities

The similarity analysis clustered sites into two major groups, each one with two sub-groups (Fig. 2a). The first group consisted of the two continental shelf sites (Abrolhos and Espírito Santo) and five VTC sites: the TMVIC and the three seamounts with the greatest habitat heterogeneity and shallowest summits (Vitória, Davis and Jaseur-East; Fig. 2a). The second group was composed by the sites with lower habitat heterogeneity (Table 1): the two easternmost, smallest, and deepest seamounts (Dogaressa and Columbia) and three seamounts relatively closer to the mainland (Almirante Saldanha, Eclairer and Jaseur; Fig. 2a). The similarity analysis among the five pre-established groups of sites showed that the continental shelf shared more species with the islands than with the closest seamounts (Fig. 2b). However, a higher overall similarity between islands and seamounts was observed, with a trend of decreasing similarity with increasing distance from the TMVIC (Fig. 2b). Richness did not decrease with distance from the mainland (Fig. 2a, b), and clustered sites have affinities in terms of habitat heterogeneity, shallowest depth and species richness (Table 1).

Highest community dissimilarity (beta-diversity) was found on the edges of the VTC, between mainland and seamounts and between seamounts and islands (Fig. 3a). Community turnover between groups of sites suggests that dissimilarity was particularly high between the mainland and the closest seamounts, decreasing towards the islands (Fig. 3b). The Mantel test detected inter-FI isolation as the most important structuring force to the assembly of fish communities on seamounts and islands ($R = 0.32$; $P = 0.04$). This result is in accordance with the “stepping-stones” hypothesis in which sites closer to each other have higher similarity. Effects of distance from a putative mainland source were not significant, even when accounting for summit area ($R = -0.19$; $P = 0.81$) or geological age ($R = 0.33$; $P = 0.56$), consequently refuting the “target-area-distance” and “age” hypotheses.

Ecological drivers of dispersal and establishment

Our model analysis pointed to the full model as the most adequate (the only one with $\Delta AIC < 2$; Table S2). The likelihood ratio tests run over the full model showed that all traits significantly influenced the species distribution range (Table 2). As expected, the model estimate showed that body size, ability to raft, multi-habitat use presented

Fig. 2 **a** Cluster analysis of the reef fish communities from the Vitória-Trindade Chain (VTC) region. The number of species per site is given. Four sub-groups of sites are highlighted: Mainland (yellow), the two islands and the three larger and shallow seamounts (blue), three seamounts relatively close to mainland and the two easternmost and deepest seamounts (green), and two relatively close to mainland seamounts and the southernmost seamount (red). **b** Similarity within the VTC regional compartments (group of sites). Number inside the ellipse refers to reef fish richness. Values outside ellipses refer to the number of species shared and Jaccard similarity between compartments (SG I: Vitória, Eclairer and Almirante Saldanha; SG II: Jaseur and Jaseur-East; SG III: Davis, Dogaressa and Columbia; TMVIC: Trindade Island and Martin Vaz Archipelago)

