REPORT

Coralline Hills: high complexity reef habitats on seamount summits of the Vitória-Trindade Chain

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Abstract Seamounts and oceanic islands play an important role as biodiversity hotspots amid the vastness of the oligotrophic open ocean. While island ecology and evolution have received a lot of attention in the last decades, the exploration and understanding of community and habitat dynamics of seamounts remain challenging. Here, we investigate the ecology and biogeography of fish and benthic communities of a recently discovered southwestern Atlantic reef system at Davis seamount. This seamount belongs to the Vitória-Trindade Chain and is located in international waters off the Brazilian coast. We present this reef system, that also occurs on other shallow seamounts of the chain, as a new reef habitat named "Coralline Hills": Its hill-shaped structure is mainly built by crustose coralline algae and rises up from the seamount summit at 60–70 m to 17 m depth. The benthic community is mainly composed by coralline algae and sponges. Fish biomass at Davis coralline hill is dominated by carnivores, mainly top predators such as nurse sharks and large groupers. The relatively shallow reef top presents higher species richness, abundance and distinct trophic structure (mostly omnivore and planktivore species) than the mesophotic zone (with higher abundance of carnivorous fishes). A biogeographic analysis revealed that the reef fish community structure is greatly influenced by a set of dispersal and establishment traits that strongly differs from that encountered on coastal reefs of the central Brazilian coast and on insular reefs of Trindade Island. Gathering information about the ecology and structure of such unique and remote habitat is timely, since the region is under imminent threat such as fishing and mining and lacks international attention.

Keywords Reef fish · Benthic community · Mesophotic ecosystems · Atlantic Ocean · Brazilian Province · Conservation

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Introduction

Seamounts and oceanic islands have been the stage of many recent discoveries, in terms of new habitats and species, as well as eco-evolutionary processes (Pinheiro et al. 2017). For instance, the importance of the role seamounts play as stepping stones for isolated environments, contributing to colonization and population maintenance of shallow water species in oceanic reefs over ecological and evolutionary timescales, has been recently highlighted (Cho and Shank 2010; Macieira et al. 2015; Simon et al. 2021). Gene flow among populations in seamounts, islands and the mainland

is a function of environmental and biological factors, which means that species with distinct traits play different roles in stepping stones processes (Simon et al. 2021). Species-level traits related to dispersal (*e.g.*, maximum body size, mobility and rafting ability) and establishment capabilities (maximum depth, multi-habitat association and brackish water dependency) influence the geographic range size (Luiz et al. 2012; Pinheiro et al. 2018) and are important drivers of community composition in seamounts and oceanic islands (Mazzei et al. 2021). However, the ways in which they shape community structure in situ remain poorly understood.

Seamounts and oceanic islands also increase primary productivity rates through interactions with oceanic currents (e.g., enclosing circulation current cells or disrupting oceanic flows), forming biomass hotspots (including of pelagic predators) surrounded by impoverished, oligotrophic deep ocean waters (Genin 2004; White et al. 2008; Morato et al. 2010; Gove et al. 2016). Moreover, because most seamounts lay beyond the range of strongest impacts (due to depth and isolation), they can act as a wilderness refuge for top predators, like sharks and groupers (Letessier et al. 2019). Depth has also been suggested as a driver for coral reefs' health status. There is evidence supporting the deep reef refuge hypothesis, which predicts that deeper reefs are less susceptible to disturbances than shallow ones (Glynn 1996; Bongaerts et al. 2010). Such evidence includes, for example, higher biomass and abundance of fishes on deeper than shallower reefs (Pereira et al. 2018). On the contrary, the composition of species of deeper reefs may differ dramatically from that of shallower ones because depth influences the structure of fish and coral communities (with effects on diversity, abundance, trophic guilds, etc.) (Rocha et al. 2018). Therefore, the study of natural communities from remote localities allows understanding ecological patterns with reduced influence of human stressors, providing insights on the effect of depth over near pristine ecosystems.

While seamount ecology is on the rise (Pitcher et al. 2008), these ecosystems figure among the last frontiers in reef studies and deserve urgent scientific and conservation efforts due to current and imminent threats such as fisheries and mining (Pinheiro et al. 2010; Vasconcelos 2012). Recently, some high sea habitats (i.e., areas beyond national jurisdiction) were recognized as Ecologically or Biologically Significant Marine Areas (EBSAs) by the Convention on Biological Diversity (CBD) of the United Nations. Some of these, the Abrolhos Bank and Vitória-Trindade Chain EBSA, are important regions for threatened and endangered species (Bax et al. 2016).

The tropical southwestern Atlantic Ocean presents a high diversity of reef ecosystems, many of them unique and extending for large areas of the continental and insular shelves (Rocha et al. 2000; Leão et al. 2003; Pereira-Filho et al. 2012; Moura et al. 2013; Teixeira et al. 2013;

Francini-Filho et al. 2018). Despite the increasing amount of studies about the reef biodiversity in the last decades (Santos et al. 2016; Aued et al. 2018; Pinheiro et al. 2018), recent efforts based on diving exploration and geophysical mapping of benthic ecosystems have yielded the discovery of unknown reef habitats (Feitoza et al. 2005; Pereira-Filho et al. 2012; Bastos et al. 2013; Morais et al. 2017; Mazzei et al. 2017). Most of these newly discovered habitats are deep and/or remote, and a comprehensive knowledge about their distribution and functioning is still lacking (Soares et al. 2018; Francini-Filho et al. 2019).

