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Research Article

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Posted Date: June 18th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9997247/v1>

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Additional Declarations: No competing interests reported.

**Habitat selection and recruitment at the southern distribution limit of
Mussismilia hispida (Verrill, 1901) on a marginal reef in the Southwestern
 Atlantic**

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Abstract:

Recruitment is a fundamental process for maintaining reef ecosystem resilience and structure. However, habitat selection and recruitment of the endemic coral *Mussismilia hispida* remain poorly understood in Brazilian reef systems. This study characterized the benthic community associated with recruit microhabitats of *M. hispida* in Ilha Grande Bay, a marginal reef system in the Southwestern Atlantic, and evaluated recruit density and distribution at depths of 3, 5, and 8 m. Microhabitats were characterized at six sites using photoquadrats, while recruit density was quantified at seven sites using belt transects. A total of 472 recruits were recorded, resulting in an overall mean density of 0.90 ± 2.34 colonies m^{-2} . Recruit abundance differed significantly among depths and sites. The highest density occurred at 5 m depth, while Sítio Forte and Lagoa Azul exhibited the highest densities among sites. Twenty-seven taxa and morpho-functional groups were recorded within recruit microhabitats, which were dominated by turf algae throughout the depth gradient. Filamentous turf exhibited the highest cover and increased with depth, whereas branching coralline turf was more abundant at 3–5 m. *Sargassum* beds were more abundant at 3 m, while *Asparagopsis taxiformis* and crustose coralline algae

increased at 8 m. *Palythoa caribaeorum* showed greater cover at 3 m, whereas the cover of adult *M. hispida* colonies increased with depth. These findings provide the first assessment of coral recruitment in Brazilian marginal reefs as well, for Brazilian coast, and highlight the importance of long-term monitoring in marginal reef systems.

Keywords: Coral Recruitment; Warm Temperate Southwestern Atlantic; brain coral; rocky reefs;

Resumo:

O recrutamento é um processo fundamental para a manutenção da resiliência e da estrutura dos ecossistemas recifais. No entanto, a seleção de habitat e o recrutamento do coral endêmico *Mussismilia hispida* permanecem pouco compreendidos nos sistemas recifais brasileiros. Este estudo caracterizou a comunidade bentônica associada aos micro-habitats de recrutas de *M. hispida* na Baía da Ilha Grande, um sistema recifal marginal do Atlântico Sudoeste, e avaliou a densidade e a distribuição dos recrutas em profundidades de 3, 5 e 8 m. Os micro-habitats foram caracterizados em seis locais por meio de fotoquadrados, enquanto a densidade de recrutas foi quantificada em sete locais utilizando transectos em faixa. Um total de 472 recrutas foi registrado, resultando em uma densidade média geral de $0,90 \pm 2,34$ colônias m^{-2} . A abundância de recrutas diferiu significativamente entre as profundidades e os locais amostrados. A maior densidade foi observada a 5 m de profundidade, enquanto Sítio Forte e Lagoa Azul apresentaram as maiores densidades entre os locais avaliados. Foram registrados 27 táxons e grupos morfofuncionais nos micro-habitats dos recrutas, os quais foram dominados por algas turf ao longo de todo o gradiente de profundidade. O turf filamentoso apresentou a maior cobertura e aumentou com a profundidade, enquanto o turf de algas calcárias articuladas foi mais abundante entre 3 e 5 m. Bancos de *Sargassum* foram mais abundantes a 3 m, enquanto *Asparagopsis taxiformis* e as algas coralináceas incrustantes aumentaram a 8 m. *Palythoa caribaeorum* apresentou maior cobertura a 3 m, ao passo que colônias adultas de *M. hispida* aumentaram com a profundidade. Esses resultados fornecem a primeira avaliação do recrutamento de corais em recifes marginais brasileiros, bem como na costa brasileira e na Baía da Ilha Grande, e destacam a importância do monitoramento de longo prazo em sistemas recifais marginais.

Palavras chave: Recrutamento de corais; Temperado Quente do Atlântico; Coral cérebro; Recifes rochosos;

INTRODUCTION

72

73 Recruitment is a fundamental process for maintaining the emergent
 74 properties of reef systems, such as the preservation of coral cover and resilience in
 75 the face of disturbances and environmental changes (Hughes and Tanner, 2000;
 76 Ritson-Williams et al., 2009; Bramanti, 2016). It can be defined as the establishment
 77 of new individuals within a population. Although asexual reproduction through
 78 budding or fission plays an important role in reef building and framework
 79 cementation, sexual reproduction is the primary mechanism responsible for
 80 recolonizing populations of most coral species, enabling the colonization of new
 81 habitats, range expansion, and the generation of genetic variability (Connell et al.,
 82 1997; Ayre and Hughes, 2000; Cowen and Sponaugle, 2009). In this context, genetic
 83 diversity is particularly important for ensuring the long-term viability of marginal
 84 populations, where genetic variability is often lower than in central populations
 85 (Peluso et al., 2018). In addition, populations inhabiting marginal environments tend
 86 to be more fragmented and, consequently, more susceptible to local extinction
 87 (Kawecki, 2008). Coral ecosystems have experienced a series of anthropogenic
 88 impacts in recent decades, both at the global scale, such as ocean warming,
 89 increasing marine heatwaves, and ocean acidification (Laffoley and Baxter, 2016),
 90 and at the local scale, including overfishing, unsustainable tourism, increased
 91 sedimentation, and pollution (Correia, 2016; Loiola, 2019). The interaction among
 92 these factors exerts increasing pressure on scleractinian coral populations, leading
 93 to higher mortality rates and consequently intensifying the need for population
 94 replenishment through sexual reproduction (Harrison, 2011). Thus, recruitment
 95 plays a fundamental role in maintaining the stability and resilience of marginal coral
 96 ecosystems under scenarios of both global and local environmental change.

97 Marginal reefs can be defined as ecosystems composed of hard-bottom
 98 communities that develop under suboptimal environmental conditions, including
 99 highly variable temperatures, low light availability, high sedimentation, and
 100 turbidity (Soares, 2020). Marginal reefs differ structurally and functionally from
 101 tropical coral reefs (Zweifler, 2021; Dee, 2022) because they are located at the
 102 boundaries between biogeographic provinces. These reefs provide suitable
 103 ecological conditions for tropical and temperate species, such as corals, occurring
 104 near the limits of their distribution ranges, as well as for locally adapted subtropical
 105 species (Beger, 2014). Although corals have well-defined ecological requirements
 106 regarding temperature, light intensity, water transparency, suspended particulate
 107 matter, and salinity, some populations persist near the limits of one or more of these
 108 environmental variables or do not perform ecological roles like those observed in
 109 typical coral reef environments. According to criterion 3 proposed by Schoepf et al.
 110 (2023), Ilha Grande Bay, in the Southwestern Atlantic (circa 23° S) can be classified

as a marginal reef system, as its local coral community is characterized by low coral cover, low species richness, and reduced reef-building ecosystem function. In addition, marginal reefs may exhibit high levels of endemism due to the selective pressures imposed by suboptimal environmental conditions (Kawecki, 2008; Beger, 2014; Soares, 2019). Populations inhabiting marginal environments may also display unique genetic characteristics or phenotypic adaptations that enhance species fitness (Haak, 2010), such as increased thermal tolerance (Oliver and Palumbi, 2011; Hume et al., 2015). Furthermore, local adaptation within transitional regions characterized by gradual environmental gradients may promote speciation processes through disruptive selection (Doebeli and Dieckmann, 2003). Therefore, marginal reefs are unique ecosystems whose biodiversity, as well as the ecological processes regulating it, require further investigation.

As ocean temperatures increase, shifts in species distribution are expected, particularly the poleward expansion of corals, fishes, and other tropical species, a hypothesis known as tropicalization (Vergés et al., 2014). In this context, tropical species are expected to use marginal reefs as climate refugia from increasingly warm tropical reefs (Laffoley and Baxter, 2016), making these environments important natural laboratories for predicting future scenarios for corals and reef ecosystems. However, the expansion of coral distributions into marginal reefs will depend, among other factors, on the availability of suitable hard substrate for larval settlement, allowing long-distance dispersal and colonization by coral species. Experiments conducted on tropical reefs indicate that more than 70% of larvae from brooding corals settle within 300 m of the source colony (Sammarco and Andrews, 1988, 1989). Therefore, transitional environments may function as marine ecological corridors for coral species migrating in search of climate refugia (Odum and Barrett, 2005; Gibson et al., 2009). Thus, understanding patterns of habitat selection and recruitment is essential for predicting the effects of tropicalization on Southwestern Atlantic reefs.

