Received: 13 November 2022 | Accepted: 9 May 2023

DOI: 10.1111/jfb.15433

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Habitat use of five sympatric predatory reef fishes at a remote island in the south-western Atlantic

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Funding information
Biodiversa+; Water JPI; Europe Union; Fundação de Amparo à Pesquisa e Inovação do Espírito Santo; RESTORESEAS Project (www.restoreseas.net)

Abstract

Density-dependent mechanisms and habitat use are important drivers of marine spatial distribution in complex ecosystems such as coral or rocky reefs. In the last decade, a few studies have assessed habitat use by reef fishes in nearshore and coastal environments along the Brazilian coast. Serranidae (groupers and sea basses) are regarded as excellent models for understanding habitat use patterns due to their diversity, long lifespan, wide distribution, morphological and functional diversity, and behavioural complexity. Their trophic position in the food web, from meso- to top-predators, grants them critical roles as top-down population controllers. Herein, we present the first assessment of habitat use by five sympatric Serranidae in a Brazilian oceanic island, Trindade. The model species selected for this assessment were the coney (*Cephalopholis fulva*), the rock hind (*Epinephelus adscensionis*), the greater soapfish (*Rypticus saponaceus*), the Creole-fish (*Paranthias furcifer*) and the hybrid between *C. fulva* and *P. furcifer*. Our findings revealed that the species showed specific associations with topographic characteristics related to shelter from predation, reproduction and feeding. Habitat use in Trindade was similar to that observed in nearshore coastal environments (where the hybrid is absent). The present work contributes to the knowledge of habitat use and niche partitioning among key species, which is a valuable tool to subsidize effective conservation initiatives such as designing marine protected areas focusing on the behaviour and habitat use of key ecological players.

KEYWORDS
ecology, functional diversity, groupers, island biogeography, population structure, sea basses

1 | INTRODUCTION

Information about the habitat use of reef fishes along the Brazilian coast has increased in the past two decades. Nevertheless, few assessments have been conducted in nearshore or coastal environments of the central and southern portions of Brazil (Anderson *et al*., 2019, 2022; Gibran, 2007). The main challenge of such studies is to understand the relationships between fish and habitat when species are phylogenetically closely related. Another important challenge is to understand the role and importance of abiotic variables (*e.g*., the reef topographic complexity) in shaping habitat use and the spatial distribution of sympatric species (Anderson *et al*., 2019; Connell, 1980; Schmitt & Coyer, 1982; Schoener, 1974; Wagner *et al*., 2012).

Serranidae (*i.e*., groupers and sea basses) are considered key marine teleost fishes, playing a crucial role as predators and mesopredators, and maintaining ecosystem structure, functioning and resilience (Baum & Worm, 2009; Bessa, 2011; Burkholder *et al*., 2013). Groupers and sea basses inhabit diverse habitats of the reef ecosystems (*e.g*., unconsolidated substrates, coral and rocky reefs), most commonly in depths <200 m (Anderson *et al*., 2014, 2019). Their high

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diversity, wide distribution, long lifespan, complex reproductive behaviour, high functional relevance and crucial ecological roles make Serranidae key model species to investigate environmental affinities and habitat associations (Anderson *et al*., 2019; Craig *et al*., 2011; Gibran, 2007). However, many species are heavily targeted by industrial and artisanal fisheries, and are overexploited and endangered (Anderson *et al*., 2014; Oliveira Freitas *et al*., 2011; Sadovy de Mitcheson *et al*., 2013). Five key sympatric Serranidae, *Cephalopholis fulva* (Linnaeus, 1758), *Epinephelus adscensionis* (Osbeck, 1765), *Rypticus saponaceus* (Bloch & Schneider, 1801), *Paranthias furcifer* (Valenciennes, 1828) and a hybrid (*C. fulva* + *P. furcifer*), were selected to assess habitat use on an isolated island from the Vitória Trindade chain (VTC), south-western Brazil. The VTC, located on the Brazilian central coast, is composed of volcanic seamounts and an island complex situated in its easternmost part, about ~1200 km offshore. Trindade is the largest island of the VTC; its fish biodiversity and populations have been studied and monitored for almost three decades (Gasparini & Floeter, 2001; Guabiroba *et al*., 2020a, 2020b; Pereira-Filho *et al*., 2011; Pinheiro *et al*., 2011, 2015; Simon *et al*., 2013). However, large knowledge gaps remain regarding the habitat use of reef fishes in this and other isolated oceanic systems of the Atlantic Ocean (*e.g*., São Pedro and São Paulo, Fernando de Noronha, Rocas Atoll). Thus, in this study we aimed to assess the following questions: (a) is 'habitat complexity' the main structuring factor regarding populational distribution and habitat use of sympatric species (*i.e*., higher complexity and area availability = less niche overlap between sympatric species/low influence of density dependent mechanisms) and (b) are habitat low structural complexity/low spatial availability drivers of niche partition of sympatric species in different compartments of the habitat?

2 | MATERIALS AND METHODS

2.1 | Compliance with ethical standards

1. Were fishes collected as part of faunal surveys? No.
2. Were fishes killed during or at the end of your experiment (*e.g*., for tissue sampling)? No.
3. Were surgical procedures performed? No.
4. Did the experimental conditions severely distress any fishes involved in your experiments? No.
5. Did any procedures (*e.g*., predation studies, toxicity testing) cause lasting harm to sentient fishes? No.
6. Did any procedure involve sentient, unanaesthetized animals that were subjected chemical agents that induce neuromuscular blockade, such as muscle relaxants? No.

2.2 | Study area

The VTC extends in an east–west alignment between 19° and 21°S latitude from 200 to 1200 km from the Brazilian shore (Figure 1). The only emerged portion of the VTC comprises the youngest (~4 my/lower Pliocene) (Pereira Monteiro *et al*., 2022) and farthermost structures of the VTC: Trindade Island (TRI; the largest) and Martin Vaz Archipelago. Field work was carried out on TRI, which harbours the richest fish fauna of the VTC, followed by the Vitória and Davis seamounts (Pinheiro *et al*., 2015). TRI has a Brazilian navy military base established in 1957. Forty navy military crew and eight researchers use the island's facilities. Every 4 months, the military crew is replaced and the scientists are replaced every 2 months, when the facilities are resupplied (Guabiroba, Santos, *et al*., 2020b; Theophilo *et al*., 2022). Recreational fishing (*i.e*., mostly angling and spearfishing) is one of the main leisure activities allowed by the Brazilian navy around the island (see Guabiroba, Santos, *et al*., 2020b). Fishing activities are higher (*e.g*., daily) at Calheta and Tartarugas, two sites located at the eastern portion of the island (see Guabiroba, Santos, *et al*., 2020b) (Figure 1).