The 1000 km long Vitória-Trindade Chain (VTC) is composed by seamounts laying along a line perpendicular to the central coast of Brazil, in a zone considered transitional between the tropical and subtropical provinces of the western Atlantic (Pinheiro et al. 2018). The Brazil Current (BC), flowing southward, is the main oceanographic feature in the region (Silveira et al. 2004). Because the BC perpendicularly crosses the VTC, one would expect that habitats and communities on the seamounts would be more similar to tropical than to subtropical reefs of the central coast. However, existing evidence so far (Simon et al. 2021) is contrary to this hypothesis, as stepping stones processes in reef fishes indicate gene flow prevalence between the VTC and reefs with subtropical affinities in the Brazilian central coast.

The majority of VTC seamounts have summits covered by rhodolith beds (Pereira-Filho et al. 2012). However, the overall flatness is locally broken by large and complex coralline algal reefs inhabited by a noteworthy diversity of species in some seamounts (Pinheiro et al. 2014, 2015; Mazzei et al. 2021; Meirelles et al. 2015). In a recent expedition, we revisited the "reef oasis" on Davis Seamount (Pinheiro et al. 2014) to investigate the ecology, biogeographic affinities and patterns and drivers of community structure of these unique reef structures. They are predominantly built of calcareous red algae, rising from the mesophotic zone toward the surface and displaying a hill-like morphology that we therefore name "Coralline Hills." We compared fish and benthic assemblages of the Davis coralline hill with reefs under tropical and subtropical influence of the mainland coast (northern and southern to the VTC, respectively) and at the eastern end of the VTC (Trindade Island). We further analyzed whether dispersal and establishment constraints of species distribution (cf. Mazzei et al. 2021) also shape the community structure in this remote system. Therefore, here we are addressing the following questions: (1) What is the taxonomic and trophic composition of fish and benthic communities? (2) How does the fish assemblage change between shallow and mesophotic depth strata? (3) Are faunal differences/similarities between Davis coralline hill and other reefs of the southwestern Atlantic related to geography (oceanic vs. mainland coast) or environment (reefs with tropical vs. subtropical affinities)? (4) What is the influence of

biological traits associated with dispersal and maintenance in shaping the community structure of Davis coralline hill?

Material and methods

Study area

Davis seamount's summit is located in international waters, approximately 600 km from the Brazilian mainland, in the middle of the Vitória-Trindade Chain (Fig. 1). The VTC is composed of many volcanic seamounts situated between latitudes 19° and 21° S, extending from approximately 200 to 1200 km off the central Brazilian coast. The islands of Trindade and Martin Vaz, at the eastern end of the chain, are the farthest and only emergent sites of the VTC. They represent the youngest volcanic episodes within the southwestern Atlantic (SWA), with igneous rocks less than 1 million years old (Mohriak 2020).

The region is influenced by the Brazil Current, which flows southward between 10° and 38° S (Silveira et al. 2004). This superficial current flow meets the VTC southeast of the Abrolhos shelf, passes through between the western-most seamounts and then reorganizes itself as a single jet (Costa

et al. 2017). It predominantly flows southwards, but cyclonic eddies moving northwards are common and can reach the seamounts of the VTC (Costa et al. 2017). Upwelling events generated by the interaction of topographical complexity and oceanic currents seem to be frequent and seasonal, promoting nutrient enrichment of the oligotrophic oceanic surface waters (Lemos et al. 2018).

We compared the Davis coralline hill with five other reef environments of the southwestern Atlantic, situated between latitudes 17° and 21°S. These reef sites encompass a transitional zone between typically tropical warm water reefs of the Abrolhos Archipelago and Northern Espírito Santo (with the prevalence of biogenic reef formations), and the subtropical-like reefs of Guarapari islands and the Southern Espírito Santo, which are mainly composed by rocky reefs under seasonal weak upwelling. Moreover, the tropical oceanic reefs of Trindade Island, at the eastern end of the chain, were also surveyed for community structure comparisons.

Data collection

Davis coralline hill was sampled in two different expeditions, during its discovery in 2011, and in 2018. Although other similar structures were detected along the VTC (e.g., Vitoria
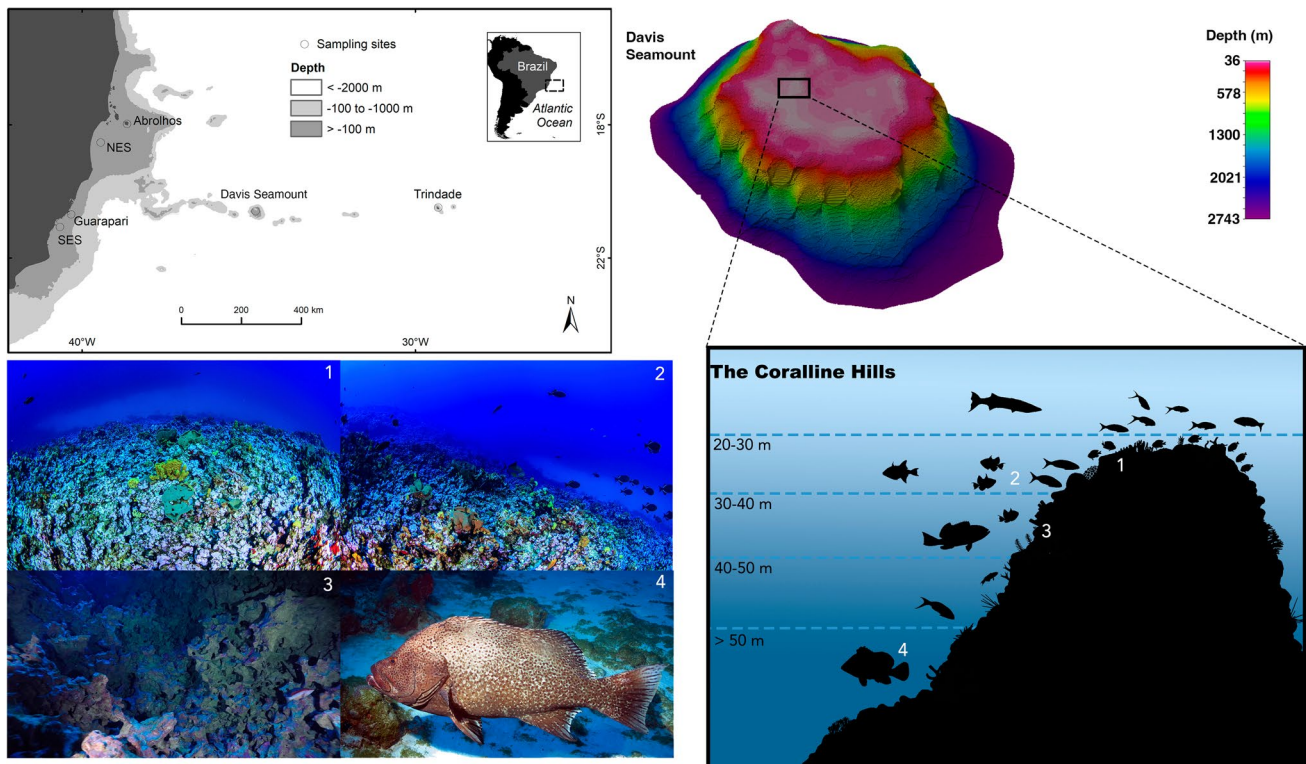
Fig. 1 Location and general morphology of coralline hill, Vitória-Trindade Chain. (1) Reef top, (2) reef slope, (3) interior of a reef cave and (4) interface at Davis Seamount. Photograph credits: L. Rocha, M.V. Bell and R.B. Francini-Filho. The acronyms SES refers to the Southern Espírito Santo reefs, and NES refers to the Northern Espírito Santo reefs