The target species of this study, *Mussismilia hispida* (Verrill, 1901) is endemic to the Brazilian coral province, occurring from the Manoel Luiz coral bank, at Maranhão state (00° 46' S) to the coast of São Paulo State (24° 28'S), including the oceanic islands of Fernando de Noronha, Rocas Atoll, and Trindade (Amaral et al., 2007; Pereira Filho et al., 2019). It is a broadcast sequential hermaphroditic species that releases gametes directly into the seawater during synchronous spawning events (Pires et al., 1999; Neves and Pires, 2002). This species exhibits slow growth rates, averaging approximately 3.6 mm year⁻¹ (Silva et al., 2019). Genetically, *M. hispida* is structured into five populations along the Brazilian coast, with the highest genetic diversity reported for the central coast of Brazil and the lowest diversity observed near its southern distribution limit, in São Paulo and Ilha

Grande Bay (Peluso et al., 2018). Although the species has been increasingly studied in recent years with respect to other ecological aspects, such as associated fauna, bleaching tolerance, and substrate cover (Oigman-Pszczol and Creed, 2006; Banha et al., 2020; Mantelatto et al., 2020), recruitment and larval habitat selection remain important knowledge gaps. Thus, the present study characterized the benthic community within the microhabitats recruited by the scleractinian coral *Mussismilia hispida* in a marginal reef of the Southwestern Atlantic, as well as evaluated recruit density and distribution. Specifically, this study aimed to: (1) assess the density and distribution of *M. hispida* recruits at three comparative depths (3, 5, and 8 m) around Ilha Grande Bay; and (2) characterize and compare the microhabitats surrounding *M. hispida* recruits at the same depths and region. Through this approach, we sought to better understand the factors potentially influencing favorable habitat selection by the species and the distribution of recruits among the different microenvironments formed by the phyto and zoobenthic assemblages of Ilha Grande Bay.

MATERIALS AND METHODS

Study site

Ilha Grande Bay (IGB) is located in the southwestern region of the state of Rio de Janeiro, Brazil (between 23°05'–23°14'S and 44°05'–44°23'W), within a transitional zone between the Tropical and Warm Temperate provinces of the Southwestern Atlantic (Spalding et al., 2007). Its waters result from the mixing of coastal waters with Tropical Water (TW) and South Atlantic Central Water (SACW), whose strongest intrusion occurs during the spring–summer period mainly on deep waters (Kjerfve et al., 2021; Sousa et al., 2026). Sea surface temperature (SST) in the region ranges from 24.4–28.4 °C during summer and from 24–26 °C during winter (Creed et al., 2007). However, Barboza and Skinner (2021) demonstrated that SST has been increasing annually, reaching up to 34 °C during years strongly influenced by El Niño events. Salinity ranges from 27–37 in shallow waters and from 32–38 at 30 m depth (Creed et al., 2007). Ilha Grande Bay presents a high availability of rocky substrates, although these are restricted to the margins of rocky shores and islands, as well as to isolated rocky outcrops, frequently not exceeding depths greater than 10 m.

The benthic community is predominantly composed of macroalgae and the zoanthid *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860), with

contributions from the hermatypic corals *Mussismilia hispida* and *Madracis decactis* (Lyman, 1859), in addition to a high diversity of sponges, ascidians, and bryozoans (Creed et al., 2007; Mantelatto et al., 2020, 2022).

Sampling design

Two field campaigns were conducted for data collection: one during austral spring, in October 2024, to perform photoquadrat sampling and characterize the microhabitats, and another, during austral winter, in July 2025, to assess recruit density (Fig. 1).

The 2024 campaign, focused on characterizing the microhabitats surrounding *Mussismilia hispida* recruits, was conducted at the following sites: Ponta do Sítio Forte (SF), Ilha da Longa (IL), Ilha da Gipóia (GI), Ilha de Imboassica (IM), Ilha de Búzios (BZ), and Ilha do Brandão (BR). These sites are located at Northern region of Ilha Grande, all inside the bay, and close to the main navigation channel. These sites include two conservation units areas (BZ and IM) and diving and recreational activities (SF, IL, GI and BR). At each site, two 20 m transects were deployed at each of the three selected depths (3, 5, and 8 m). Active searches for *M. hispida* recruits were subsequently conducted within a 20 × 2 m belt transect sampling area. Recruits were defined here as colonies visible to the naked eye measuring up to 3 cm in diameter and containing one or more polyps. For each recruit found, a 10 × 10 cm quadrat was centered around the colony and photographed using the photoquadrat technique for subsequent microhabitat characterization. Twenty photoquadrats of recruits were obtained for each replicated transect at each depth stratum, except in transects where the minimum abundance of 20 recruits was not found within the sampling area (20 × 2 m).

The 2025 campaign was conducted during winter, between June 30 and July 3, to quantify recruit density. Surveys were carried out at Ilha do Brandão, Sítio Forte, Lagoa Verde (LV), Queimada Grande (QG), Praia Vermelha (PV), Lagoa Azul (LA), and Ilhas Botinas (BO). Two 20 m transects, marked at 1 m intervals, were deployed at depths of 3, 5, and 8 m. Within each 1 m² sampling unit along the transects, all *M. hispida* recruits encountered were quantified.

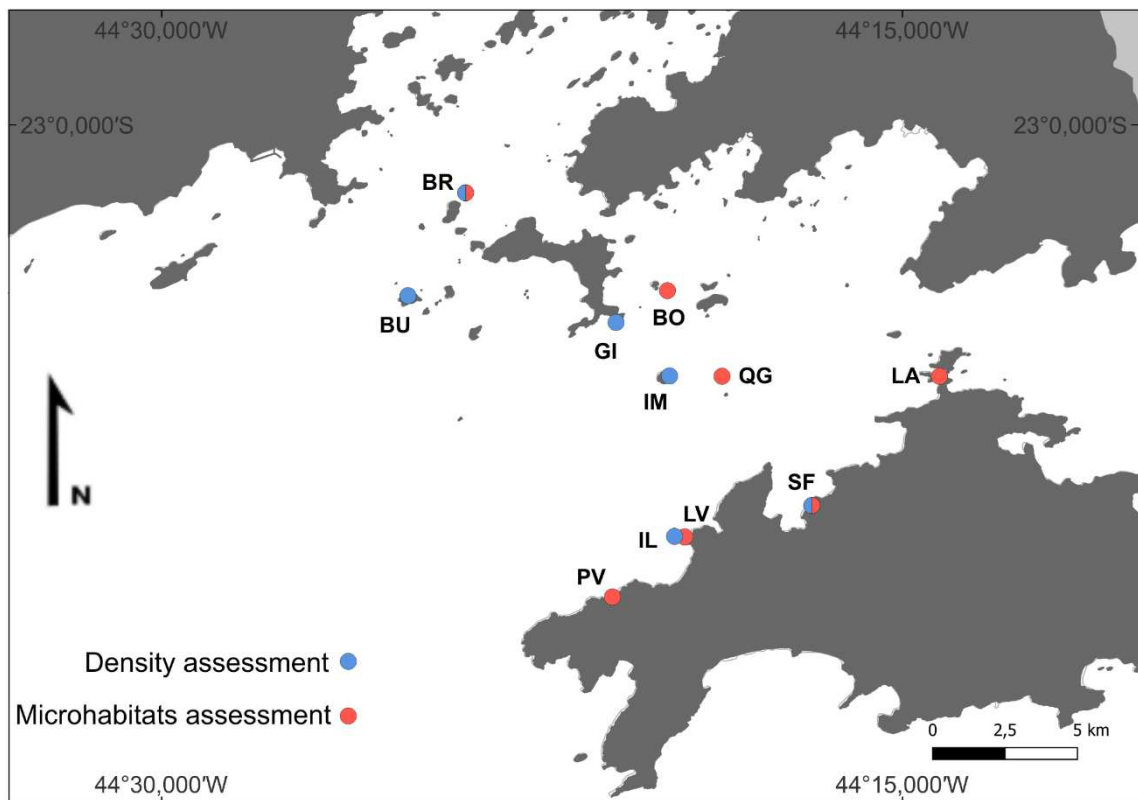
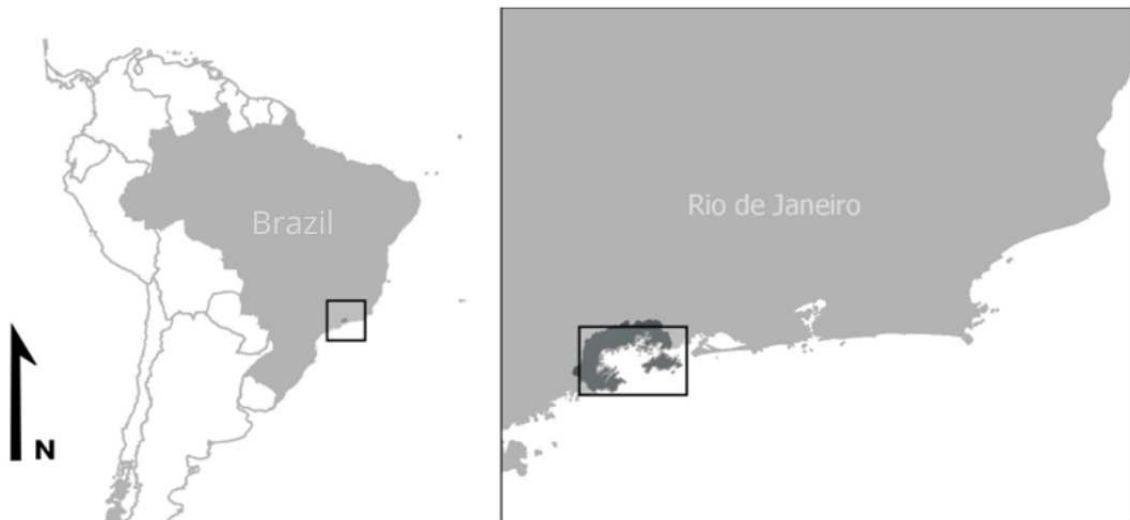


Fig. 1 Study sites arranged from north to south: BR - Ilha do Brandão, BU - Ilha de Búzios, BO - Ilhas Botinas, GI - Ilha da Gipóia, IM - Ilha Imboassica, LA - Lagoa Azul, QG - Ilha Queimada Grande, SF - Enseada do Sítio Forte, IL - Ilha da Longa, LV - Lagoa Verde, and PV - Praia Vermelha.