2.3 | Sampling design, fish counts and habitat characterization

Data were collected during two expeditions. In June/July 2016 reef bottom structural complexity data (abiotic data) were sampled. In September/October 2019 reef fish density and biomass data (biotic data) were sampled. Six sites were selected: two sites located along the eastern shore of the island (Tartarugas and Calheta), two sites on the northern shore (Ponta Norte and Farilhões) and two sites on the western shore (Racha and Eme). The eastern sites (Tartarugas and Calheta) are mostly constituted by rocky reefs covered with biogenic structures formed by crustose coralline algae (CCA), macroalgae, sponges and corals. The northern and western sites (Ponta Norte, Farilhões, Racha and Eme) are rocky reefs covered mostly by macroalgae, sponges and corals (Figure 1).

Standard 40m^2 (20 × 2 m) strip belt transects [underwater visual censuses (UVCs)] were used to estimate the Serranidae density (Anderson *et al*., 2019, 2020). A total of 120 transects were performed (*i.e*., 4800 m^2), 20 (*i.e*., 800 m^2) in each of the six sites. Water transparency ranged from 10 to 50 m, sample depth varied between 5 m (Calheta) and 25 m (Racha), and water temperature ranged from 25 to 28°C. All transects were performed in the morning when all selected species were active (Anderson *et al*., 2019; Gibran, 2007).

Five species were selected as models to access habitat use due to their high density and biomass: the coney *C. fulva* (Linnaeus, 1758), the rock hind *E. adscensionis* (Osbeck, 1765), the greater soapfish *R. saponaceus* (Bloch & Schneider, 1801), the Creole fish *P. furcifer* (Valenciennes, 1828) and the hybrid between *C. fulva* and *P. furcifer*, which is commonly detected at the island (Pinheiro *et al*., 2009; Reece, 2002). Two species are targeted by fisheries, *C. fulva* and *E. adscensionis* (Guabiroba, Santos, *et al*., 2020b). The five species selected for this study are not listed as threatened (IUCN, 2022).

Fish were counted and identified while the diver unrolled the tape measure along the length of the transect. The position of each individual in the water column (*e.g*., its distance from the bottom, including when sheltered) was recorded together with its body size (Anderson *et al*., 2019). Biomass was later estimated by the weight–length relationship ($W = a^{*}TL^{b}$) for each species (i.e., W is the total body weight

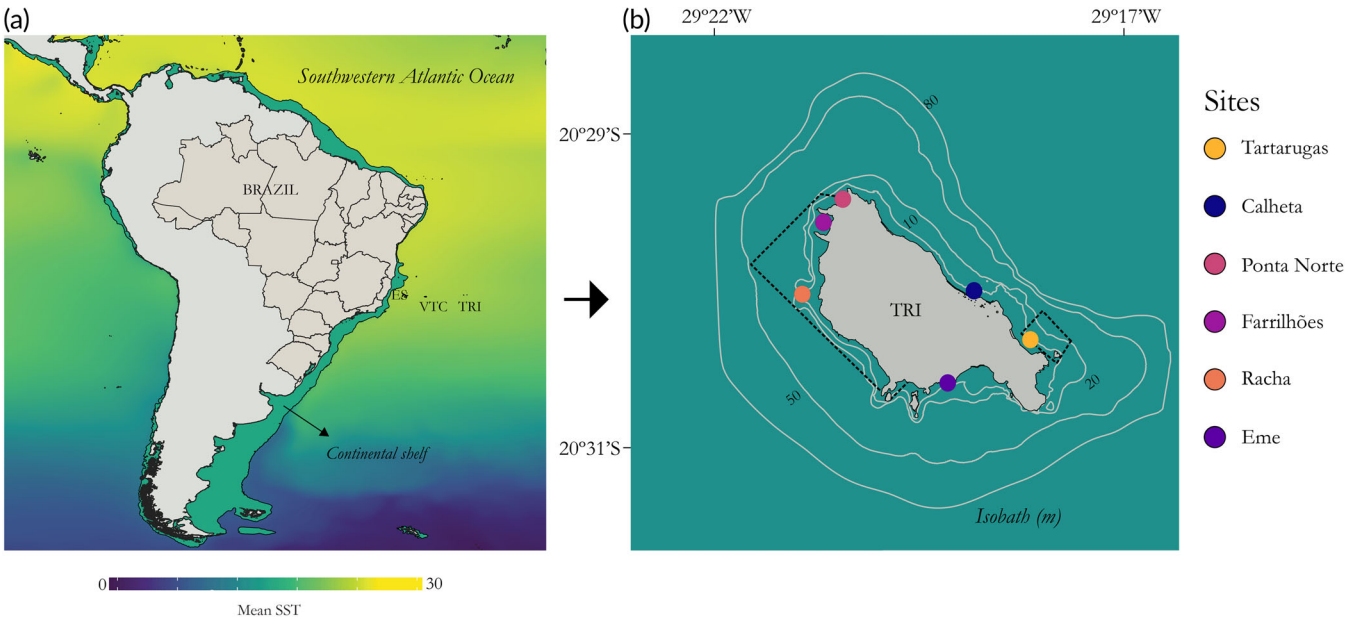

FIGURE 1 Study area. (a) Map showing the position of Vitória Trindade chain (VTC) at the central portion of the Brazilian coast. The gradient scaled horizontal bar represents the average sea surface temperature. (b) Map showing the position of sampled sites around Trindade Island (TRI). The dashed polygons represent the protected sites (fisheries restricted area).

(g), *TL* is the total lenght of the individual (cm), *a* and *b* are the coefficients of the functional regression between W and TL) (Froese & Pauly, 2022).

While rolling back the tape measure, the diver also recorded the following environmental variables every 5 m: (a) the rocky reef slope (angle inclination in °), (b) the number of small (radius = $r < 10$ cm), medium ($r = 10$–50 cm) and large ($r > 50$ cm) rocky boulders, and (c) the number of small (opening = $o < 10$ cm), medium ($o = 10$–50 cm) and large ($o > 50$ cm) holes/shelters (adapted from Anderson *et al.*, 2019). A total of 480 habitat complexity measurements (samples) were taken. The habitat complexity sampling covered the majority of topographic features of TRI reefs (*e.g.*, shallow and deep habitats, biogenic and rocky reefs).