seamount), they were not sampled quantitatively. During the 2011 expedition, sampling was performed through video transects (55 min) conducted along a depth gradient, including shallow (20–30 m) and mesophotic (30–60 m) zones. Videos were recorded by divers slowly swimming one meter above the reef. Fish abundance was estimated from frames taken every 10 s from video transect. A total of 33 frames were analyzed from 20 to 30 m depth, 17 frames from 31 to 40 m, 185 frames from 41 to 50 m and 93 from 51 to 60 m. The greater number of frames in deep habitats is due to the larger reef area and greater amount of time spent exploring mesophotic reefs.

To compare the reef community of Davis coralline hill with other reef ecosystems of the southwestern Atlantic, fish and benthic communities were assessed, respectively, through underwater visual censuses and photo-quadrats conducted on the top of the reef structure (18 to 30 m depth) during our expedition in 2018. Each census consists of a strip transect measuring 20 m long and 2 m width, in which a diver swims the transect line identifying, estimating the size and counting all fishes observed in the transect area. Fish lengths were grouped into 5-cm (1–5 cm and 6–10) and 10-cm (11–20, 21–30 cm, etc.) classes. Five photo-quadrats (measuring 50×50 cm) were conducted every 5 m within each transect used for censuses (Photo-quadrats and censuses were conducted in the same transect). For each transect, depth was measured using a dive computer, while rugosity was visually assigned into three categories following Pinheiro et al. (2013): low (flattened substrate with no holes or crevices), intermediate (substrata with small boulders and holes less than 1 m of size) and high (substrata composed of big boulders and holes equal or greater than 1 m of size). In 2018, using these sampling methodologies, a total of 18 transects were performed on the coralline hill and 20 in Trindade Island.

Data of reef fish communities in shallow waters reefs (3–30 m depth) were compiled from several expeditions carried out between 2008 and 2018 on the continental shelf and in Trindade. All studies used the same methodology (censuses using SCUBA). Overall, 881 censuses were conducted (Davis coralline hill $n = 18$ UVCs in the present study; Trindade $n = 144$ present study; Southern Espírito Santo reefs $n = 129$ from Pinheiro et al. (2013); Guarapari $n = 239$ from Simon et al. (2011, 2013a); Northern Espírito Santo reefs $n = 53$ from Mazzei et al. (2017); and Abrolhos Archipelago $n = 298$ from Guabiroba et al. (2022)).

Data analyses

Fish species were classified into trophic groups following Ferreira et al. (2004) and Pinheiro et al. (2018). Individual biomass was estimated through the growth model $W = aTL^b$ (Froese 2006), where W is the calculated weight of fishes,

TL is the total length (using the center of the length class estimated in the census), and *a* and *b* are the regression parameters of each species, obtained from FishBase (Froese and Pauly 2018). Biomass is considered a good metric to evaluate environmental health, as it reflects size spectra and determines the energy flux among communities and ecosystems (Brown et al. 2004). Thus, contrasting biomass of comparable sites can give an idea about the health status of different localities.

Fish abundance and biomass were analyzed using a matrix based on Bray–Curtis similarity index (one of the most widely used measures of dissimilarity using abundance data), while composition was analyzed through a presence–absence matrix based on the Jaccard index (a robust method for minimizing the influence of differences in sample size, it is considered the most appropriate to measure changes in taxonomic dissimilarity) (Fattorini 2010; Villéger and Brosse 2012). A non-metric multi-dimensional scaling (nMDS), based on the Jaccard index, and a second-stage nMDS were performed to explore the variations in fish composition among sites (Clarke et al. 2006). SIMPER analyses were conducted to assess species and trophic groups' contribution to within-groups similarity and among-groups dissimilarities.

A PERMANOVA design (Anderson et al. 2008) was built considering sites and rugosity as fixed factors and depth as covariate. Analyzes were run using the permutation of residuals under a reduced model and the Type I sum of squares (SS). In order to search for differences between each pair of site combinations, pairwise analyzes were conducted using the same permutation method above, but with Type III SS. For SIMPER and PERMANOVA analyses, sites were grouped in three categories, according to their geographic position, as coastal (Abrolhos, north Espírito Santo, Guarapari and south Espírito Santo), seamount (Davis coralline hill) and island (Trindade Island).