Data analysis

For recruit abundance and distribution data, overall means and standard deviations were calculated for each sampled depth and site. Differences among

means were evaluated in the R software using the Kruskal-Wallis test followed by Wilcoxon post hoc pairwise comparisons (R Core Team, 2024), due to the lack of normality and the heterogeneity of variances. Frequency of occurrence was calculated as the ratio between the number of samples containing recruits and the total number of samples analyzed, with results expressed as percentages.

The percentage cover of the *Mussismilia hispida* microhabitats at comparative depths of 3, 5, and 8 m was analyzed using Coral Point Count with Excel extensions (CPCe) (Kohler and Gill, 2006). A total of 49 equidistant points arranged in a grid were used for each image. From this, mean percentage cover values were obtained overall, among depths, and among sites. Hellinger transformation was applied to the dataset (Legendre and Gallagher, 2001), followed by PERMDISP analysis to test the homogeneity of multivariate dispersions using the betadisper function from the vegan package (Oksanen et al., 2024) in R. Multivariate dispersions showed significant heterogeneity among sites, whereas no significant differences were detected among depths. Therefore, PERMANOVA was applied only to the depth factor, followed by pairwise PERMANOVA comparisons among depths as a post hoc test. Subsequently, SIMPER analysis was performed to identify the percentage contribution of each taxon/functional group to the observed similarity among depths. Analyses were conducted in R using the vegan (Oksanen et al., 2024) and pairwiseAdonis (Martinez Arbizu, 2020) packages.

Non-metric multidimensional scaling (nMDS) analysis was performed to visualize relationships among samples according to site and depth. Similarities among sampled sites and depths were calculated using the Bray-Curtis index to generate dendrograms through the UPGMA clustering method. Correlations between taxa/functional group vectors and nMDS ordination axes were then calculated. Vector significance was assessed through permutation tests and expressed as p-values, whereas vector length was used as a measure of the strength of association between each vector and the ordination. These analyses were conducted in R using the vegan (Oksanen et al., 2024), cluster (Maechler et al., 2024), and stats (R Core Team, 2024) packages.

Finally, the diversity of sessile invertebrate and algal assemblages within the microhabitats was evaluated for each depth stratum using descriptive indices, including species richness, Margalef richness, and Simpson (1 - D) diversity, in R with the vegan package (Oksanen et al., 2024).

RESULTS

Spatial and bathymetric distribution and density of recruits

A total of 472 recruits were recorded across the seven sampled sites, resulting in an overall mean density of 67 recruits per site and 0.90 ± 2.34 colonies m^{-2} . Recruit abundance differed significantly among depths (Kruskal-Wallis, $\chi^2 = 21.63$; $\text{df} = 2$; $p < 0.001$) and among sites (Kruskal-Wallis, $\chi^2 = 138.69$; $\text{df} = 6$; $p < 0.001$). Regarding depth, the highest mean density was recorded at 5 m (1.11 colonies m^{-2}), followed by 3 m (0.95 colonies m^{-2}) and 8 m (0.22 colonies m^{-2}) (Table 1; Fig. 2). Pairwise comparisons using the Wilcoxon post hoc test indicated significant differences between 3 and 5 m ($p < 0.05$), 3 and 8 m ($p < 0.05$), and more markedly between 5 and 8 m ($p < 0.001$).

The highest mean recruit densities were recorded at Sítio Forte and Lagoa Azul (Fig. 3). Sítio Forte exhibited the highest recruit density among all localities, particularly at 5 m depth (Fig. 4). High densities were also observed at Ilha Queimada Grande and Praia Vermelha, whereas the lowest densities were recorded at Lagoa Verde and Brandão. No recruits were found at 8 m depth at either Lagoa Verde or Brandão. Finally, no recruits were recorded at Botinas during the sampling period. Significant differences among sites were detected for the comparisons LA-LV, LA-BR, and LA-BO ($p < 0.05$). In contrast, no significant differences were observed for BR-BO, LA-QG, QG-SF, and SF-PV ($p > 0.05$).

Table 1 Mean density (colonies m^{-2}) of *Mussismilia hispida* recruits across localities and depths in Ilha Grande Bay.

Site	Mean density (col. m^{-2})	3 m (col. m^{-2})	5 m (col. m^{-2})	8 m (col. m^{-2})
Sítio Forte	2.3	2.17	2.42	-
Lagoa Azul	2.1	2.27	1.92	-
Praia Vermelha	1.65	0.6	1.45	-
Queimada Grande	1.43	0.35	1.65	0.9
Lagoa Verde	0.13	0.22	0.17	0
Brandão	0.08	0.15	0.1	0

Botinas	0	0	0	-
Depth (overall mean)	0.9	0.95	1.11	0.22

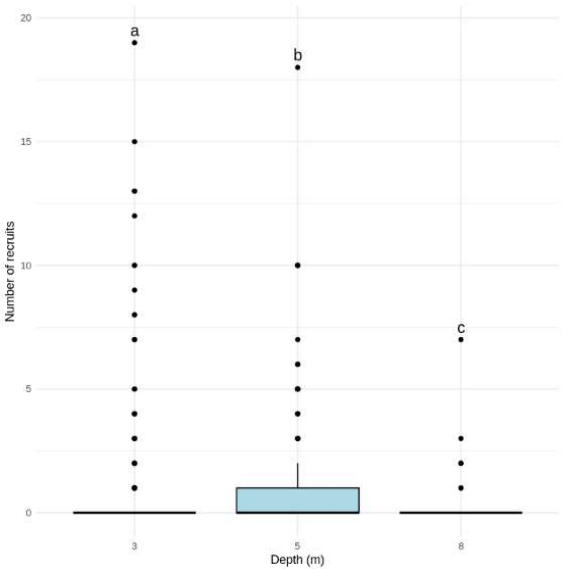


Fig. 2 Boxplot of *Mussismilia hispida* recruit density (colonies m⁻²) at 3, 5, and 8 m depth in Ilha Grande Bay. Different letters indicate significant differences among depths according to pairwise Wilcoxon tests.

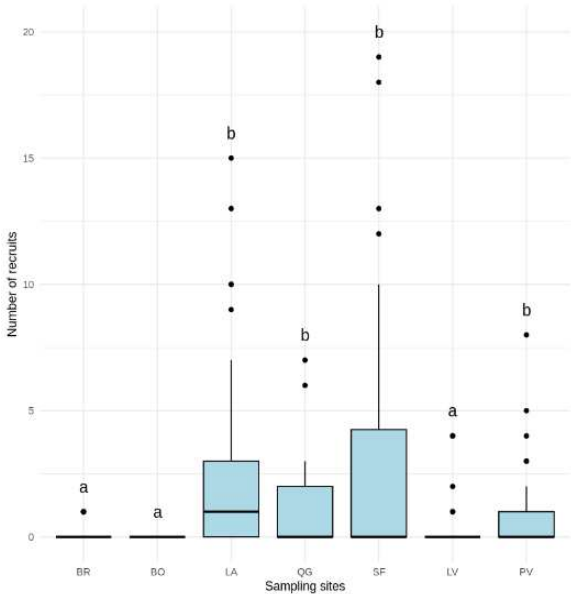


Fig. 3 Boxplot of *Mussismilia hispida* recruit density (colonies m⁻²) across the sampled localities in Ilha Grande Bay. Localities: Brandão (BR), Botinas (BO), Lagoa Azul (LA), Queimada Grande (QG), Sítio Forte (SF), Lagoa Verde (LV), and Praia Vermelha (PV). Different letters indicate significant differences among localities according to pairwise Wilcoxon tests.