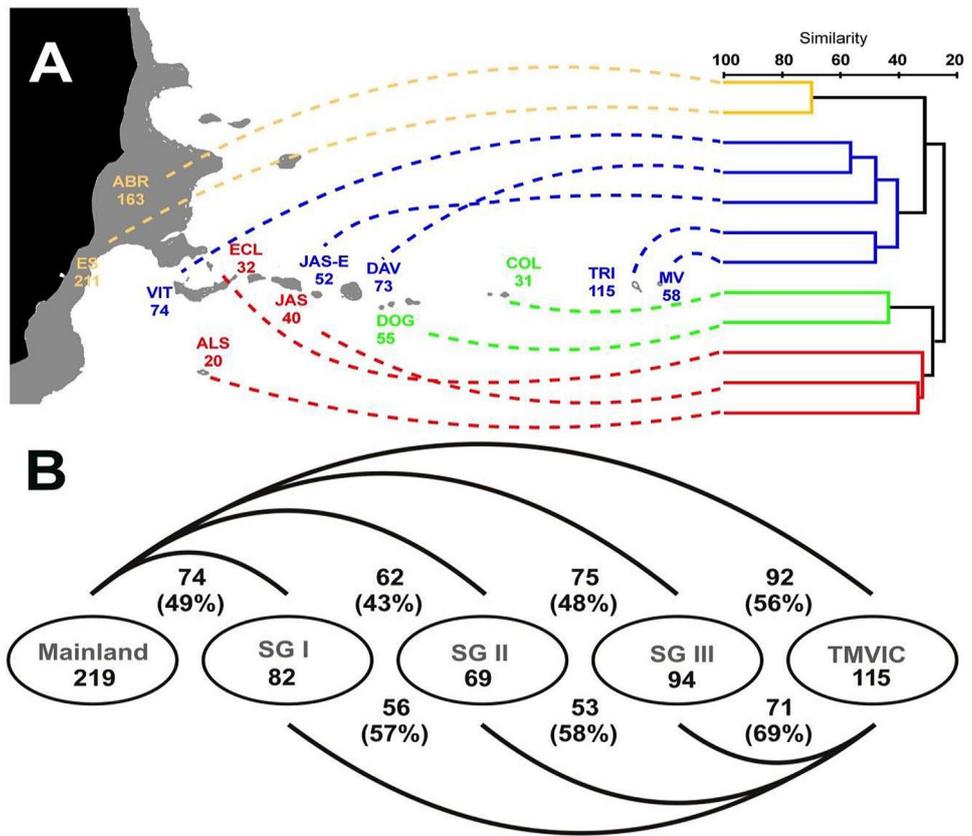
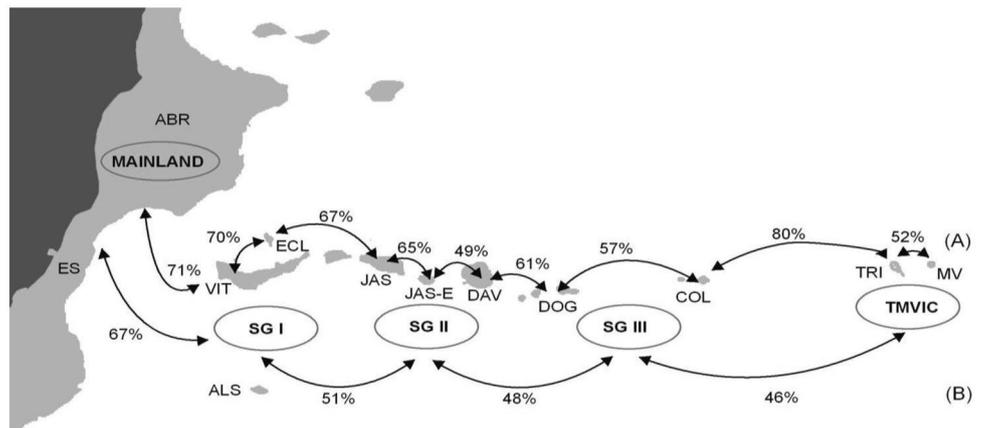


Fig. 3 Community turnover (beta diversity) along the VTC region between each location and its neighbors **a** and between consecutive regional compartments (group sites) **b** (Jaccard coefficient). The proportion refers to community dissimilarity between regional compartments (SG I: Vitória, Eclairer and Almirante Saldanha; SG II: Jaseur and Jaseur-East; SG III: Davis, Dogaressa and Columbia; TMVIC: Trindade Island and Martin Vaz Archipelago)