Species were classified according to traits associated with dispersal and establishment in seamounts and oceanic islands, following Mazzei et al. (2021). Dispersal traits considered were: maximum body size (total length in cm); mobility, considered as a binomial variable (sedentary or mobile), with sedentary species being those that do not usually move among habitats; and the ability to raft with floating objects (binomial variable). The establishment traits considered were the maximum depth (m); the multi-habitat use (binomial variable based on whether a species inhabits multiple habitats or not); and brackish water dependency (binomial variable), considering whether a species requires coastal or estuarine habitats to complete its life cycle. The average maximum depth and maximum length (body size) of the assemblage within each transect were calculated using the value of each species weighted by their total number in the transect. The abundance of the other binomial variables

was analyzed as proportion in each transect. Dispersal and establishment trait variables were tested for differences among localities (mainland coast, coralline hill and Trindade Island) with the nonparametric Kruskal–Wallis test. In case of significant result, a Dunn test was conducted to test for differences in each pair of locality combinations. Analyses were conducted in R software using "dplyr" and "FSA" packages and functions "kruskal.test" and "dunnTest."

Photo-quadrats were analyzed in Coral Point Count with Excel Extensions software (Kohler and Gill 2006). In each quadrat, 30 random points were randomly overlaid and the individual organisms or substrates below each point were identified to the lowest taxonomic level. Benthic cover comparisons between Davis coralline hill and Trindade Island were conducted using a Bray–Curtis similarity matrix. PERMANOVA and SIMPER analyses were run in the same way as for fishes (see details above). The relationship between the Bray–Curtis similarity of benthic cover and reef fish assemblages of Davis coralline hill and Trindade Island was assessed with a Mantel analysis with 999 permutations, to test the hypothesis whether transects with higher benthic similarities would also have higher fish similarities.

Results

General remarks on Davis coralline hill morphology

The coralline hill comprises a highly complex reef emerging from mesophotic depths (60–70 m) up to shallow waters near the surface (up to 17 m on Davis seamount). The hilltop (17–25 m depth) presents many depressions and caves (Fig. 1), while the walls sharply drop down to about 60 m, where there is an interface between the reef and adjacent sandy/rhodolith bottoms (Fig. 1). The structural complexity of the reef is increased by small crevices and large holes, forming a network of hollow structures, with sponge-like features at a much broader scale. Strong, alternating currents may originate from (and enter in) the reef well below the reef top, evidencing this spongy structure extends into the reef interior. This structural complexity provides refuge and living habitat for a variety of species, from the smallest to the largest ones. Crustose coralline algae are mostly dead in the internal parts of the reef (Fig. 1). The sea urchin *Diadema antillarum* is abundant, as confirmed during two 2011 night dives in coralline hills both on Davis and on the Vitoria seamount, during which hundreds of individuals were observed (few can be seen during the day). The coralline hill habitat type was only analyzed in detail on Davis seamount, but it was also found in other VTC seamounts such as Vitória (structures rising from 70 to 35 m depth), Jaseur-East (~ 55 to 45 m) and Columbia (~ 84 to 80 m).

Most of the VTC remains unexplored, but bathymetric maps indicate the probable presence of similar structures on other seamounts.
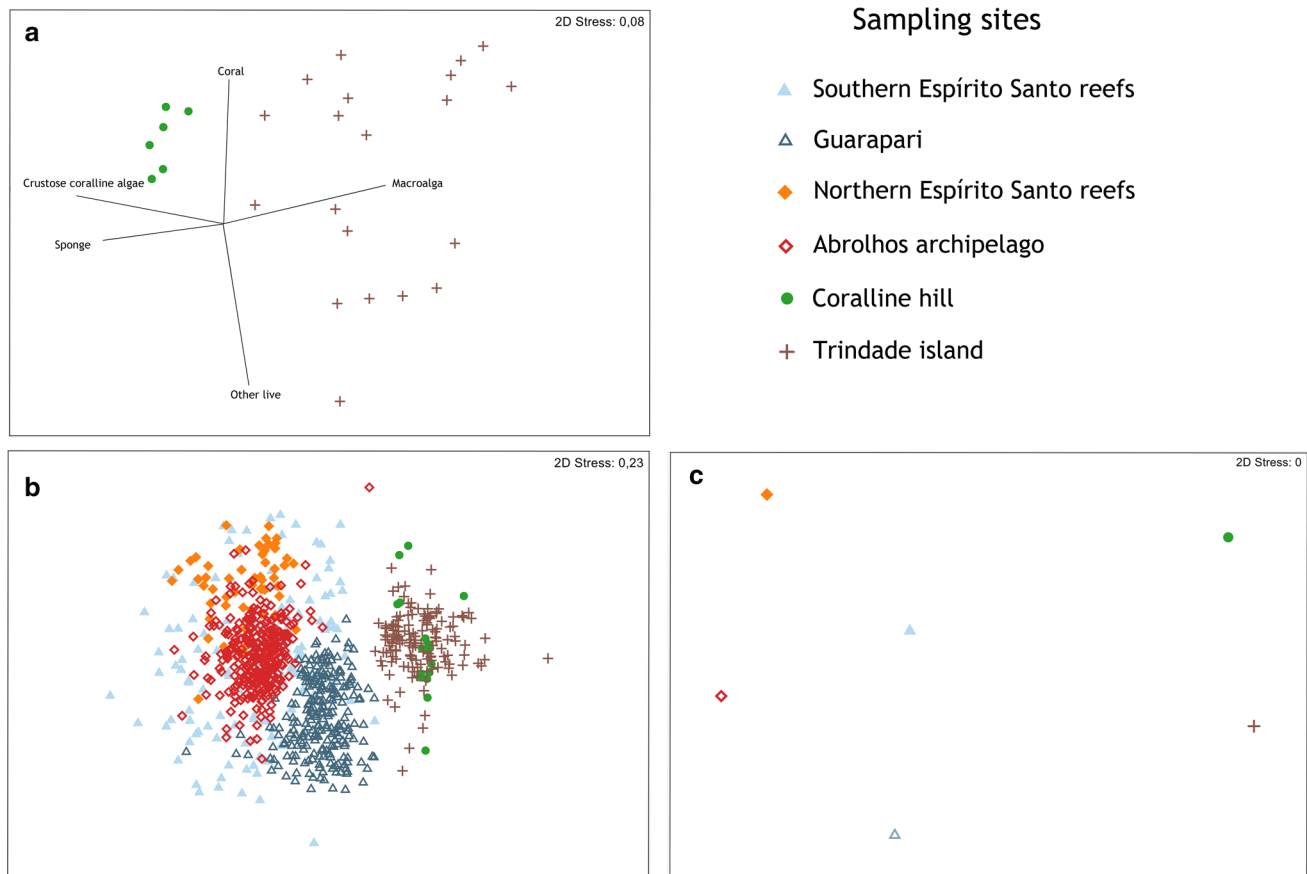
Coralline hill benthic cover