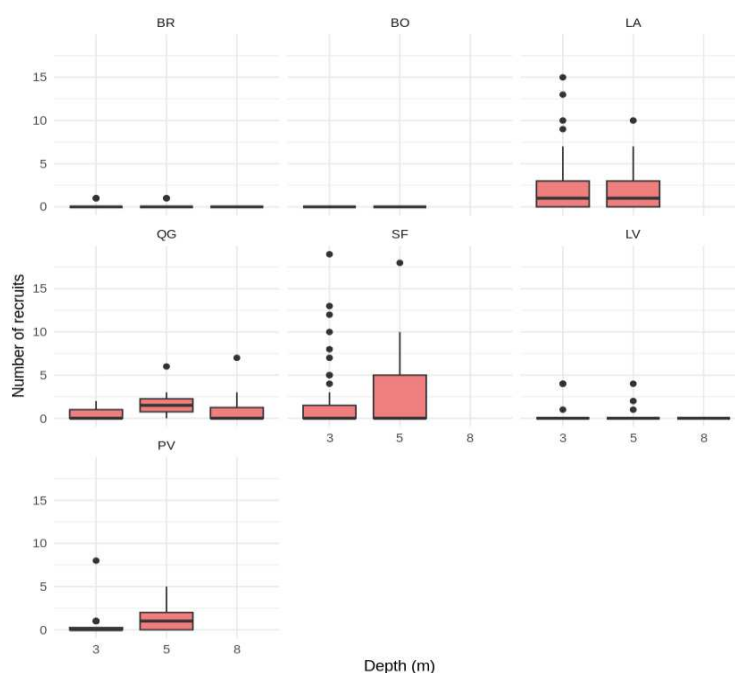


Fig. 4 Boxplot of *Mussismilia hispida* recruit density (colonies m⁻²) across the sampled localities at 3, 5, and 8 m depth in Ilha Grande Bay. Localities: Brandão (BR), Botinas (BO), Lagoa Azul (LA), Queimada Grande (QG), Sítio Forte (SF), Lagoa Verde (LV), and Praia Vermelha (PV). Different letters indicate significant differences among localities

The overall frequency of occurrence of recruits in the region was 25.57%, with values of 22.72% at 3 m, 34.54% at 5 m, and 8.75% at 8 m (Table 2; Fig. 5). Among the surveyed localities, Lagoa Azul exhibited the highest frequency of occurrence, whereas the lowest frequencies were recorded at Brandão, Lagoa Verde, and Botinas (Fig. 6). When locality-depth combinations were considered, the highest frequency of occurrence was observed at Ilha Queimada Grande at 5 m depth, followed by Praia Vermelha and Lagoa Azul at the same depth (Fig. 7).

Table 2 Frequency of occurrence (%) of *Mussismilia hispida* recruits across localities and depths in Ilha Grande Bay.

Site	Mean	3 m (%)	5 m (%)	8 m (%)
	frequency of occurrence (%)			
Lagoa Azul	61.25	55	67.5	-

Praia Vermelha	47.5	25	70	-
Queimada Grande	46.6	30	75	35
Sítio Forte	32.5	27.5	37.5	-
Brandão	8.3	15	10	0
Lagoa Verde	5	7.5	7.5	0
Botinas	0	0	0	-
Regional mean	25.57	22.72	34.54	8.75

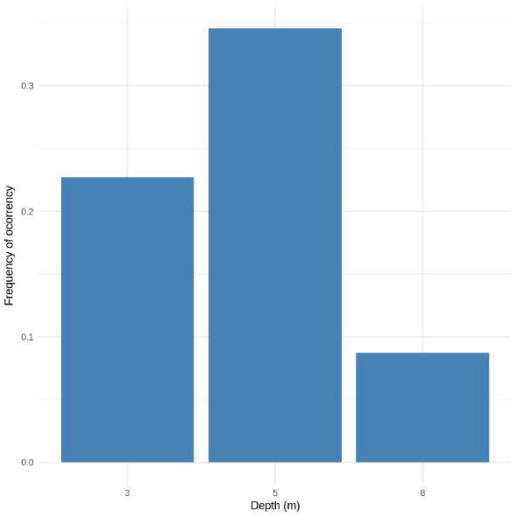


Fig. 5 Frequency of occurrence of *Mussismilia hispida* recruits at 3, 5, and 8 m depth in Ilha Grande Bay.

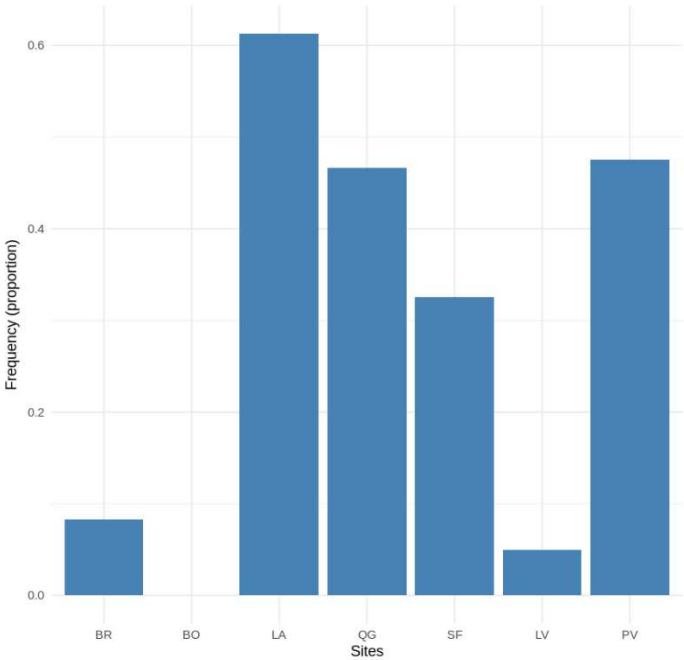


Fig. 6 Frequency of occurrence of *Mussismilia hispida* recruits across the sampled localities. Localities: Botinas (BO), Brandão (BR), Lagoa Azul (LA), Lagoa Verde (LV), Praia Vermelha (PV), Queimada Grande (QG), and Sítio Forte (SF).

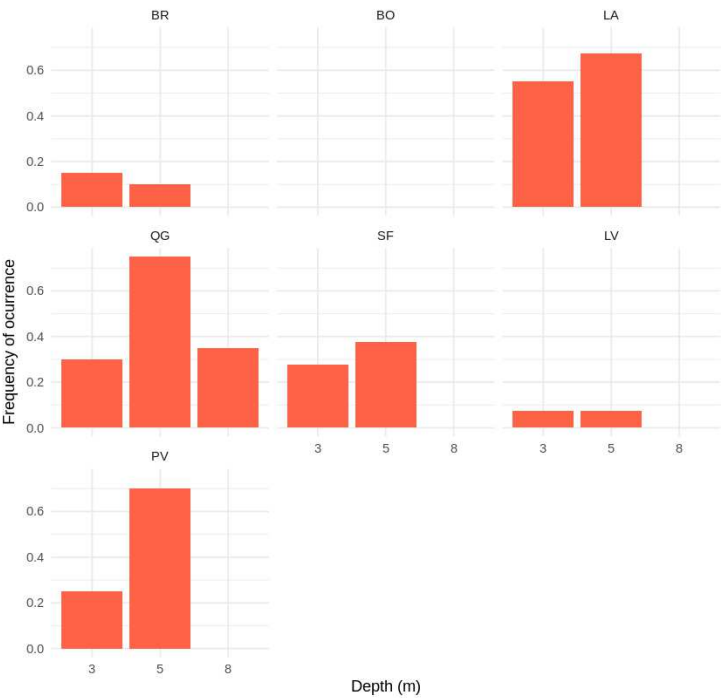


Fig. 7 Frequency of occurrence of *Mussismilia hispida* recruits across the sampled localities at 3, 5, and 8 m depth. Localities: Brandão (BR), Botinas (BO), Lagoa Azul (LA), Queimada Grande (QG), Sítio Forte (SF), Lagoa Verde (LV), and Praia Vermelha (PV)

Structure and composition of the microhabitat associated with *M. hispida* recruits