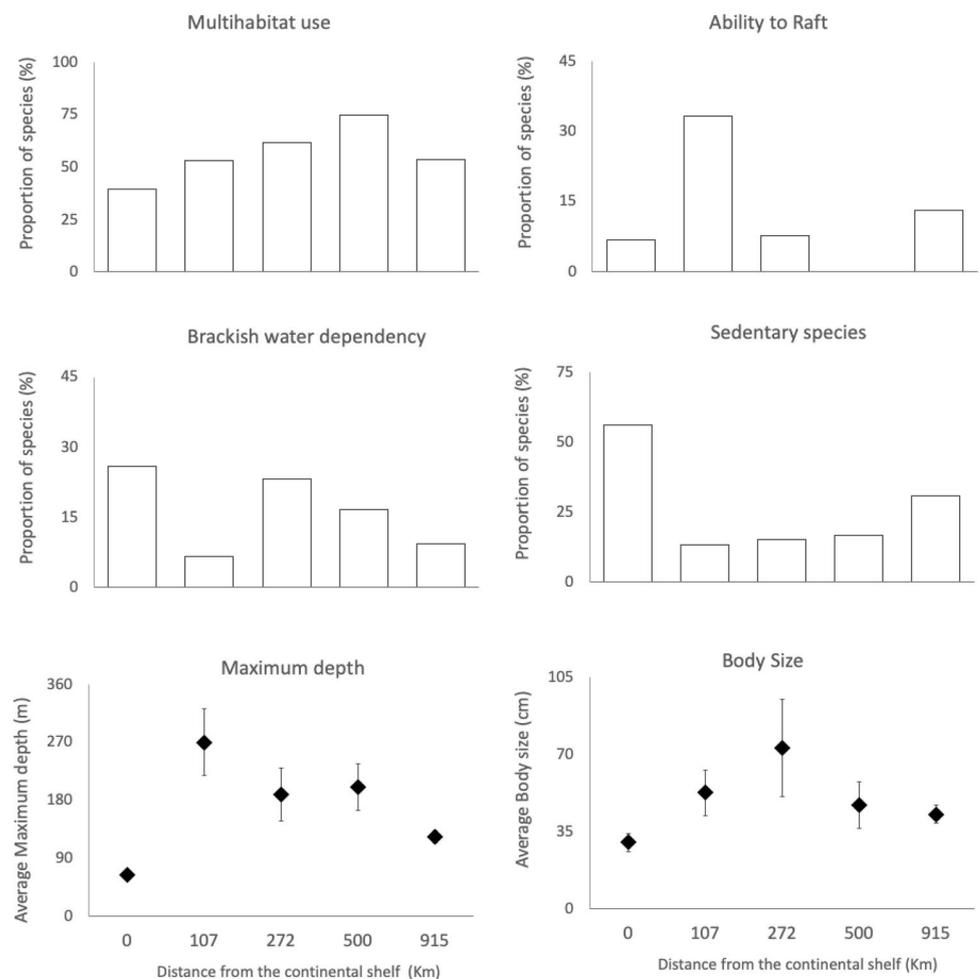
a positive relationship with the maximum distance from continental shelf, while brackish dependency was negative (Table 2). However, differently to our predictions, maximum depth showed a negative relationship, and sedentary mobility a positive relationship, with maximum distance from continental shelf (Table 2). These unexpected trends were mainly driven by the species found in the islands, at the end of the chain, which showed intermediate characteristics (Fig. 4). For instance, insular species showed a lower average of maximum depth and higher proportion

of sedentary species compared with seamounts, and higher average of maximum depth and lower proportion of sedentary species compared with the continental shelf (Fig. 4). Notwithstanding insular characteristics, and accordingly to our predictions, a general higher proportion of multi-habitat users and of rafting-capable species, as well as higher averages of body size, were found on oceanic sites compared to species restricted to the continental shelf, while the opposite pattern was shown by brackish water dependent species (Fig. 4).

Table 2 Summary of the generalized linear mixed model statistics for the effects of species traits over the distribution of reef fishes along the VTC

| | Estimate | SE | z value | LRT | VIF |
|---------------------------------|----------|------|---------|--------|------|
| Intercept | 2.32 | 0.53 | 4.33 | | |
| Dispersal traits | | | | | |
| Body size (cm) | 2.90 | 0.01 | 20.32 | 414.25 | 1.70 |
| Mobility | | | | | |
| Sedentary | 8.28 | 0.05 | 17.97 | 336.12 | 1.33 |
| Roving | 6.87 | 0.04 | 17.55 | | |
| Rafting | | | | | |
| Yes | 1.48 | 0.03 | 4.40 | 19.08 | 1.10 |
| Establishment traits | | | | | |
| Depth (m) | -4.82 | 0.00 | -7.24 | 52.69 | 1.14 |
| Multi-habitat | | | | | |
| Yes | 1.72 | 0.01 | 12.83 | 165.71 | 1.03 |
| Brackish-water | | | | | |
| Yes | -1.13 | 0.02 | -7.46 | 56.08 | 1.02 |
| Sample size (n) | 237 | | | | |
| Genus/family (random effect SD) | 3.41 | | | | |
| Family (random effect SD) | 2.36 | | | | |
| R^2 | 0.4 | | | | |

Fig. 4 Proportion of species according to multihabitat-use, rafting ability, brackish-water dependency, sedentary mobility, and average of maximum depth and body sizes in accordance to the maximum distance reached in the Vitória-Trindade Chain region. Thus, 0 only shows species restricted to the continental shelf, and 915 shows species that reach the islands (but are not necessarily present on all seamounts). Percentages add up to 100% for each sector reached. Diamond represents the mean value and bars standard errors



Discussion

Here, we identify potential mechanisms regulating the assembly of shallow water reef fish communities on seamounts. By contrasting seamounts with mainland and oceanic islands, we find no fundamental, single biogeographic or ecological process driving distinct species composition. We find, for example, no support for a major effect of distance from mainland on species richness. These findings support Hachich et al. (2015; 2019), which identified the large dispersal capacity of most marine species as a mechanism blurring the effects of distance predicted by the theory of island biogeography. Contrarily to other studies in the VTC (Leal and Bouchet 1991; Paiva 2006; O'Hara et al. 2010), we observed that habitat heterogeneity and shallowest depth are more important to the similarity and richness of fish communities on seamounts and oceanic islands than geographic isolation.