Benthic assemblages of Davis coralline hill (Table S1) were mainly represented by crustose coralline algae (67.1%), sponges (26.9%), the stony corals *Agaricia fragilis* (4.1%) and Equinoderma (1.8%). PERMANOVA's main test revealed that benthic cover structure is significantly different between the coralline hill and Trindade Island (pseudo-$F = 14.3$; $p = 0.001$) (Fig. 2A). SIMPER analysis showed biogenic coverage at Davis coralline hill is typified by coralline algae (52.1%) and sponges (29.9%), while in Trindade coralline algae (32.6%), macroalgae (32.2%) and sponges (18.8%) dominate. Mean dissimilarity between these two sites was 41.3% due to differences in cover of macroalgae (37.8%), coralline algae (19.9%) and other living organisms (15.7%). The similarity in benthic assemblages of Davis coralline hill and Trindade island was not significantly correlated with the similarity of fish assemblages (Mantel test, $r = 0.0002$, $p = 0.494$).

Reef fish community structure at Davis coralline hill

Twenty-six species belonging to 13 families were recorded in the censuses performed on the upper coralline hill habitat (~ 17 to 30 m depth; Table S2). Labridae was the most speciose family (four species), followed by Epinephelidae and Pomacentridae (three species each). The most speciose trophic group was roving herbivores (five species), followed by carnivores and sessile invertebrate feeders (four species each), omnivores, piscivores, planktivores and territorial herbivores (three species each) and mobile invertebrate feeders (one species; *Amblycirrhitus pinos*).

Thalassoma noronhanum was the most abundant species (mean of 16.6 ± 3.9 SE indiv.40 m^{-2}), followed by *Paranthias furcifer* (9.67 ± 3.52), *Clepticus brasiliensis* (9.11 ± 2.83) and *Melichthys niger* (7.56 ± 1.36). Fish biomass was dominated by *Ginglymostoma cirratum* (mean of 4422 ± 2853 SE g.40 m^{-2}; in response to a low number of large individuals), followed by *Melichthys niger* (2722 ± 489 SE; high number of small individuals), *Sphyraena barracuda* (861 ± 321 SE; high number of large individuals, > 50 cm TL) and *Mycteroperca venenosa* (752 ± 403 SE; high number of large individuals, > 50 cm TL). Although not recorded in visual censuses, large individuals (60–80 cm) of the marbled grouper *Dermatolepis inermis* were frequently sighted in 2011 (authors pers. obs.).

Planktivores were the most abundant trophic group (56.8% of total fish counted), followed by roving herbivores (14.8%), omnivores (12.8%), territorial herbivores (6.3%),

Fig. 2 Non-metric multi-dimensional scaling (nMDS) of benthic cover in the Coralline Hill and Trindade Island (**A**), with vectors indicating benthic groups with Pearson correlation greater than 60%. Reef fish species composition among sites (**B**), and second-stage nMDS of reef fish composition (**C**). The Bray–Curtis index was used for benthic community and Jaccard index for reef fish composition. nMDS is based on presence–absence data and Jaccard index

carnivores (5.5%), piscivores (2.6%), sessile invertebrate feeders (1.0%) and mobile invertebrate feeders (0.3%). Carnivores were the trophic group with the highest biomass due to larger size of individuals (47.3% of total biomass), followed by omnivores (23.0%), piscivores (11.5%), planktivores (8.5%), roving herbivores (8.0%) and territorial herbivores, sessile and mobile invertebrate feeders, each contributing less than 1% of total biomass.

Fish community varied along a depth gradient (data from video transects), with mean abundance (pseudo-$F = 27.4$; $p = 0.001$) and richness (pseudo-$F = 3.8$; $p = 0.008$) higher in shallow areas (20–30 depth strata, Fig. S1). In this sense, trophic structure also differed among depth strata (pseudo-$F = 9.6$; $p = 0.001$) with prevalence of omnivores and planktivores in shallow habitats (Fig. S1; Table S3).

