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An exclusion experiment to study the influence of habitat structure provided by *Mussismilia* corals (Cnidaria; Anthozoa) on the predation of associated crustaceans

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Abstract

Predation is an interaction between species that influences community organisation by the direct consumption of prey, influencing prey numbers, behaviours and traits. The intensity of predation is greatly influenced by the environment, and the physical structure of habitats may influence predation intensity by providing refuge for prey or reducing the foraging efficiency of predators. In this context, the aim of the present study is to verify the influence of predation on the richness and density patterns of crustaceans inhabiting different species of *Mussismilia* corals, which provide various habitat structures for the associated fauna. We conducted an exclusion experiment to include total, partial and no cage treatments. The richness and density of crustaceans differed among coral species and cage treatments, except between partial cage and no cage treatment. *Mussismilia harttii* showed higher richness and density in uncaged and partial cage treatments compared with *M. braziliensis*, which in turn showed higher values than *M. hispida*. These findings indicate the importance of predation in the structure of crustacean assemblage associated with *Mussismilia* species and that differences in the richness and abundance of associated fauna result from the different habitat structures provided by each species of *Mussismilia*.

Keywords: Habitat structure, Habitat complexity, Habitat heterogeneity, Scleractinian corals, Associated fauna, Artificial cage

Background

Predation is an intra- and interspecific interaction that is thought to markedly influence community organisation by the direct consumption of prey, influencing prey numbers, behaviours and traits. However, some studies found that predation did not significantly influence the structure of communities [1, 2]. Predators and prey are almost always part of complex communities with multiple species interactions and a diversity of indirect interactions [3]. Therefore, understanding the impact of predation is an immense challenge. Manipulative studies may provide

important tools to identify such processes, as suggested by Virnstein [4], Posey and Ambrose Jr. [5] and Galván et al. [6].

Predator effects may increase community diversity at intermediate intensity levels, but at low or high intensity, they may decrease diversity [7]. These effects may influence the community by enhancing species coexistence, preventing resource monopolies by reducing superior competitors and releasing niche space for other species [8]. However, they can also hamper the coexistence of species, e.g., by forcing prey into a limited number of refuges, leading to more intense competition for resources within the spaces [3, 9], or when predators preferentially feed on rare species, leading to local extinction [10]. As Begon et al. [11] suggested, the effect of predation on a community depends on different factors, such as predation intensity, ecosystem

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productivity, and, partly, the characteristics of the prey species. Gilinsky [12], in a study evaluating both the predation effect and role of habitat structure, emphasized the importance of predator identity, the season of the year and the complexity level of the habitat.

The effects of predation in various marine environments, for example, soft bottom [1, 2, 6], artificial reefs [13], coral reefs [14], offshore rock outcrops [5], and marine rock intertidal communities [8, 15] are well documented. Although the effects of predation are often studied by manipulating predator density, in some cases, this strategy may not be the most efficient. Hall et al. [1] observed that predators enclosed in cages failed to feed on the available prey and lost weight, whereas Karlson [16] manipulated the density of echinoids and verified that there was not significant differences on the local macrofauna.

The intensity of predation (the probability that an individual prey will be killed by a predator) is strongly influenced by both physical and biotic characteristics of the environment [17]. The physical structure of the habitat, for instance, may reduce the impact of predation by providing a refuge for prey and/or reduce the foraging efficiency of predators [12, 15, 18]. Habitat structure has been defined as a two axis concept: habitat complexity, represented by the amount of a physical structure; and habitat heterogeneity, which represents the addition of different kinds of physical elements to the system [19–21].

Scleractinian corals are one of the organisms that provide habitat and shelter for invertebrates in coral reefs. Their large carbonate skeletons harbour a great variety of invertebrate species, and their morphological patterns of growth may influence the distribution of these invertebrates. Despite the fact that crustaceans represent the majority of species living directly associated with corals, most coral reef research has focused on fish species, while invertebrates have been neglected [22].

Nogueira et al. [23], evaluating the effects of the habitat structures provided by three different species of the endemic Brazilian coral *Mussismilia*, identified *M. harttii* as the species harbouring a richer and more abundant collection of associated crustaceans, compared to the congeners *M. braziliensis* and *M. hispida*. The larger number of species associated with *M. harttii* corals is related to its phaceloid growth pattern, in which the polyps grow at distance from each other, providing space in between (Fig. 1). Based on the suggestion by Menge and Sutherland [18] that habitat structure effects the foraging efficiency of predators, we aimed to evaluate if predation is important in influencing the richness and abundance of crustaceans associated with the habitat structures provided by three different *Mussismilia* coral species. We tested if there was a difference in the richness and abundance (density) of crustaceans associated with *Mussismilia* species in colonies subjected to total cage, partial cage and uncaged treatments.