2.4 | Data analysis

To assess whether reef topography, species distributional patterns of density and biomass, and species habitat use change among sites, Bayesian generalized linear models (Bayesglms) with default priors were performed using the 'arm' R package (Gelman & Su, 2021). The program is a modification of classic generalized linear models which uses an approximate expectation–maximization (EM) algorithm to update the betas at each step using an augmented regression to represent the prior information (Gelman & Su, 2021). The algorithm applies Student *t* prior distributions for the coefficients. The prior distribution for the constant term is set so it applies to the value when all predictors are set to their mean values (Gelman & Su, 2021). To select the best Bayesglms models, two information criterions were considered: Akaike information criterion (AIC) (Akaike, 1998) and Bayesian information criterion (BIC) (Neath & Cavanaugh, 2012; Schwarz, 1978). The lowest AIC and BIC values indicate the best models (Akaike, 1998; Neath & Cavanaugh, 2012; Schwarz, 1978). Both information criteria were obtained using the function 'summ' from the 'jtools' R package (Long, 2022). Graphs and diagrams were designed and plotted using the 'circlize' (Gu *et al.*, 2014) and 'ggplot2' (Wickham, 2016) R packages. All analyses were conducted in the R computing environment (R Development Core Team, 2021). Data were assumed to have a positive Poisson distribution (Brown & Zhao, 2002; Legendre & Legendre, 2012; Zar, 1999).

3 | RESULTS

3.1 | Trindade Island's reef topographic features

Compared to the other sites, Racha showed significantly higher reef structural complexity (*i.e.*, higher number of small, medium and large rocks) and shelter availability (*i.e.*, higher number of small, medium and large holes) (Bayesglm = $Pr[>|z|] < 0.05$) (Figure 2c). This site also presented significantly higher habitat spatial availability (*i.e.*, higher reef inclination and height) (Figure 3c). Farilhões showed significance for two variables indicative of shelter availability, small rocks and small holes, Ponta Norte only for small rocks and Eme for small holes (Figure 2c). Compared to other sites, Tartarugas and Calheta presented high reef structural complexity, heterogeneity and shelter availability, but no statistical significance regarding any environmental variable analysed (Figure 2c).

3.2 | Population structure

Considering all species *versus* all sites, most individuals had body size between 15 and 30 cm Total Lenght (TL) (83.11%, or 453 individuals,

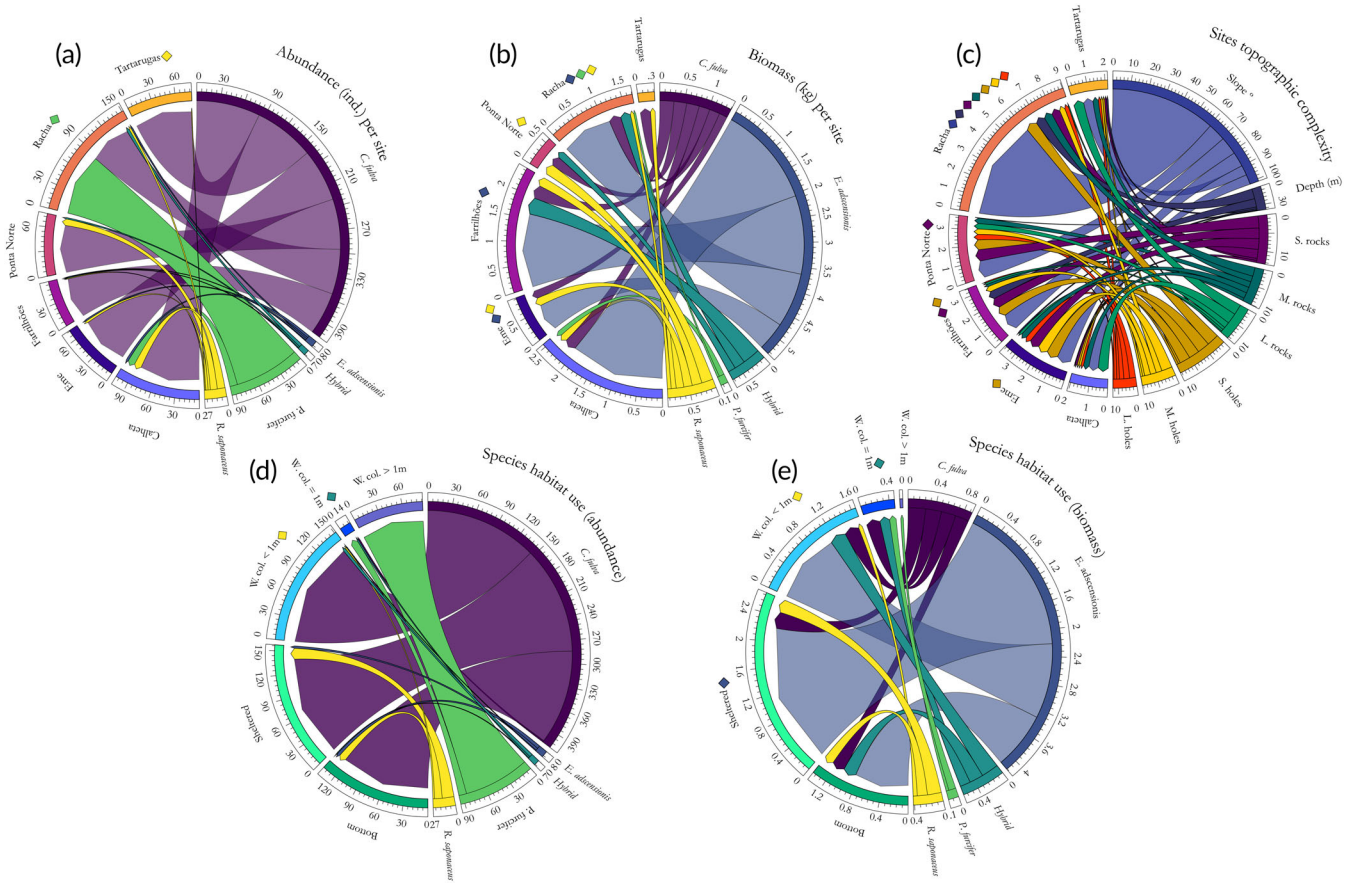

FIGURE 2 Chord diagrams showing quantitative relationships among density and biomass of species *vs*. sites (a, b). Chord diagram showing topographic complexity indicative variables *vs*. sites ©. Chord diagrams showing quantitative relationships among density and biomass of species *vs*. habitat use indicative variables (d, e). Diamonds represent significant differences of quantitative relationships among species density and biomass *vs*. sites (a, b), among topographic complexity indicative variables *vs* sites (c), and among density and biomass of species *vs*. habitat use indicative variables (d, e) (Bayesglm = $Pr(>|z|) < 0.05$)). The colours of the diamonds represents the species (a, b, d, e) and reef complexity variables (c).