Effects of geography and environment on the fish community

Reef fish composition at Davis coralline hill was more similar to the tropical and remote reefs of Trindade Island (average dissimilarity = 65.5%) than to coastal reefs (average dissimilarity = 90.8%) (Table S4). Despite some similarity and overlap presented in nMDS analyses, species composition differed significantly among sites (PERMANOVA main test: pseudo-$F = 59.0$; $p = 0.001$) (Fig. 2B, C, Table S5 for PERMANOVA results). Unexpectedly, tropical reefs of the VTC (Davis coralline hill and Trindade) were more similar to the subtropical reefs of the Espírito Santo coast (Guarapari and the Southern Espírito Santo reefs) than the tropical reefs of the Abrolhos shelf (Abrolhos and the Norther Espírito Santo reefs; Fig. 2C).

Abundance similarity within the coralline hill was maintained by *Thalassoma noronhanum* (18.2%), *Melichthys niger* (16.7%), *Clepticus brasiliensis* (10.4%), *Scarus zelindae* (10.0%) (Table S6). The main contributors to

within-group biomass similarity were *Melichthys niger* (35.8%), *Cephalopholis fulva* (11.6%) and *Scarus zelindae* (9.0%) (Table S6).

Total biomass differed among sites (Fig. S2) with 94.4% of average dissimilarity between Davis coralline hill and coastal reefs (Table S7). The main contributors for such dissimilarity were *Melichthys niger* (13.7%), *Cephalopholis fulva* (5.4%), *Ginglymostoma cirratum* (5.2%) and *Sphyraena barracuda* (5.0%) (Table S7). All of these species had higher biomass at the coralline hill and were nearly absent in coastal reefs. On the other hand, the average dissimilarity in species biomass between coralline hill and Trindade reefs was 71.9% (Table S7). This difference was driven by *Melichthys niger* (8.3%), *Cephalopholis fulva* (8.3%) and *Kyphosus* spp. (8.1%), which showed higher biomass in Trindade, while *Sphyraena barracuda* (5.7%) and *Ginglymostoma cirratum* (5.6%) showed higher biomass at the coralline hill.

Reef fish community structure differed among coralline hill, coastal and island communities, both in biomass of species (pseudo-$F = 63.5$; $p = 0.001$) and trophic groups (pseudo-$F = 58.4$; $p = 0.001$) (Fig. S3). Depth and rugosity were also significant drivers for both species and trophic groups (Table S5). Biomass of fish trophic groups was dissimilar between Davis coralline hill and coastal reefs (67.6%) with omnivores (20.2%) and carnivores (19.6%) presenting higher biomass in the former, while mobile invertebrate feeders were more common (14.4%) in the later. Trophic dissimilarity between Davis coralline hill and Trindade reefs was about 48.4% and driven by higher biomass of roving herbivores (19.6%), carnivores (19.5%) and mobile invertebrate feeders (15.7%) in Trindade Is. reefs (Table S8).

Assembly rules

All dispersal and establishment traits were significantly different among localities (Fig. 3). The proportion of mobile and brackish water non-dependent fishes and the average depth of the fishes were higher in Davis coralline hill and Trindade than in mainland sites (Fig. 3). Multi-habitat users and the average body size of the fishes reached a higher proportion at Davis coralline hill than at Trindade and mainland reefs (Fig. 3). Rafting-capable fishes presented higher proportions in the community of Trindade, followed by Davis coralline hill, and mainland (Fig. 3).

Discussion

The unique reef morphology and assemblages found at the Davis coralline hill we explored differed from other reefs at Trindade and on the continental shelf of the southwestern Atlantic. Since Davis and many other VTC seamounts were exposed during low-stand sea levels, we can infer that the

coralline hills habitat started to develop on seamount summit during the last sea-level rise. We hypothesize coralline hills would follow the pattern of most Brazilian coral reef systems, which grew during the last 8–7 ky after the flooding of the continental shelf (Leão et al. 2003). Thus, the vertical growth rate of the tallest known coralline hill would be between 3.3 and 5.3 mm.y^{-1} (40 m height in 7.5–12 ky), lower than reefs of the Brazilian coast (~ 7–8 mm.y^{-1}; Leão et al. 2003). Due to similarities in composition, the coralline hills vertical growth rate should be similar to that of Rocas Atoll (3.1 mm.y^{-1}), the only atoll of the South Atlantic (Leão et al. 2003). Rocas Atoll is unique for being built primarily of calcareous algae (Gherardi and Bosence 2001), but it grows about twice as fast as rhodoliths in the Abrolhos Bank (Amado-Filho et al. 2012) or crustose coralline algae in the Great Barrier Reef (Lewis et al. 2017). The relatively slow growth of coralline hills might be a result of geologic (e.g., age, subsidence, uplift), oceanographic (e.g., temperature, currents) and biological (e.g., bioerosion) drivers that have prevented the reefs from emerging. These constraints, associated with the low diversity of reef-building corals, might have prevented the development of atolls in the SWA despite the exposure of VTC seamounts during the low sea-level stands.

The structure of the coralline hill reef community is also remarkable. Fish biomass was dominated by large carnivores, such as *Ginglymostoma cirratum*, *Sphyraena barracuda* and *Mycteroperca venenosa*. The biomass of these species and of large carnivores in general is much lower in most Brazilian reefs and worldwide, mainly due to overfishing (Jackson et al. 2001; Morais et al. 2017; Ruppert et al. 2017; Guabiroba et al. 2020a). Indeed, only *S. barracuda* was recorded in coastal sites, but at biomass 2.5-fold lower than at Davis´ coralline hill. Mean biomass of predator fishes (macrocarnivores and piscivores) at the coralline hill (~ 176 g m^{-2}) is higher than those found on protected and relative healthy areas across the Caribbean, such as the Bahamas, Cuba and Mexico (~ 122 g m^{-2}), and those reported for reefs in the Pacific, such as the Northern Hawaiian Islands (~ 132 g m^{-2}) (Friedlander and DeMartini 2002; Valdivia et al. 2017). Even old and enforced Brazilian MPAs, like the National Parks of Abrolhos (coastal) and Fernando de Noronha (oceanic), have lower biomass of top predators compared to the coralline hill (Francini-Filho and Moura 2008; Krajewski and Floeter 2011; Ilarri et al. 2017; Guabiroba et al. 2022; this study). Notwithstanding, the nurse shark *Ginglymostoma cirratum*, widely distributed in the Atlantic Ocean and endangered in Brazil, was only recorded in our visual censuses in Trindade (0.014 ind./40m^2) and in the Coralline Hill (0.17 ind./40m^2), with a 14-fold higher average biomass found in the latter.