331

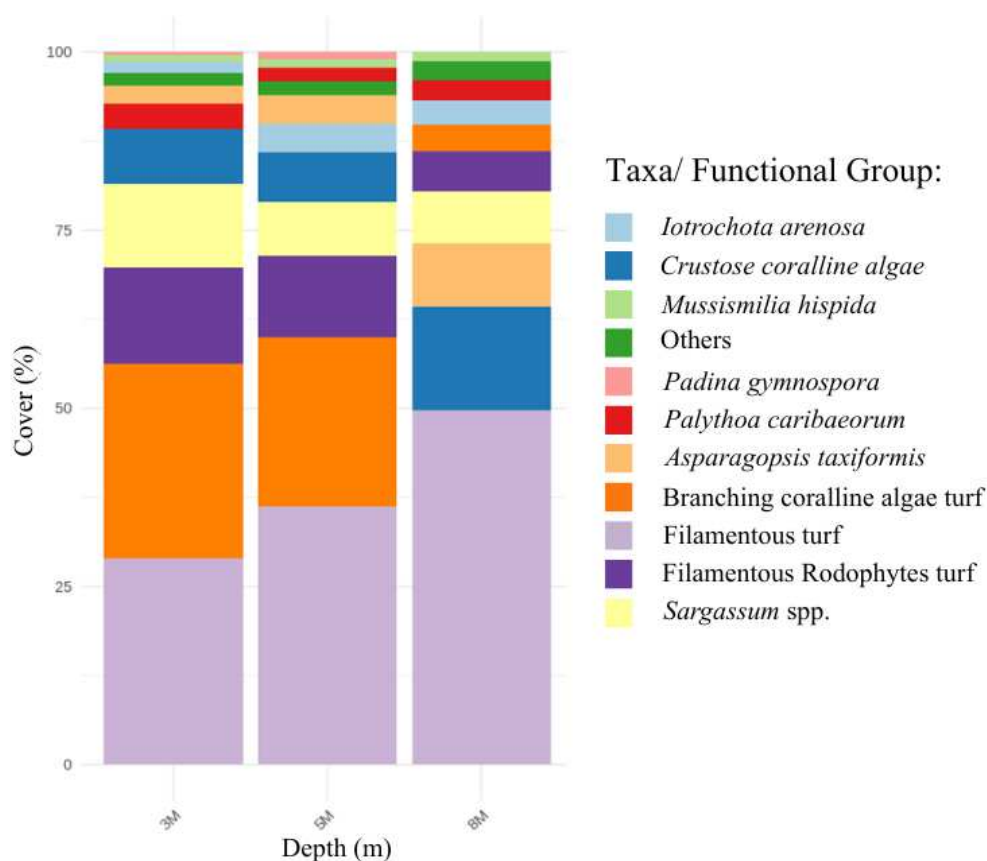
332 The microhabitats associated with *M. hispida* recruits in Ilha Grande Bay
 333 were composed of 27 taxa or morpho-functional groups. These included the algae:
 334 turf algae, crustose coralline algae (CCA), *Asparagopsis taxiformis*, *Lophocladia*
 335 *trichoclados*, *Champia compressa*, *Sargassum furcatum*, *Sargassum vulgare*,
 336 *Dictyota* sp., *Padina gymnospora*, *Jania adhaerens*, *Lobophora variegata*, and
 337 *Hypnea* sp.; and the following invertebrates: Porifera - *Iotrochota arenosa*,
 338 *Desmapsamma anchorata*, *Tedania ignis*, *Darwinella* sp. 1, *Darwinella* sp. 2,
 339 unidentified Porifera, the Cnidaria *Palythoa caribaeorum*, *Mussismilia hispida*,
 340 *Tubastraea* spp., *Madracis decactis*, *Zoanthus sociatus* an unidentified Hydrozoa,
 341 the Ascidiacea *Ascidia sydneiensis* and *Phallusia nigra*, and the Bryozoa
 342 *Schizoporella errata*.

343 Benthic cover within the microhabitats along the depth gradient (3–8 m) in
 344 Ilha Grande Bay was dominated by turf algae, which exhibited high and similar
 345 values at 3 and 5 m (70,54% and 72,2%, respectively), followed by a decrease at 8
 346 m (59,83%), considering all turf algal taxa/functional groups combined (Fig. 8).
 347 Within this group, filamentous turf algae were the most abundant functional group
 348 at all depths. This functional group increased with depth, from 29.02% at 3 m to
 349 36.23% at 5 m, reaching 49.75% at 8 m. In contrast, branching coralline turf algae
 350 were more representative at shallower depths (27.27% at 3 m and 23.79% at 5 m),
 351 decreasing markedly at 8 m (3.76%). Filamentous rhodophyte turf was more
 352 abundant at 3 m (13.53%) and decreased with depth, as was canopy-forming algae
 353 *Sargassum* spp. (11.58%). However, *Asparagopsis taxiformis* exhibited greater
 354 cover at 8 m (8.86%). Crustose coralline algae showed lower cover at shallow depths
 355 (7.83% at 3 m and 6.96% at 5 m) and increased at 8 m (14.56%).

356 Among invertebrates, the cover of *M. hispida* within the microhabitats
 357 increased slightly with depth (0.88% at 3 m, 1.25% at 5 m, and 1.36% at 8 m). The
 358 zoantharian *Palythoa caribaeorum* showed the highest cover at 3 m (3.45%),
 359 decreasing at the other depths (1.87% at 5 m and 2.94% at 8 m). The sponge
 360 *Iotrochota arenosa* reached its highest cover at 5 m (4.04%). The invertebrates
 361 *Madracis decactis*, *Tubastraea* spp., *Schizoporella errata*, *Zoanthus sociatus*,
 362 *Darwinella* spp., *Desmapsamma anchorata*, unidentified Hydrozoa, unidentified
 363 Porifera, and the algae *Lobophora variegata*, *Champia compressa*, *Padina*
 364 *gymnospora*, *Dictyota* sp., and *Lophocladia trichoclados* individually accounted for
 365 less than 1% of total benthic cover.

366

Fig. 8 Percentage cover of benthic organisms within microhabitats occupied by *Mussismilia hispida* recruits in Ilha Grande Bay at 3, 5, and 8 m depth.



367

368 The cover of the main species/functional groups varied among the sampled
 369 sites. Imboassica exhibited the highest contribution of filamentous turf algae among
 370 all localities, ranging from 52.99% at 3 m to 85.17% cover at 8 m (Fig. 9). In contrast,
 371 branching coralline turf algae were the dominant category at shallow depths (3–5
 372 m) at Gipóia (47.38% and 30.76%, respectively). At Sítio Forte, branching coralline
 373 turf algae reached the highest cover recorded among all localities at 3 m (51.83%),
 374 but were almost completely replaced by filamentous turf algae at 8 m (69.38%). At
 375 Gipóia and Ilha da Longa, *Asparagopsis taxiformis* made an important contribution
 376 at 8 m (25.92% and 23.90%, respectively). *Sargassum* spp. reached its highest cover
 377 at 8 m at Ilha da Longa (19.67%) and at 3 m at Sítio Forte (19.93%), in addition to
 378 showing an important contribution between 3 and 5 m at Gipóia (16.54% and
 379 15.68%, respectively). Crustose coralline algae showed their highest cover at Búzios
 380 at 8 m (22.82%). At Brandão, the highest cover occurred at 3 m (21.43%), whereas
 381 at Ilha da Longa the highest value was recorded at 5 m (17.7%).

382 *Palythoa caribaeorum* was present at all localities and reached its highest
 383 cover at Brandão at 3 m (15.26%), although high percentages were also recorded at
 384 other depth strata, such as at Búzios at 8 m (9.45%) and at Gipóia at 8 m (11.58%).
 385 Adult colonies of *M. hispida* were present within the microhabitats at all sites, with

the highest cover recorded at Gipóia at 8 m (4.34%). The sponge *Iotrochota arenosa* was also present at all sites, reaching its highest cover at Ilha da Longa at 5 m (8.92%).