considered herein subadults or adults) (Figure 3a). In contrast, small 5–10 cm TL individuals (considered herein juveniles) represented only 6% (33 individuals) of the population distributed across six sites (Figure 3a,b). Similarly, large individuals (productive breeders) (Barneche *et al*., 2018; Saenz-Agudelo *et al*., 2015) with body sizes of 35–60 cm TL were rare and represented only 10% (59 individuals) of the serranid assemblage (Figure 3a). The population structure of species exhibited a similar pattern: the majority of *C. fulva* individual body sizes ranged from 15 to 30 cm (80.14%/327 individuals, subadults and adults) (Figure 2a). Juveniles (5–10 cm) represented only 7.3% (30 individuals) of the population (Figure 3a,b). Large females/reproductive males (individuals 30–40 cm) represented only 12.5% (51 individuals) of the population (Figure 3a). *C. fulva*'s larger individuals and juveniles were detected mostly at Calheta (Figure 3a,b). Most *E. adscensionis* individuals were adults (40–60 cm; 87.5%, seven individuals). No juveniles were recorded in any of the six sites (Figure 3a,b). The *R. saponaceus* population recorded consisted of subadults and adults with body sizes ranging from 10 to 35 cm. No large breeders or juveniles were detected (Figure 3a,b). The *P. furcifer* population recorded consisted mostly of juveniles (86.3%/82 individuals), and adults (individuals ≥20 cm) represented 13% (13 individuals) of the population. Most juveniles of *P. furcifer* were detected at Racha (Figure 3a). All hybrids were adults (20–30 cm) and no juveniles were recorded (Figure 3a,b). Most hybrids were recorded at Racha (Figure 3a,b). Considering the sites as a potential nursery habitat for the studied species, Racha showed significance regarding the distribution of young individuals of the Creole-fish (Figure 3b).

3.3 | Frequency of occurrence and spatial distribution

A total of 545 individuals were sighted. *C. fulva* presented the highest density [408 individuals/frequency of occurrence (FO) 75%] followed by *P. furcifer* (95 individuals/FO 17%), *R. saponaceus* (27 individuals/FO 5%), *E. adscensionis* (eight individuals/FO 1%) and the *fulva-furcifer* hybrid (seven individuals/FO 1%). *C. fulva* presented the highest biomass (95.06 kg/81.26%), followed by *E. adscensionis* (11.12 kg/FO 9.5%), *R. saponaceus* (4.6 kg/FO 4%), *P. furcifer* (4.5 kg/FO 3.89%)