High biomass of large carnivores could be explained by bottom-up processes, supported by the hypothesis of
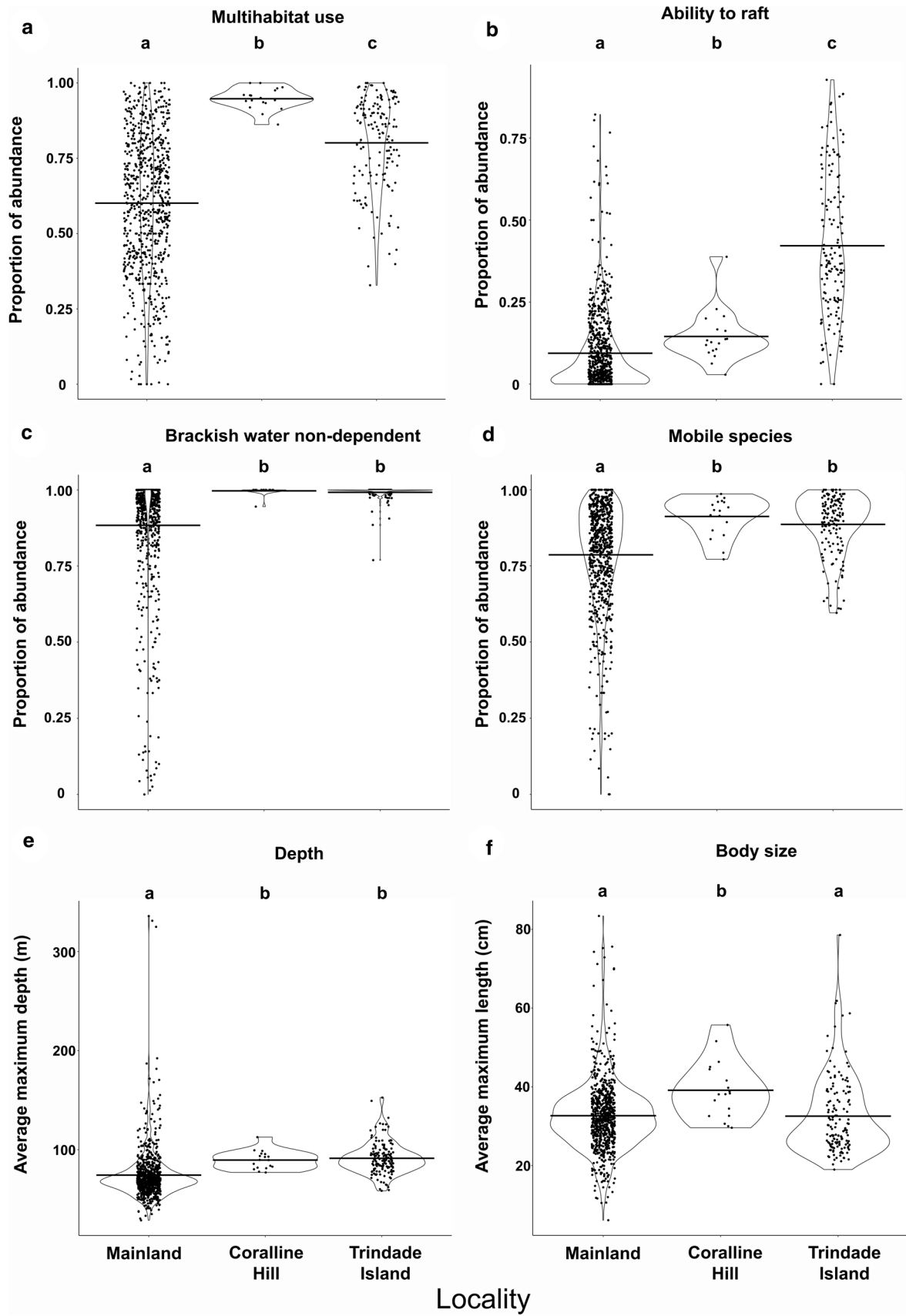
◄**Fig. 3** Proportion of abundance according to multi-habitat use (**A**), rafting ability (**B**), brackish water non-dependent species (**C**), non-sedentary species (**D**) and average of maximum depth (**E**) and body size (**F**) in different localities (mainland, Coralline Hills at Davis seamount and Trindade Island). Upper letters indicate whether there are significant differences (different letters) or not (same letters) among localities

increased primary productivity on seamount waters related to ocean currents (Mendonça et al. 2012; Gove et al. 2016). Davis seamount is known to experience high chlorophyll-a concentration due to an upwelling enrichment caused by the interaction of the Brazil Current with the VTC features (Lemos et al. 2018). Increased primary production may have cascade consequences over the entire community, from benthic reef-building organisms (crustose coralline algae and stony corals) to piscivorous fishes (Gove et al. 2016). The great abundance of planktivorous fishes and high sponge coverage (which feed primarily on picoplankton) at Davis coralline hill also support the hypothesis on primary production subsidizing bottom-up processes, and therefore regulating the ecology of these ecosystems. Moreover, myriads of planktivore fishes are also common around islands and habitats such as artificial reefs (Pinheiro et al. 2011; Simon et al. 2013b). The abundance of these smaller fishes often attracts larger ones from surrounding habitats (Simon et al. 2011). Coralline hills, as underwater islands emerging from the seamount flat summits, can contribute to locally trap the plankton through a topographic blockage mechanism (Isaacs and Schwartzlose 1965; Genin 2004), further boosting the trophic chain (Gove et al. 2016). The combination of upwelling and island effects could explain the high biomass of reef fishes, especially predators, found in the coralline hill at Davis seamount.