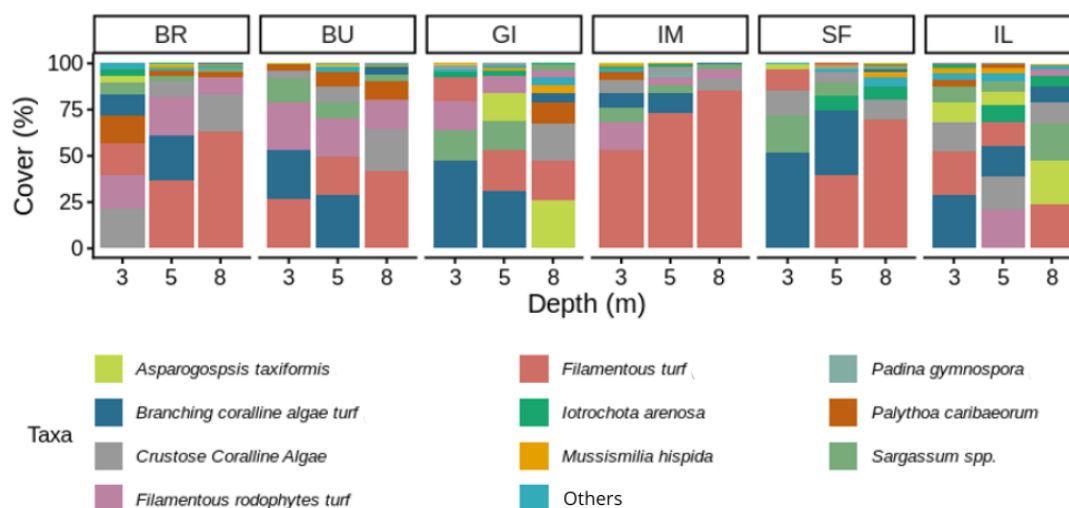
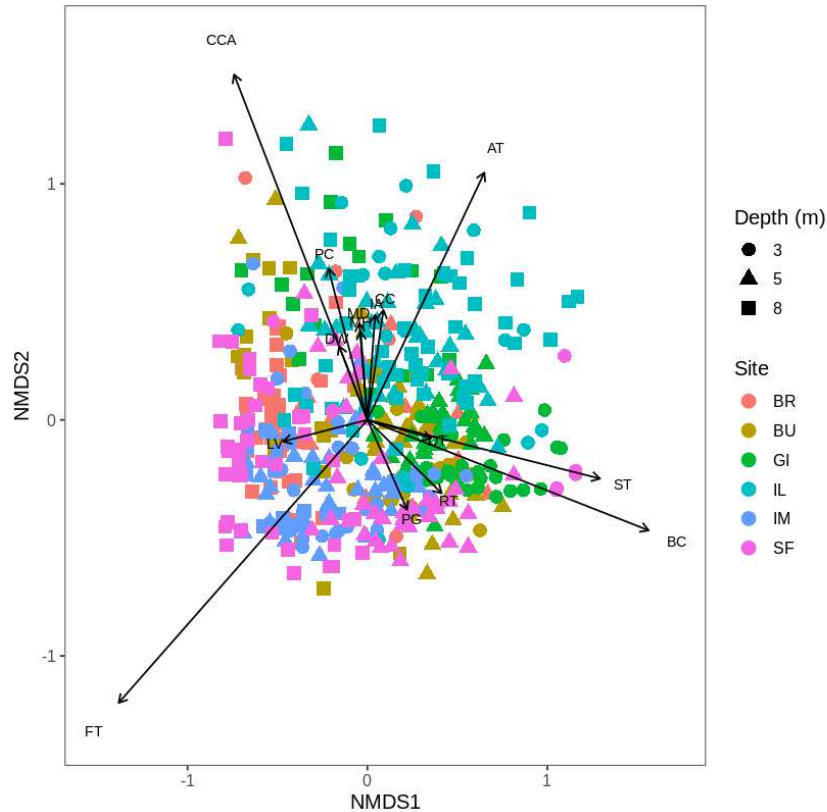


Fig. 9 Percentage cover of benthic groups within *Mussismilia hispida* recruit microhabitats at the sampled sites in Ilha Grande Bay at 3, 5, and 8 m depth. Sites: Brandão (BR), Búzios (BU), Gipóia (GI), Ilha da Longa (IL), Imboassica (IM), and Sítio Forte (SF)

The nMDS ordination revealed trends in sample grouping according to depth and sampling sites. However, benthic community structure showed high overlap among samples and a relatively high stress value (0.21) in the ordination (Fig. 10). Filamentous turf algae and crustose coralline algae showed the strongest negative correlations with nMDS axis 1 (Table 3), grouping most of the 8 m samples, particularly from Sítio Forte, Imboassica, Brandão, and Gipóia. In contrast, branching coralline turf algae, *Sargassum* spp., and *Asparagopsis taxiformis* exhibited stronger positive correlations with nMDS axis 1. Vectors associated with branching coralline turf and *Sargassum* spp. were mainly related to samples from 3 and 5 m depths, whereas *A. taxiformis* was more strongly associated with samples from Ilha da Longa. Regarding the sampling sites, BU and IL, as well as BR and SF, showed greater proximity in the ordination. Despite the overall similarity among sites and depths (up to 0.6), dendrogram revealed the formation of three major groups inside this region (Fig. 11). The first group comprised IM_5, IM_8, and SF_8, indicating a high degree of similarity among these communities. The second group consisted exclusively of SF_3, highlighting its distinct community composition relative to all other samples. The third group included all remaining locality-depth combinations. Within this larger cluster, subgroups were observed involving samples from different depths at BR, BU, IL, and GI, as well as IM_3 and SF_5,

411 indicating similarities among these communities despite differences in depth and
 412 location.



413

Fig. 10 Non-metric multidimensional scaling (nMDS) ordination based on Bray-Curtis similarities of benthic communities within *Mussismilia hispida* recruit microhabitats across a depth gradient (3, 5, and 8 m) at six sites in Ilha Grande Bay. Sites: Ilha do Brandão (BR), Ilha de Búzios (BU), Ilha da Gipóia (GI), Ilha da Longa (IL), Ilha Imboassica (IM), and Enseada do Sítio Forte (SF). Vectors: filamentous turf (FT), branching coralline algae turf (BC), *Sargassum* spp. (ST), *Asparagopsis taxiformis* (AT), crustose coralline algae (CCA), *Palythoa caribaeorum* (PC), filamentous red algal turf (RT), *Lobophora variegata* (LV), *Champia compressa* (CC), *Iotrochota arenosa* (IA), *Padina gymnospora* (PG), *Madracis decactis* (MD), *Mussismilia hispida* (MH), *Dictyota* turf (TD), and *Darwinella* spp. (DW). Stress = 0.21.

414

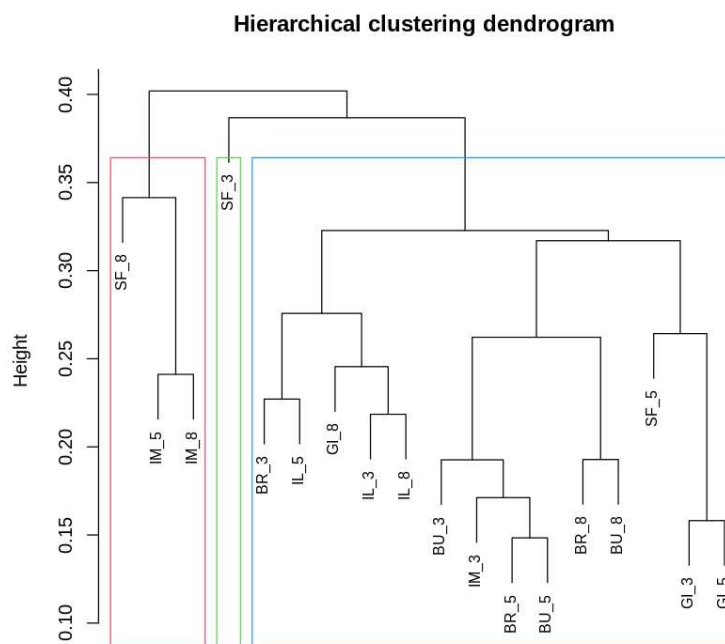


Fig. 11 Hierarchical clustering dendrogram based on Bray-Curtis dissimilarity.

Table 3 Correlation between benthic group vectors and nMDS axes.

Taxa/ Functional group	NMDS1	NMDS2	pval	Length
Filamentous turf	-0.69	-0.59	0.001	0.91
Crustose coralline algae	-0.37	0.73	0.001	0.82
Branching coralline algae turf	0.78	-0.23	0.001	0.81
<i>Sargassum</i> spp.	0.64	-0.12	0.001	0.65
<i>Asparagopsis</i> <i>taxiformis</i> turf	0.32	0.52	0.001	0.61
<i>Palythoa caribaeorum</i>	-0.10	0.32	0.001	0.33
Filamentous rhodophyte turf	0.20	-0.15	0.001	0.25

<i>Lobophora variegata</i>	-0.23	-0.04	0.001	0.23
<i>Champia compressa</i>	0.04	0.23	0.001	0.23
<i>Iotrochota arenosa</i>	0.02	0.22	0.001	0.22
<i>Padina gymnospora</i>	0.11	-0.19	0.001	0.22
<i>Madracis decactis</i>	-0.02	0.20	0.002	0.20
<i>Mussismilia hispida</i>	-0.01	0.18	0.001	0.18
<i>Dictyota</i> turf	0.17	-0.03	0.001	0.18
<i>Darwinella</i> spp.	-0.07	0.15	0.001	0.17

419

420 PERMANOVA detected significant differences for the factor “Depth”
 421 (Pseudo-F = 56.445; $R^2 = 0.1046$; $p = 0.001$). Pairwise PERMANOVA comparisons
 422 revealed significant differences between 3 and 8 m, and between 5 and 8 m (Pseudo-
 423 F = 40.420; $R^2 = 0.1177$; adjusted $p = 0.0015$; and Pseudo-F = 43.928; $R^2 = 0.1066$;
 424 adjusted $p = 0.0015$, respectively), whereas no significant differences were found
 425 between 3 and 5 m (Pseudo-F = 1.859; $R^2 = 0.0063$; adjusted $p = 0.093$).

426 SIMPER analysis identified mean similarities within the sampled depth strata
 427 ranging from 48.76% to 53.67%, revealing patterns related to species contributions
 428 along the vertical gradient (Table 4). Filamentous turf algae showed the highest
 429 contribution to benthic community similarity at all depths, with a progressive
 430 increase toward 8 m. In contrast, branching coralline turf algae contributed strongly
 431 at shallow strata (3–5 m), together with filamentous rhodophyte turf and *Sargassum*
 432 spp. At 8 m depth, crustose coralline algae and *Asparagopsis taxiformis* showed
 433 greater contributions to community similarity.