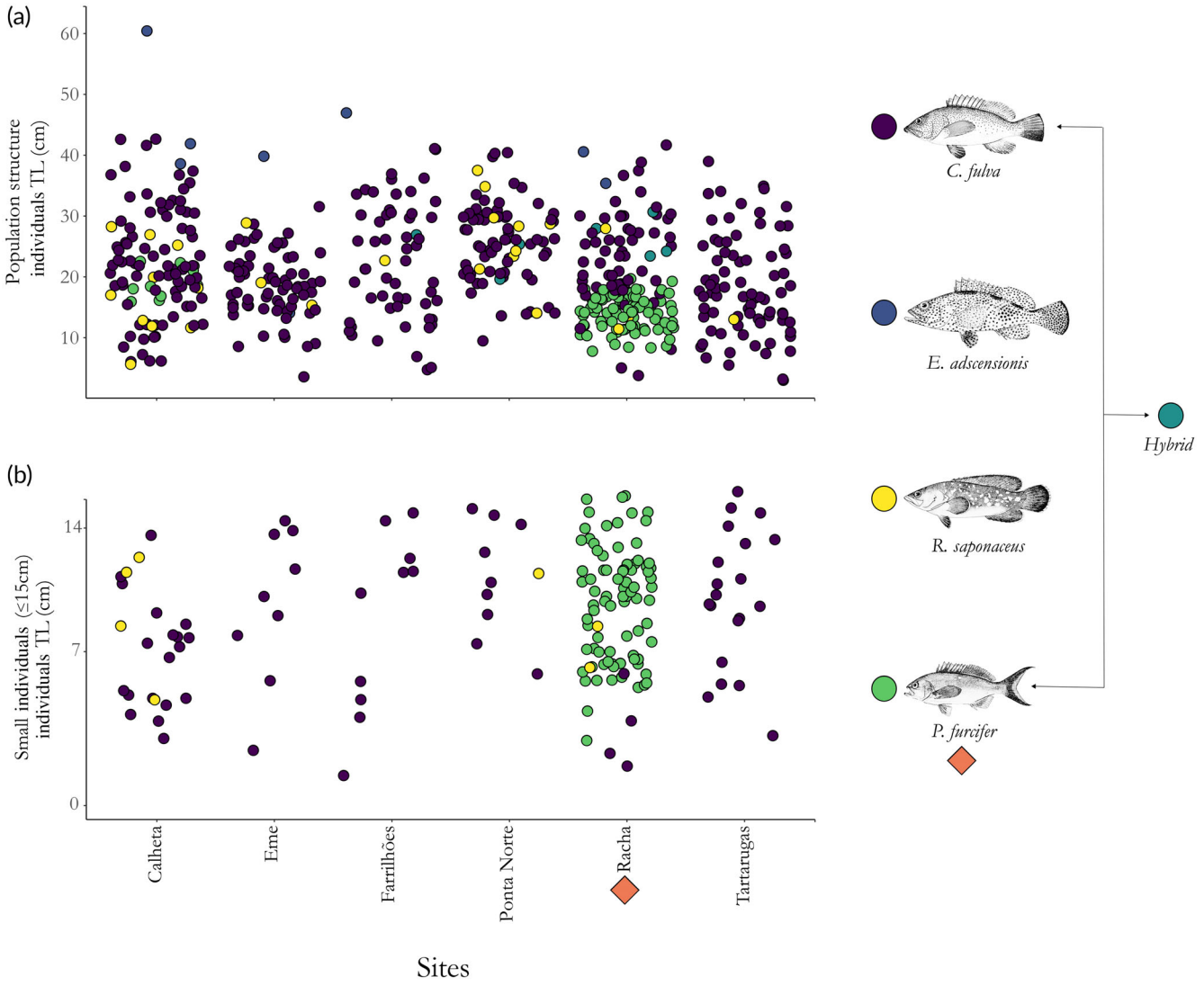

FIGURE 3 Scatterplots showing the population structure of serranids across six sites of TRI. (a) Species individuals' sizes *vs*. sites. (b) Serranid subadults and juvenile sizes (cm) *vs*. sites. Small circles represent the species, different colours represent the species, diamonds represent statistical significance (Bayesglm = Pr(>|*z*|) < 0.05) and different colours represent the sites.

and the hybrid (FO 1.33%). *C. fulva*'s spatial distribution of density and biomass showed no significant differences among sites (Bayesglm = Pr(>|*z*|) > 0.05) and showed the highest density among the studied species at all sites (Figure 2a,b). *E. adscensionis* density showed no significant difference among sites (Figure 2a). The highest biomass was detected at Calheta and Farilhões (Figure 3b); Racha, Farilhões and Eme showed significant differences in biomass among sites (Figure 2b). *R. saponaceus* was detected at all six sites, but the highest density was detected at Calheta (Figure 2b). *R. saponaceus* individuals were significantly larger at Ponta Norte compared to all other sites (Figure 2b). *P. furcifer* was detected at two sites, Calheta and mainly Racha. The latter site showed significant differences in density and biomass compared to the other sites (Figure 2a,b). Hybrids were detected at Racha, Farilhões and Ponta Norte, and while density and biomass seemed higher at Racha (Figure 2a,b), no significant difference in either variable were detected among sites.

3.4 | Habitat use

All species presented associations (*e.g*., feeding, reproduction, sheltering from predation) with the habitat's structural complexity (Figure 2c, e). *C. fulva* showed a high niche plasticity, inhabiting multiple subcompartments of the habitat: near the bottom, sheltered (*i.e*., inside cavities or holes) or foraging in the water column ≤1 m from the reef bottom (Figure 2d,e). *E. adscensionis* individuals were detected at the bottom of the reef or at the water column <1 m above substrate; the majority of individuals were detected sheltered (*i.e*., inside holes or crevices) (Figure 2d,e). *E. adscensionis* biomass was significantly higher for the variable 'sheltered' (Figure 2d,e). Most *R. saponaceus* individuals were detected sheltered (Figure 2d,e). Density and biomass showed significance regarding the habitat use variable 'water column <1m' (Figure 2d,e). *P. furcifer* was detected in the water column, with most specimens swimming >1 m above the reef bottom (Figure 2d,e).

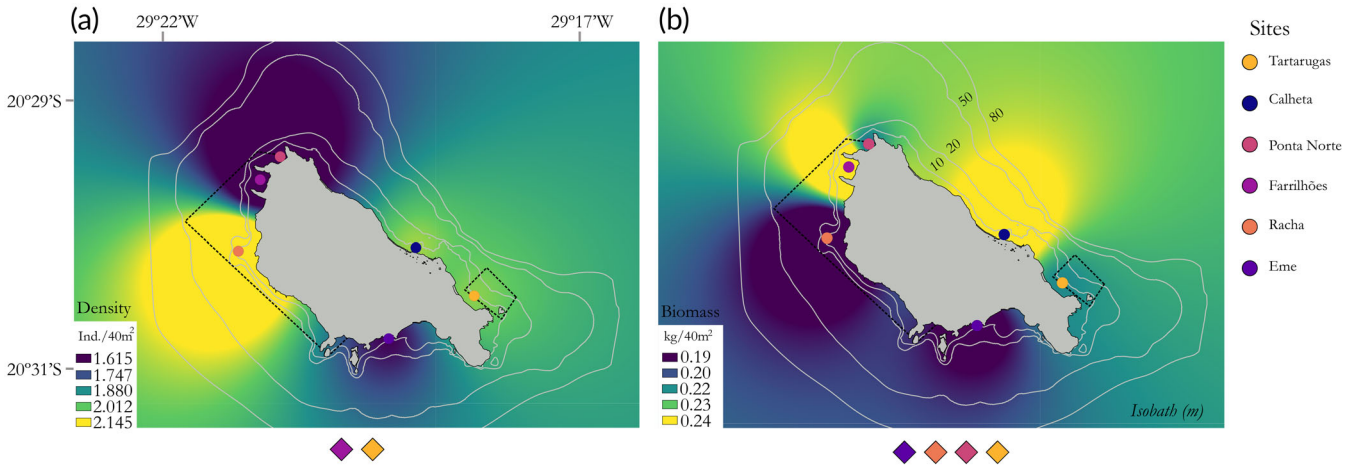

FIGURE 4 Distributional patterns of average density and biomass among sites. Interpolated colours represent the average distributional values among sites. Diamonds represent statistical significance (Bayesglm = Pr(>|z|) < 0.05). The colours of the diamonds represent the sites.

Density and biomass showed no significance regarding any of the habitat use variables (Figure 2d,e). Hybrids were detected near the reef bottom and in the water column (Figure 2d,e). Hybrid density and biomass showed significance for the habitat use variable 'water column = 1m' (Figure 2d,e).

3.5 | Average density and biomass across sites

Our results indicate that habitat complexity is a key driver of structuring the spatial distribution of density and biomass of species across sites (Figs. 2c and 4). The density and biomass of focal species were heterogeneously distributed (Figure 4a). The stacked average density varied among sites from 1.61 to 2.14 individuals per UVC. Significant difference in density was detected for Farilhões and Tartarugas (Figure 4a). The stacked average biomass varied from 0.19 to 0.24 kg per UVC (Figure 4b). Significant differences in average biomass were detected for Eme, Racha, Ponta Norte and Tartarugas (Figure 4b). See suplementary material (Appendix S1) Bayesglms outputs.