Recently, dispersal and establishment traits of fishes were found to contribute in determining the species composition along the remote seamounts and islands of the VTC, driving a stepping-stone assembly rule in the chain (Mazzei et al. 2021). Now going further, in this current research we disclose that these ecological mechanisms are also shaping differences in fish community structure among mainland, coralline hills and island reefs. For instance, many invertebrate feeders, such as haemulids, are highly abundant along the Western Atlantic, but less abundant or absent in many oceanic sites (Pinheiro et al. 2011; Melo et al. 2020). In open ocean or insular waters, the family is likely to be limited by the absence of shallow or brackish environments for recruitment. In addition, the remarkable high abundance of *Scarus zelindae* at Davis coralline hill and its apparent absence at other VTC sites has also been suggested to be a result of habitat requirement to its establishment and maintenance in oceanic ecosystems (Mazzei et al. 2019). As for community composition (Mazzei et al. 2021), the number of fishes in the community capable of rafting increases along the chain.

However, attributes such as body size and multi-habitat use are more important at Davis coralline hill than on mainland or Trindade shores, providing an additional contribution to colonization and maintenance in this extreme environment. Therefore, dispersal and establishment traits work as strong filters capable of influencing the abundance and community structure in remote oceanic localities.

The coralline hill and Trindade show ample similarity in reef fish community, but differ in benthic cover. The near-absence of fleshy macroalgae in coralline hills may be explained by the high abundance of herbivorous fish and *Diadema* sea urchins. The latter are likely to control macroalgae abundance through grazing (Morrison 1988), at the same time that it may contribute to the impressively high structural complexity of the coralline hills through bioerosion (O'Leary and McClanahan 2010). We expect this bioeroder to be the main responsible for the spongy structure of coralline hills, but confirmation of this hypothesis will need further studies. Also, herbivory over coralline algae can favor the increase in its own structural complexity in a predator–prey profitable interaction, since the constant meristematic removal results in tissue differentiation and redirection growth forming castle-like novel structures (Littler and Littler 2013).

Davis seamount has been suggested to shelter one of the highest levels of fish diversity of the VTC (Pinheiro et al. 2015; Guabiroba et al. 2020b), potentially representing one of the last shallow-water stepping stone connecting the mainland and Trindade Island (most of the VTC seamounts have summits below 35 m depth while Davis shallower area is about 17 m deep) (Meirelles et al. 2015). However, conversely to our expectation, the fish biodiversity of the tropical coralline hill is more similar to the subtropical reefs of the southern Espírito Santo (SES) than tropical reefs of Abrolhos Bank. This result supports the body of work that suggests the Brazil Current as a biogeographic barrier between the mainland coast and the VTC (Pinheiro et al. 2015, 2017; Mazzei et al. 2021; Simon et al. 2021). Following this rationale, the main drivers of dispersal in the region could be northward eddies, rings and gyres created by the passage of the Brazil Current between the VTC and the continental shelf (Mill et al. 2015; Costa et al. 2017).

Although Davis coralline hill has some features of a relatively pristine environment, evidence of fishing activities (lost anchors, traps and fishing lines observed during dives and reports from commercial fisheries) portrays an eminent risk for this remote and vulnerable ecosystem. Seamount fish communities are particularly vulnerable to overfishing because of a combination of factors including their isolation (that limit larval replenishment), reduced area (which limit population size) and life history of many species (slow growth and late maturation). Fishing activities on these remote locations are characterized by a

"boom and bust" cycle, yielding high catches in the first years and followed by the near collapse of target populations (e.g., Guabiroba et al. 2020a). In Trindade, for instance, a few years of commercial fishing overexploited local populations of sharks and yellowfin grouper (*Mycteroperca venenosa*) (Pinheiro et al. 2010); the latter are still commonly seen on coralline hills of the CVT (Pinheiro et al. 2015). The characteristics of the community structure allow us to conclude that Davis coralline hill is probably experimenting low fishing effort, and that opportunities for conservation actions for this and other VTC sites are still open.

While mining for carbonates is an eminent threat to VTC seamounts, especially in Davis (Vasconcelos 2012), the Brazilian government recently created a very large MPA mosaic including Columbia seamount inside a no-take MPA, the first seamount with this level of protection in Brazil. Very little is known about the biodiversity or ecology of Columbia seamount, but its summit depth, with the shallowest record of 84 m, suggests that there is suitable habitat only for mesophotic and deeper communities. Therefore, Columbia seamount might offer limited contributions to the recovery of overexploited shallow water populations in Trindade and Martin Vaz islands (the same would apply to Dogaressa seamount; see Simon et al. 2021). On the other hand, Davis seamount has been included in a proposal of Marine Biosphere Reserve, and the Brazilian government claims it within the United Nations Convention on the Law of the Sea (UNCLOS) as an extension of its exclusive economic zone (EEZ). The creation of a Marine Biosphere Reserve or the extension of the Brazilian EEZ could help to promote the protection of coralline hills on Davis and other seamounts located in areas beyond national jurisdiction (Heffernan 2018). The present research details the ecology of a unique and extremely remote ecosystem that shelters most of the shallow water populations found on the VTC seamounts. With still preserved communities, the coralline hills deserve precautionary measures, comprehensive ecological mapping and conservation studies before its biodiversity is potentially lost to predatory practices such as mining and unmanaged fishing.

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