434

435 **Table 4** Similarity Percentage (SIMPER) analysis of benthic communities within
 436 *Mussismilia hispida* recruit microhabitats across a depth gradient (3, 5, and 8 m)
 437 at six sites in Ilha Grande Bay.

Taxa/ Functional group		Contribution (%)	Cumulative (%)
Depth: 3 m			
Average similarity =	Filamentous turf	24.29	24.29
48.76			

		Branching coralline algae turf	22.54	46.83
		Filamentous rhodophyte turf	15.15	61.98
		<i>Sargassum</i> spp.	13.56	75.54
Depth: 5 m				
Average	similarity =	Filamentous turf	27.34	27.34
53.67				
		Branching coralline algae turf	21.82	49.16
		Filamentous rhodophyte turf	13.16	62.32
		<i>Sargassum</i> spp.	10.07	72.39
Depth: 8 m				
Average	similarity =	Filamentous turf	36	36
49.32				
		Crustose coralline algae	16.93	52.93
		<i>Sargassum</i> spp.	8.81	61.74
		<i>Asparagopsis taxiformis</i>	8.63	70.37
		Filamentous rhodophyte turf	7.91	78.28

438

439 Species richness varied little among depths, with identical values recorded
 440 at 3 m (10) and 8 m (10), and a slight increase at 5 m (11) (Table 5). This pattern
 441 was accompanied by higher diversity values at 5 m, whereas 8 m showed the lowest
 442 diversity indices, indicating reduced diversity and greater dominance. Among sites,
 443 Ilha da Longa exhibited the highest diversity values, followed by Gipóia. In contrast,
 444 Imboassica and Sítio Forte displayed the lowest richness values and diversity
 445 indices, particularly Imboassica, indicating more dominated microhabitats.

446

447 **Table 5** Species richness, Margalef richness, and Simpson diversity indices of
 448 benthic communities within *Mussismilia hispida* recruit microhabitats across a
 449 depth gradient (3, 5, and 8 m) at six sites in Ilha Grande Bay.

Categor y	Richnes s	Margale f	Simpson (1 - D)
3 m	10	0.98	0.64
5 m	11	1.08	0.65
8 m	10	0.93	0.56
BR	9	0.83	0.56
BU	9	0.97	0.69
GI	9	1.16	0.71
IL	11	1.29	0.71
IM	8	0.79	0.45

SF	8	0.83	0.54
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DISCUSSION

Spatial and bathymetric distribution and density of recruits

Although several aspects of the biology of *M. hispida* have already been described (Oigman-Pszczol and Creed, 2006; Banha et al., 2020; Mantelatto et al., 2020), the intensity of recruitment in this species remains poorly explored, particularly in marginal reefs such as Ilha Grande Bay. The high recruitment observed in the region contrasts with the low results reported by Oigman-Pszczol et al. (2004) and Carlos-Junior et al. (2025) for the Búzios region. Recruitment rates recorded in Ilha Grande Bay are comparable to those reported for subtropical reefs, such as the Florida Keys and Australia, ranging from 0.8 to 3.2 colonies m⁻² (Chiappone and Sullivan, 1996; Hoey et al., 2011; Lachs et al., 2021). However, they remain lower than those reported for tropical reefs in the Caribbean (Edmunds, 2004; Williams et al., 2017), Indian Ocean (Dajka et al., 2019), and Pacific Ocean (Thompson et al., 2019; Speare et al., 2024), where recruit densities frequently exceed 10 colonies m⁻² and may reach 40–70 colonies m⁻². Nevertheless, Price et al. (2019) reported a global decline in coral recruitment on tropical reefs, accompanied by increasing recruitment at subtropical latitudes, reinforcing the tropicalization hypothesis proposed by Vergés et al. (2014). In this context, increasing recruitment rates are expected in marginal reefs located at the transition between tropical and temperate biogeographic provinces. However, no previous studies in the region allow us to conclude that the high recruitment observed in Ilha Grande Bay is directly associated with increasing seawater temperatures. Therefore, further long-term studies are necessary to better understand recruitment dynamics under ongoing climate change scenarios.

Our data indicate higher recruit densities at 5 m depth, with reduced densities at 3 m and minimum values at 8 m. This pattern in Ilha Grande Bay is associated with the high cover of the zoantharian *Palythoa caribaeorum* on shallow substrates (Mantelatto et al., 2020), which is reflected in the greater cover of this species within microhabitats at 3 m depth, exerting a strong local effect on *M. hispida* recruitment. Its encrusting growth pattern, combined with its ability to monopolize the substrate through the production of allelopathic compounds (palytoxins) and overgrowth of the surrounding benthic community (Suchanek and Green, 1981; Ramos and Vasconcelos, 2010; Silva, 2015), may inhibit larval

settlement or cause post-settlement mortality of recruits from other invertebrates (Maida et al., 1996).

Palythoa caribaeorum is a dominant species in shallow habitats from Florida, the Gulf of Mexico, and the Caribbean to the Brazilian coast, particularly at the Abrolhos Bank (Francini-Filho et al., 2013) and between southern Espírito Santo and Santa Catarina (Aued et al., 2018; Schroeder et al., 2025). This zoantharian is well known for limiting the occurrence of corals along shallow reef fringes in these regions, as well as restricting other invertebrates and algae (Suchanek and Green, 1981; Hill et al., 2021). Mean cover of *Palythoa caribaeorum* on rocky reefs in Ilha Grande Bay ranges from 20% to 52%, and the species may dominate shallow areas (2–4 m) (Castro, 1999; Lages and Meurer, 2007; Koutsoukos, 2012; Mantelatto et al., 2020). In the present study, however, its cover within *M. hispida* microhabitats was lower, even at sites such as Brandão (15.26%). Thus, the observed pattern suggests a negative interaction with recruitment, possibly through settlement avoidance or post-settlement mortality caused by overgrowth (Suchanek and Green, 1981), as observed in the field (pers. obs.), supporting the reduction in recruit density and frequency of occurrence at 3 m depth.

The decrease in mean recruit density at 8 m relative to 5 m was recorded at all sites where this depth stratum was sampled (Queimada Grande, Brandão, and Lagoa Verde). This pattern may be associated with changes in substrate type at this depth range, where the transition between consolidated and unconsolidated substrates commonly occurs. At this interface, greater sediment accumulation is expected, which may negatively affect larval settlement and recruit survival. Another potential factor is the stronger seasonal influence of South Atlantic Central Water (SACW) intrusion at this depth (Kjerfve et al., 2021; Sousa et al., 2026), which may interfere with recruit survival, as recruits are particularly vulnerable during this life stage to critical events such as sudden cooling of seawater. Nevertheless, this depth may also represent a refuge zone for *M. hispida*, particularly during marine heatwaves or El Niño events (Barboza and Skinner, 2021; Carvalho et al., 2025). These findings reinforce the need for long-term monitoring of this species in the region.

Differences in recruit distribution and density among sites in Ilha Grande Bay, particularly between BO, BR, and LV versus LA, QG, SF, and PV, may be related to circulation patterns and larval dispersal processes. Water residence time in Ilha Grande Bay averages approximately 30 days (Santos et al., 2018), although it may be longer within sheltered bays and embayments and shorter in more exposed areas, such as the bay entrance and regions near the central channel. The larval duration of *M. hispida* ranges from 7 to 10 days and may reach up to 15 days (Pires et al.,

2016; Peluso et al., 2018). Thus, sites with longer water residence times are expected to exhibit greater larval retention and, consequently, higher recruit abundance. Reduced circulation may favor recruitment and enhance coral larval settlement by increasing larval residence time near the substrate (Figueiredo et al., 2013; Gouezo et al., 2020). The highest mean recruit densities observed at Lagoa Azul and Enseada do Sítio Forte coincide with areas characterized by longer water residence times, estimated at 70–90 days during the summer. In contrast, localities that are more exposed or more strongly influenced by the central channel of the bay, such as Praia Vermelha, Lagoa Verde, and Ilha Queimada Grande, exhibit shorter residence times, ranging from 30 to 60 days during the summer, and lower recruit densities (Santos et al., 2018). However, Praia Vermelha and Queimada Grande showed higher frequencies of occurrence at 5 m than Sítio Forte and Lagoa Azul at the same depth. This pattern suggests that areas with greater circulation tend to exhibit a more dispersed spatial distribution of recruits, resulting in higher frequencies of occurrence, whereas areas with lower circulation may promote more aggregated recruit distributions, leading to higher local densities. However, this pattern was not observed at Brandão and Botinas. Despite being areas with relatively high water residence times, recruit densities remained low, indicating that larval retention alone does not explain the observed recruitment patterns. At Botinas, where no recruits were recorded, the site is shallow (< 5 m) and subjected to intense daily tourism activity, including anchoring by numerous boats. High sedimentation was also observed in the field at this site. Sediment accumulation may hinder larval settlement by covering available substrate and may additionally cause recruit mortality through burial or abrasion.