4 | DISCUSSION

The heterogenic reef topography of TRI provides different habitats (Coelho *et al*., 2012) (*e.g*., eastern portion constituted mostly by shallow rocky reefs covered by biogenic CCA structures, the western portion constituted mostly of deeper rocky reefs) that appear to influence the species' spatial distribution and habitat selectivity (Almany, 2004a; Anderson *et al*., 2019; Gibran, 2007). Our work presents remarkable similarities of habitat use patterns for serranids to those reported by previous works conducted on nearshore and coastal environments (Anderson *et al*., 2019; Gibran, 2007). Species spatial distribution and habitat use in both isolated and coastal environments seems to be influenced by the reef's topographic complexity and density-dependent mechanisms (*e.g*., inter and intraspecific competition, predation) (Almany, 2004a, 2004b; Anderson *et al*., 2019, 2020; Gibran, 2007).

4.1 | Species density and biomass spatial distribution

The *C. fulva* populations showed a homogenous distribution in density and biomass among the six sites. Compared to the other species studied, the densities and biomass of *C. fulva* were higher at all sites. Such homogenous distributional patterns explain why no significant differences among sites were found when *C. fulva*'s populational descriptors were analysed *versus* the factor 'sites'. Our findings corroborate the results reported by Coelho *et al*. (2012) regarding the spatial distribution of *C. fulva* across 11 sites around TRI. According to Coelho *et al*. (2012), no significant differences were detected for *C. fulva* density, either horizontally (across sites) or vertically (across different depth strata) (see Coelho *et al*., 2012). According to Guabiroba, Santos, *et al*. (2020b) *C. fulva* is highly targeted by angling and spearfishing activities in TRI. According to Coelho *et al*. (2012), *C. fulva*'s population on TRI is the densest compared to the Caribbean and coastal Brazilian populations. Despite the unusual high density of *C. fulva*'s populations on TRI, constant anthropic pressure has reduced the populations over time (Guabiroba, Santos, *et al*., 2020b).

The *R. saponaceus* population also showed a homogeneous distributional pattern, being detected in all six sampled sites. However, its higher density and biomass found at Calheta indicate an affinity towards shallow habitats. The populational descriptors (*i.e*., density and biomass) of *R. saponaceus* across TRI can be considered lower compared to those of *C. fulva*. *R. saponaceus* is found to be mainly solitary and its feeding habits (*i.e*., solitary ambush predator) contribute to dispersing individuals across the reefs they inhabit. The great majority of *Rypticus* are solitary species, found on shallow reefs positioned motionless on the bottom, inside or near shelters (Froese &

Pauly, 2022; Randall & Schraml, 2010). The species is not targeted by fishing activities on TRI and the population appears stable.

The other serranids in this study showed heterogeneous distributional patterns across sites. The highest density and biomass of *E. adscensionis* were detected at Racha (high vertical complexity deep reef) and Calheta (high horizontal complexity shallow reef), both sites with high reef topographic complexity. Individuals of *E. adscensionis* were not detected in two of six sites (Ponta Norte and Tartarugas) and throughout the study a small number of individuals were detected. Pinheiro *et al.* (2011) reported that *E. adscensionis* was detected in 16% of all UVCs conducted around TRI, showing a mean abundance of 0.28 individuals per UVC and a biomass of 575 g per UVC. According to Guabiroba, Santos, *et al.* (2020b), *E. adscensionis* is highly targeted by angling and spearfishing on TRI, and severe populational declines have been detected overtime. Moreover, during fish population monitoring expeditions in 2012 and 2013 on TRI, no *E. adscensionis* individuals were detected during UVC sampling campaigns, indicating that the species' stocks had severely declined (Guabiroba, Santos, *et al.*, 2020b). Conservation initiatives regarding *E. adscensionis* populations on TRI must be considered immediately to avoid the functional extinction of the species in the near future.

P. furcifer, a gregarious planktivore (Froese & Pauly, 2022), was detected in two sites, Racha and Calheta, and the highest density and biomass were detected at Racha, an environment with high reef slope angle inclination and high bottom complexity. Racha, positioned on the western portion of TRI, is the site where all the species studied herein were detected, indicating an environment with high ichthyofaunistic diversity and therefore zooplankton availability (*i.e.*, direct and indirect food resource). Planktivorous reef fishes are able to seek out plankton where it is most concentrated (Clarke *et al.*, 2005; Hamner *et al.*, 1988; Jones, 1987). The Racha site is an islet with a rocky reef structure formed by vertical basaltic walls, reaching 30 m at the bottom, providing strong local currents and an abundant three-dimensional foraging space for planktivorous species (Kingsford & MacDiarmid, 1988).

Hybrids were absent at Eme, Tartarugas and Calheta, which indicates a selectivity towards deeper rocky reefs. Hybrids of *C. fulva* and *P. furcifer* exhibit morphological traits of both species: the head is similar to *P. furcifer* and the posterior body portion is similar to *C. fulva* (*e.g.*, truncate caudal fin instead of forked). Such hybridization occurs in other oceanic environments where both species are sympatric (*e.g.*, Cuba, Bermuda, Brazil) (Bostrom, 2000; Bostrom *et al.*, 2002; Pinheiro *et al.*, 2009; Smith, 1966). According to Bostrom (2000) the morphology of the hybrids enables the specimens to prey on items included in the *C. fulva* diet (*i.e.*, crustaceans and fish) and the *P. furcifer* diet (*i.e.*, zooplankton). Considering the small size of the hybrid mouth compared to *C. fulva*'s mouth structure, specialists claim that hybrids feed mostly on zooplankton (Bostrom, 2000; Bostrom *et al.*, 2002), which may explain the hybrids' selectivity for deeper rocky reef sites with the presence of stronger currents (*e.g.*, Racha).

4.2 | Species populational structure across sites

The populations of *C. fulva* across TRI sites can be considered healthy (Begon & Townsend, 2020) and spatially homogeneous. The majority of individuals detected were between 15 and 30 cm (TL) (*i.e.*, subadults and adults) (Froese & Pauly, 2022). Juveniles were detected in all studied sites, indicating local recruitment (*i.e.*, spawning aggregations and subsequent larval settlement are occurring in local scale) (Jones *et al.*, 1999; Strathmann *et al.*, 2002). The presence of the *C. fulva* juveniles was higher at Tartarugas and Calheta, indicating young individuals' affinity with TRI western shallow rocky reefs covered with biogenic CCR structures (*i.e.*, potential nursery areas) (Aburto-Oropeza *et al.*, 2007; Nagelkerken *et al.*, 2012). TRI western sites also showed a higher macroalgal cover and diversity compared to other sites, which can positively influence reef fish recruitment (Evans *et al.*, 2014; Fulton *et al.*, 2019, 2020). Regardless of the intense anthropic pressure on *C. fulva* populations on TRI (Guabiroba, Santos, *et al.*, 2020b), the species seems to be thriving at all studied sites, exhibiting one of the densest populations compared to the Caribbean and other sites along the north-east and central Brazilian coasts (Coelho *et al.*, 2012). The unusual high density of *C. fulva* populations across TRI sites may also indicate a mesopredator release effect (*e.g.*, low populational density of larger groupers and sharks) (Feit *et al.*, 2019; Guabiroba, Santos, *et al.*, 2020b; Sandin *et al.*, 2010).