Moreover, our results showed that the similarity between seamounts and islands communities is driven by a stepping stones process and that it decreases towards mainland, with the highest species turnover found between mainland and seamounts. This scenario indicates that despite strong differences, seamount communities are still more similar to those of islands than to those of the continental shelf. Therefore, it is likely that seamounts work as stepping stones for marine organisms at both evolutionary and ecological time scales (e.g.: Pinheiro et al. 2017). This does not necessarily mean that all species hop over each and every seamount towards the most remote functional island, but rather that environmentally similar and adjacent sites contribute more to each other's similarity than distant ones.

In addition, we found support for the hypothesis that reef fish traits related to both dispersal and establishment underlie species' distribution ranges over seamounts and islands, thus influencing community assembly processes and local biogeography. Although endemic reef fish communities in remote locations do not show specific dispersal potential favoring colonization or self-recruitment processes (Robertson 2001), the limitation in dispersal ability along the VTC might be associated with the Brazil Current (Lemos et al. 2018), previously suggested as an ecological barrier that constrains connectivity and influences the high turnover between the continental shelf and the VTC (Pinheiro et al. 2015a). Limited establishment potential, as inferred by traits related to habitat dependency, seems also to influence colonization and recruitment. For instance, despite having high dispersal abilities and/or wide geographical distributions, several species show limited distribution along the VTC. The high diversity found in the larval pool of the VTC (Stocco and Joyeux 2015), and

the widespread distribution of some VTC endemics (i.e. *Halichoeres rubrovirens* and *Sparisoma rocha*) along the chain, indicate that larval dispersal, although important, does not constitute the main driver for species distribution.

Sea level fluctuations across geological times have played a critical role on the biological connectivity among seamounts and oceanic islands of the VTC, driving the origin and persistence of a number of endemic species and distinct populations specific to this system (Gasparini and Floeter 2001; Simon et al. 2013a; Macieira et al. 2015; Pinheiro et al. 2015a; 2017). During low sea level stands [i.e., 90% of the time during the Pleistocene, Lambeck et al. (2002)], many seamounts were exposed and island habitats became available, increasing connectivity for small and shallow-water dependent species (weak dispersers) through the chain. Sea-level transgressions worked as a vicariant barrier, and species unable to persist over submerged seamount summits became extinct. Adaptation to deeper environments may explain many of the depth range extensions found on deeper reefs of the VTC (Pinheiro et al. 2015a), also evidenced for corals (Vermeij and Bak 2002; Diekmann et al. 2003; Polato et al. 2010). High sea-level stand periods would also have driven speciation for sedentary species, tidepool residents and shallow-water dwellers on the insular reefs (Simon et al. 2013a; Macieira et al. 2015; Pinheiro et al. 2015a; 2017; Andrades et al. 2018). Thus, historical sea-level changes have a direct influence on contemporary community structure and biogeography of seamounts and oceanic islands, explaining the intermediate ecological characteristics of the biodiversity found in the islands (Fig. 4), where, in contrast to seamounts, shallow habitats for sedentary species are available.

Seamounts have been suggested to contribute to the dispersal of reef organisms over vast oceanic distances (Hubbs 1959; Wilson and Kaufmann 1987), and species dispersal capabilities seem to directly influence genetic connectivity between seamounts and islands (Cho and Shank 2010) and stepping-stone gene flow patterns elsewhere (Crandall et al. 2012). Our study highlights the importance of considering species' establishment strategies for a better understanding of the ecology and evolution of seamount and island communities. Here we conclude that the assembly rules of reef fishes on seamounts and oceanic islands of the VTC are driven by a stepping stone process rather than propagule rain. Thus, establishment and dispersal mechanisms, shaped by historical sea-level changes, regulate the persistence of species and similarity in community composition among adjacent and environmentally similar sites of the VTC.

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Author contributions EFM and HTP conceived the idea for this study; EFM, HTP, TS, RM, RMM, RBF, JLG and JCJ collected and compiled the data; EFM, HTP, TS, RM, CRP, JBT, SRF, CELF, RBF, JPQ and JCJ analyzed the data; EFM, HTP, TS, RM, J-CJ led the writing and RMM, CRP, JBT, SRF, CELF, RBF, LAR, JPQ, and JLG reviewed the manuscript.

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Availability of data and material Data are provided as supplementary material.

Declarations

Conflicts of interest The authors declare no conflict of interest.

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