Structure and composition of the microhabitat associated with *M. hispida* recruits

Most *M. hispida* microhabitats in Ilha Grande Bay were dominated by turf algae at all depths, with a slight decrease at 8 m, where crustose coralline algae (CCA) became more abundant. Although competition with filamentous turf algae is a documented cause of mortality in both adult corals and recruits on tropical coral reefs (Swierts and Vermeij, 2016; Jorissen et al., 2020), high recruitment rates have also been reported on subtropical reefs dominated by turf algae (Tanvet, 2022). The results of the present study support the idea that turf algae constitute an important microhabitat for coral recruitment on marginal reefs of the Southwestern Atlantic. The coexistence between corals and turf-dominated assemblages, which are abundant throughout the Brazilian coral province (Paula, 2002; Figueiredo et al.,

2008; Aued et al., 2018), suggests that local corals may be evolutionarily associated with substrates with high algal cover and may therefore exhibit greater tolerance to recruitment within these microhabitats. This differs from patterns commonly reported for tropical reefs in the Indo-Pacific and Caribbean, where increasing interactions between corals and turf algae have been widely associated with declining environmental quality, including reductions in coral cover, loss of herbivores, and intensification of climate change effects, ultimately resulting in algal-dominated phase shifts (McManus and Polsenberg, 2004; Hughes et al., 2007; Birrell et al., 2008). In these systems, high turf algal cover generally limits coral recruitment through mechanisms of spatial competition and reduced post-settlement survival (Hoey et al., 2011; Webster et al., 2015). Taken together, these findings suggest that turf algae on marginal reefs of the Southwestern Atlantic may play a distinct ecological role from that commonly reported for tropical reefs.

Differences between the microhabitats at 3–5 m and 8 m reflect changes in the benthic community of Ilha Grande Bay along the depth gradient. The cover of crustose coralline algae (CCA) within the microhabitats increased with depth, following a pattern previously described for the region (Mantelatto et al., 2020; 2022). In shallow waters (< 6 m), this group generally exhibits low cover (1.9–2.87%) (Lages et al., 2011; Vançato et al., 2023), whereas higher values (~15%) have been recorded at greater depths (up to 16 m) (Mantelatto et al., 2020). In the present study, CCA cover within the microhabitats was higher than expected at 3–5 m and similar to values previously reported in the literature at 8 m, suggesting a preferential association between *M. hispidus* recruits and this functional group. The relationship between CCA and scleractinian coral recruitment is well documented and is frequently attributed to chemical cues produced by these algae that induce coral larval settlement (Ritson-Williams et al., 2009; Price, 2010; O’Leary et al., 2012; Segal et al., 2012; Gómez-Lemos et al., 2018). In this context, the recurrent occurrence of recruits within microhabitats with higher CCA contribution reinforces the hypothesis of settlement facilitation in the study area. Crustose coralline algae are capable of persisting under low-light conditions and frequently occur beneath turf algal mats (Muniz et al., 2013). Therefore, the turf algal cover recorded in the present study may be masking an even greater contribution of underlying CCA beneath the epiphytic algal matrix. As a result, part of the substrate visually classified as turf may, in fact, consist of extensive areas of underlying crustose coralline algae that chemically attract coral larvae.

Branching coralline algae turf exhibited higher cover at depths of 3–5 m. Heyward and Negri (1999) demonstrated that species within this functional group may act as chemical inducers for coral larval settlement and recruitment. Similar effects have also been reported for other benthic invertebrates, such as gastropods

and sponges, in which the presence of branching coralline algae is associated with increased recruitment success (Carballo and Ávila, 2004; Williams et al., 2008).

Assemblages formed by canopy-forming macroalgae such as *Sargassum* spp. were present at all sites and depths, with the highest cover recorded at 3 m. In Ilha Grande Bay, the vegetative development of *Sargassum* spp. reaches maximum values between October and February, corresponding to the period of greatest thallus growth (Széchy et al., 2006). Dense *Sargassum* beds, which are common on shallow rocky reefs in Ilha Grande Bay (Creed et al., 2007; Koutsoukos et al., 2012), tend to limit coral recruitment, probably due to reduced light availability and substrate occupation. In these environments, the sessile benthic community associated with the surrounding thalli is predominantly composed of organisms adapted to low-light conditions, such as sponges and ascidians (Kornder et al., 2021). On the other hand, under low to moderate densities, canopy-forming macroalgae may exert a potentially facilitative effect, in which partial shading reduces photoinhibitory stress and favors the initial establishment and survival of recruits. Francini et al. (2002) reported a spawning event of *M. hispida* during April in the Santos region (São Paulo State), near Ilha Grande Bay. If spawning in Ilha Grande Bay occurs during the same or a similar period, it would coincide with the seasonal decline of *Sargassum*, which may favor settlement and recruitment of *M. hispida* in the region.

Adult colonies of *Mussismilia hispida* were present within the same microhabitats occupied by recruits at all depths, with slightly higher values recorded at 8 m. This pattern may indicate the occurrence of intraspecific facilitation, a process previously described for coral larvae that preferentially settle near conspecifics in response to chemical cues and structural characteristics associated with adult colonies (Heyward and Negri, 1999; Raimondi and Morse, 2000; Doropoulos et al., 2016).

Iotrochota arenosa was the sponge with the highest cover within the analyzed microhabitats, reaching maximum values at 5 m depth. This species is recognized for its capacity to overgrow and cause mortality in *Tubastraea* spp. corals (Silva et al., 2017), suggesting a strong competitive potential for space occupation. In general, sponges produce high concentrations of secondary metabolites that may inhibit coral larval settlement (Arnold, 2011; Brandt et al., 2019). However, in the present study, the highest density of *M. hispida* recruits was also recorded at this depth, indicating that the presence of *I. arenosa* did not act as a limiting factor for coral recruitment. Nevertheless, it cannot be ruled out that part of recruit mortality may be associated with overgrowth by *I. arenosa*.

The low cover of other invertebrates within the recruit microhabitats, particularly *Tubastraea* spp. and *Desmapsamma anchorata*, which are abundant in the benthic community of Ilha Grande Bay (De Paula and Creed, 2005; Lages et al., 2011), suggests that algae-dominated substrates may provide more suitable conditions for the settlement and early survival of *M. hispida*. Both taxa are strong spatial competitors and can negatively affect corals through overgrowth or the production of allelopathic compounds (Aerts, 1999; Da Silva et al., 2022).

CONCLUSION

This study provides the first assessment of recruitment and microhabitat characteristics associated with *Mussismilia hispida* recruits in Ilha Grande Bay, a marginal reef system at the southern limit of the species distribution. Recruit density and frequency of occurrence were highest at 5 m depth and lowest at 8 m, indicating that recruitment is not uniformly distributed along the bathymetric gradient. Sites located in sheltered areas, particularly Lagoa Azul and Sítio Forte, exhibited the highest recruit densities, suggesting that longer water residence times may contribute to recruitment success.

The benthic community associated with recruits was dominated by turf algae throughout the depth gradient, whereas crustose coralline algae became more abundant at 8 m depth. The results also indicate that turf algae may constitute an important recruitment microhabitat for corals on marginal reefs of the Southwestern Atlantic, contrasting with the predominantly negative role often reported for turf-dominated assemblages on tropical reefs. In addition, adult colonies of *M. hispida* were consistently present within recruit microhabitats, suggesting the possible occurrence of intraspecific facilitation. Conversely, the higher cover of *Palythoa caribaeorum* in shallow habitats, together with reduced recruit density and frequency at 3 m depth, supports the hypothesis that this zoantharian may limit recruitment through spatial competition. Overall, these findings highlight the importance of habitat characteristics and local environmental conditions in shaping recruitment patterns of *M. hispida* and reinforce the need for long-term monitoring to evaluate the response of marginal coral populations to ongoing environmental change.

Acknowledgements

Authors would like to thanks to Fundação Carlos Chagas de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) through financial support to the Project MONITOMAR (SEI-260003/002213/2021), in the person of Dr. Mônica Marques Calderari. To the Aquamaster Scuba Center and its technical director, Wellington Vieira, for the support during expeditions. To the suggestions to a former version of this manuscript performed by Dr. Helena Passeri Lavrado. This study was conducted under research authorization from SISBIO (#80994) and INEA (009/2025 and 016/2022).

Data availability statements

The datasets generated and/or analysed during the current study are available from the corresponding author upon reasonable request.

Competing Interests

The authors declare no competing interests.

Author Contributions: GLGP and LFS conceived, elaborated, conducted, and executed the work. Both authors contributed to the development of the study, data collection, analysis, interpretation of the results, and preparation of the manuscript. All authors reviewed and approved the final version of the manuscript.

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