The secretive, solitary and nocturnal *R. saponaceus* (Courtenay Jr, 1967; Froese & Pauly, 2022) was also present homogeneously across the TRI sites. In contrast, juveniles (<15 cm) were detected in three sites, Calheta (higher juvenile density), Ponta Norte and Racha. Juveniles of *R. saponaceus* seem to have habitat affinities with Calheta environmental characteristics: shallow rocky reef covered by biogenic CCA structures and high benthic diversity (*e.g.*, macroalgae, sponges and coral cover) (Evans *et al.*, 2014; Fulton *et al.*, 2019, 2020). Such a pattern of habitat selectivity by juveniles of a reef fish species validates Calheta as a potential nursery environment for reef fish. *R. saponaceus* populations are not targeted by fisheries across TRI sites (Guabiroba, Santos, *et al.*, 2020b).

The largest individuals of *E. adscensionis* were recorded at Calheta and no juveniles were detected in any of the six sites. *E. adscensionis* is highly targeted by local systematic angling fishing activities, which may have contributed to the depletion of the population (Guabiroba, Santos, *et al.*, 2020b; Pinheiro *et al.*, 2010, 2011, 2015). Fisheries pressure and populational declines of *E. adscensionis* populations at TRI have been reported since 2010 (Guabiroba, Santos, *et al.*, 2020b; Pinheiro *et al.*, 2010, 2011, 2015). According to Pinheiro *et al.* (2010) there is evidence that overfishing may have been responsible for local extinctions of reef species on other Brazilian oceanic islands. Local conservation initiatives (*e.g.*, exclusion of the species from the local fishing target list) are urgent to avoid the total collapse of *E. adscensionis* stocks around TRI.

P. furcifer juveniles were detected at Racha, indicating an affinity with deep, high structural complexity rocky reefs. The Racha site seems to be the optimum environment (*i.e.*, nursery and foraging

FIGURE 5 Three different cryptic patterns of the coney (*C. fulva*) while foraging on different types and colours of substrate: (a) red morph, foraging near red algae (coralline crustose algae [CCA]); (b) red camouflage morph, foraging near green algae and yellow sponges; (c) dark morph, foraging near/against shelters and crevices; (d) black and white morph, foraging near CCA and green macroalgae. Images taken at TRI from 2016 to 2019 by Anderson A. B.

habitat) for *P. furcifer* compared to the other five sites. The high density of juveniles <10 cm at Racha indicates self-recruitment of a species highly associated with specific environmental conditions. Local zooplankton circulation around TRI may also influence the settlement of juveniles of *P. furcifer* (Boehlert & Mundy, 1993; Clarke *et al*., 2005; Kingsford & MacDiarmid, 1988; Rodríguez *et al*., 2001).

No hybrid juveniles were recorded. The hybrids' populational structure and spatial distribution across TRI are the consequences of a stochastic phenomenon (*i.e*., interspecific hybridization of the parental species *C. fulva* + *P. furcifer*). Several processes have been proposed to explain the abundance of hybrid reef fish in a specific area: external fertilization, density-dependent mechanisms (*e.g*., competition for limited spawning grounds) and spatial or dietary overlap in parental species (Montanari *et al*., 2012; Pyle & Randall, 1994). The high density of both parental species at Racha may explain the constant presence of hybrids across TRI. Hybrids are not targeted by fisheries at TRI.

4.3 | Species habitat use

C. fulva individuals were detected sheltering (inside holes and crevices) motionless at the reef bottom and swimming in the water column (vertically <1 m and at 1 m), but never swimming above 1 m vertically distant from the bottom. The species displayed a plastic and efficient habitat use, being detected in nearly all environmental substrata analysed herein, except vertically higher than 1 m from the bottom, where planktivores and omnivores are expected to be foraging (Mendes *et al*., 2019; Silvano & Güth, 2006). The proportional distribution of *C. fulva* density and biomass across different strata of the habitat explains why no significant differences among habitat use were found. *C. fulva* is a protogynous hermaphrodite carnivorous fish that feeds mostly on teleostei and crustaceans (Coelho *et al*., 2012; Froese & Pauly, 2022; Gathaz *et al*., 2013). *C. fulva*'s morphological traits [*e.g*., truncate caudal fin, small body size (maximum TL 44 cm), high reproductive rate (150×10^3 to 280×10^3 eggs per female) and fast sexual maturation ($\sim$ 20 cm TL to sex change)] (Froese & Pauly, 2022) enable it to colonize and thrive at different microhabitats found around TRI. During the sampling campaigns, four distinct camouflage patterns were recorded for *C. fulva* individuals: the red morph (foraging close to rocky and CC Areefs), the red camouflage morph (foraging close to yellow sponges, macroalgae, rocky and CCA reefs), the dark morph (foraging near holes and dark crevices), and the black and white morph (foraging at the bottom near macroalgae, rocky and CCA reefs) (Figure 5). The rapid colour change (*i.e*., camouflage) aptitude of *C. fulva* may increase the capture success rates, enabling the species to use several 'subcompartments' of the ecosystem. Different colours were recorded mostly when individuals were foraging in a solitary way. Similar camouflage patterns were reported by Anderson *et al*. (2019) for *Mycteroperca acutirostris* (Valenciennes, 1828) at subtropical reefs of the southern

Brazilian coast. Rapid colour change was also documented for *E. adscensionis* at the Gulf of Mexico (see Kline *et al*., 2011).

E. adscensionis individuals were detected mostly sheltered (inside holes and crevices), motionless at the reef bottom and swimming in the water column (vertically <1 m), never swimming above 1 m vertically distant from the bottom. Significant association of the species was detected with the habitat use variable 'sheltered', which indicates high habitat selectivity or a higher specificity of *E. adscensionis* regarding the environment compared with *C. fulva*, which may have contributed to less competition (niche segregation). All large individuals (> 40 cm) were detected inside holes and crevices, and others never far from their shelters. The rock hind is a long-lived (~30–45 years lifespan) aggressive territorial protogynous grouper, with rapid colour changing camouflage aptitude (Burton *et al*., 2012; Kline *et al*., 2011; Marques & Ferreira, 2018). According to Kline *et al*. (2011), *E. adscensionis* rapid colour change is used for confronting territory intruders and displays of aggression towards females. All *E. adscensionis* individuals displayed overly skittish behaviour when approached. The intense anthropic pressure (angling and spearfishing) on the fragile population of *E. adscensionis* at TRI over time (Guabiroba, Santos, *et al*., 2020b) may have selected, artificially (Griffin *et al*., 2022), aggressive, furtive and evasive individuals. Anthropic pressure on the *E. adscensionis* population at TRI may have altered the species diel cycles (Griffin *et al*., 2022; Harmange *et al*., 2021).

R. saponaceus individuals were recorded mostly sheltered, with a large number motionless at the bottom, inside holes and crevices, and a few individuals in the water column (never >1 m) were detected while avoiding other fish. Significant differences in density and biomass of *R. saponaceus* were detected for the habitat use variable 'water column <1m', which can be explained by considering the higher density and biomass values for the habitat use variables 'sheltered' (*i.e*., inside holes and crevices) and 'bottom' (*i.e*., motionless at the reef bottom). *R. saponaceus* is a nocturnal solitary sea bass with little available information regarding its growth, reproduction and feeding habits (Froese & Pauly, 2022). Considering our results and the evolutive features of the species (*e.g*., slender body shape, large mouth and buccal cavity, rounded caudal fin), one may assume that *R. saponaceus* is an efficient ambush nocturnal predator, highly associated with the reef three-dimensional complexity, relying on holes and crevices during the day to repose.

All *P. furcifer* individuals were recorded swimming in small shoals in the water column; no specimens were detected sheltered, near or at the bottom. The density and biomass of the species varied according to the use of the water column. Considering the density, the great majority of the population was detected in the water column, vertically >1 m from the bottom. The biomass, in contrast, was higher at the water column strata near the bottom (*i.e*., water column = 1 m), indicating a partition of habitat use: smaller individuals foraging above larger individuals. The niche partition by groups of the same species may reduce intraspecific competition (Frédérich *et al*., 2009; Pekcan-Hekim *et al*., 2016) in a small and isolated environment (*i.e*., an oceanic island) where food and space are considered limited resources (MacArthur & Wilson, 2016).

Hybrids were detected at the reef bottom, swimming in the water column <1 m from the reef bottom and swimming in the water column 1 m from the bottom. All individuals were solitary and skittish (Batista *et al*., 2012). The density and biomass of hybrids were significant for the habitat use variable 'water column = 1m'. The lowest number of individuals (density) and the smallest (biomass) were detected at 1 m vertically distant from the reef bottom, which explains the significant difference for the 'water column = 1 m' variable compared to all others. The morphological traits of hybrids, inherited from *P. furcifer* (*e.g*., head shape) and *C. fulva* (*e.g*., body shape), enable the unusual specimens to use both habitat subcompartments where *P. furcifer* and *C. fulva* forage Batista *et al*. (2012) reported several hybrid specimens, measuring from 15 to 25 cm, observed in shallow areas of the Rocas atoll (off the north-eastern Brazilian coast), alone or in pairs, swimming near the reef wall, using the crevices for shelter. Hybridization among serranids is documented worldwide, especially in oceanic islands and archipelagos (Batista *et al*., 2012; Bostrom, 2000; Locke *et al*., 2013; Payet *et al*., 2016).

5 | CONCLUSIONS

Populational spatial distribution of reef fish species, populational structure and habitat use are driven synergically by environmental structural complexity, evolutionary traits and density-dependent mechanisms. In both isolated and coastal ecosystems, reef fish species are associated with the topographic complexity of the environment and rely on such rugosity to feed, reproduce and take shelter from predation. The structural complexity and three-dimensional heterogeneity seem to govern species spatial distribution and habitat use. The unusual density and biomass of *C. fulva* across TRI sites may indicate a mesopredator release effect, potentialized by anthropic pressure (*i.e*., overfishing) on other targeted predatory fish (*e.g*., larger groupers and sharks). The populations of *E. adscensionis* should be monitored with great concern, considering the small population recorded and the absence of juveniles over time. *P. furcifer* tend to use different strata of the water column in different ontogenetic stages to avoid niche overlap. The present study has contributed to the knowledge of habitat use and thus spatial partitioning of key target species. Such information is a valuable tool in improving the knowledge of stakeholders, conservation scientists and politicians, which will contribute to the design of Marine Protected Areas in the near future.

AUTHOR CONTRIBUTIONS

A.B.A. contributed to manuscript conceptualization, manuscript preparation and review, and data analysis. H.T.P. and R.B.F.-F. contributed to manuscript preparation and review. C.E.L.F. and J.J.-C. contributed to manuscript review.

ACKNOWLEDGEMENTS

We thank the RESTORESEAS project (www.restoreseas.net), financed by Water JPI, Biodiversa+ and Europe Union, for A.B.A. postdoctoral fellowship and research funding, Fundação de Amparo à Pesquisa e

Inovação do Espírito Santo, Brazil for A.B.A. postdoctoral fellowship and research funding, and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (2019/24215-2; 2021/07039-6) for H.T.P. research fellowship and research funding. Thanks to PELD-ILOC and the Brazilian Navy for logistics support.

FUNDING INFORMATION

RESTORESEAS project (www.restoreseas.net), BIODIVERSA+, Water JPI and Europe Union (A.B.A. postdoctoral fellowship and research funding). Fundação de Amparo à Pesquisa e Inovação do Espírito Santo, Brazil, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil (A.B.A. postdoctoral fellowship and research funding). Hope for Reefs Initiative of the California Academy of Sciences and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (H.T.P. fellowship and funding, 2019/24215-2 and 2021/07039–6).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Anderson, A. B., Pinheiro, H. T., Francini-Filho, R. B., Ferreira, C. E. L., & Joyeux, J.-C. (2023). Habitat use of five sympatric predatory reef fishes at a remote island in the south-western Atlantic. *Journal of Fish Biology*, 1–12. https://doi.org/10.1111/jfb.15433