Methods

To identify the effectiveness of habitat structures in *Mussismilia* corals as refuges for invertebrates against predators, a field experiment was carried out at Caramuanas reef (Todos-os-Santos Bay, Salvador, Bahia State, Brazil) in March 2013. Cages were systematically placed along the top of the reef, at least 3 metres apart, around *Mussismilia* corals (*M. harttii*, *M. braziliensis* and *M. hispida*) to exclude predators. These coral species were selected due to their close phylogenetic relationships; in this way, the influence of other factors, such as chemical defences is unlikely. The same species were never encaged consecutively (e.g., after sampling *M. harttii*, the following species caged was *M. braziliensis*, then *M. hispida*). Each cage was constructed in a cylindrical format, with plastic mesh (0.5 cm aperture) attached to 2 iron circles (40 cm diameter and 30 cm height). To fix these cages to the bottom, 3 iron pickets were inserted into the substratum for each cage, which was tied to the pickets with plastic cable

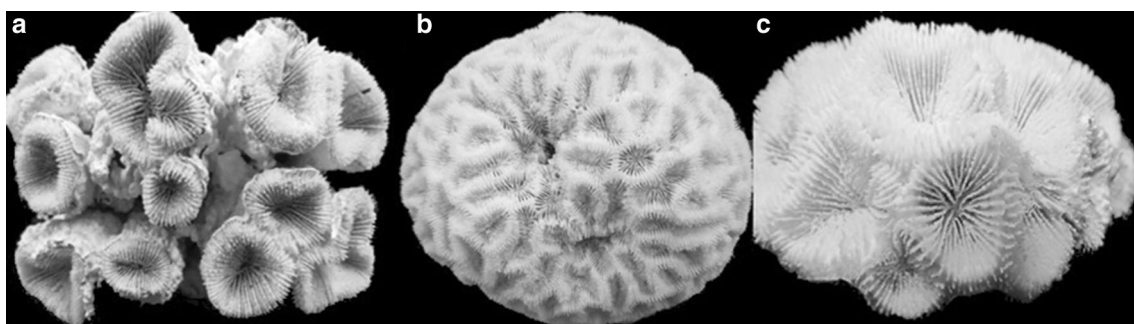


Fig. 1 Images showing the morphological pattern of *Mussismilia* species: **a** *Mussismilia harttii*, **b** *M. braziliensis* and **c** *M. hispida* (modified from Nogueira et al. [23])

ties (Fig. 2). To avoid forming a gap between the cage and the substratum bottom, the cage mesh was attached to the iron picket base. To identify possible damage and certify the efficiency of cages in excluding predators, the experiment was checked every 15 days until the final sampling, to remove seaweed and other debris.

To identify the influence of cages, rather than the exclusion of predators, we constructed partial cages (procedural controls) with 5 apertures (20 cm diameter) (4 on the side and 1 on the top (Fig. 2), to allow access for predators) surrounding each coral species, intercalating them with caged corals and corals without cages in a systematic sampling.

The experiment was set up for 3 months and when the cages were removed (in June 2013) the corals were immediately covered with plastic bags and collected by free diving with a hammer and chisel. For each coral species, we systematically placed 8 complete cages, 8 partial cages and 8 corals without cages, interspersed at a distance of at least three metres.

At the end of experiment, only five cages from each treatment were found and sampled, due to some cages being removed by people. In this case, we also collected 5 colonies of each coral species that had not undergone the treatment, to identify the effects of coral habitat structure under predation influence.

After sampling, corals were washed and the water was filtered in a 150 µm mesh and fixed in 70% alcohol. Then, with the aid of a stereomicroscope, crustaceans were

sorted and separated into groups of numbered morphospecies (when there were more than one morphospecies of a single taxonomical level, they were numbered consecutively). The number of individuals was divided by the coral diameter, providing a density value and preventing the effect of different coral areas.

We transformed richness and density of the crustaceans associated with *Mussismilia* species into log $x + 1$ (base 10) to achieve normality. We conducted a two-way ANOVA in the open-source software R Program, to compare the difference in richness of associated crustaceans between *Mussismilia* species under cage treatments, and we performed the same procedure to identify differences in density of associated crustaceans. A post hoc analysis with Tukey's test was also completed for paired comparisons. Significance was set at $p < 0.05$. Species that contributed most to significant dissimilarities between the coral species were determined using the SIMPER (similarity percentages) procedure from the Primer 6 package.

Results

We collected 6158 individual crustaceans, comprising a total of 102 different taxa, of which the most abundant group was Copepoda (4280), Peracarida (1149), Ostracoda (569) and Decapoda (159). Among Copepoda, the *Halectinosoma* sp., *Idomene* sp. and Canuelidae 1 species were the most abundant. In uncaged corals, all three copepods were more abundant in *M. harttii* and the same pattern was observed in partially caged corals. However,

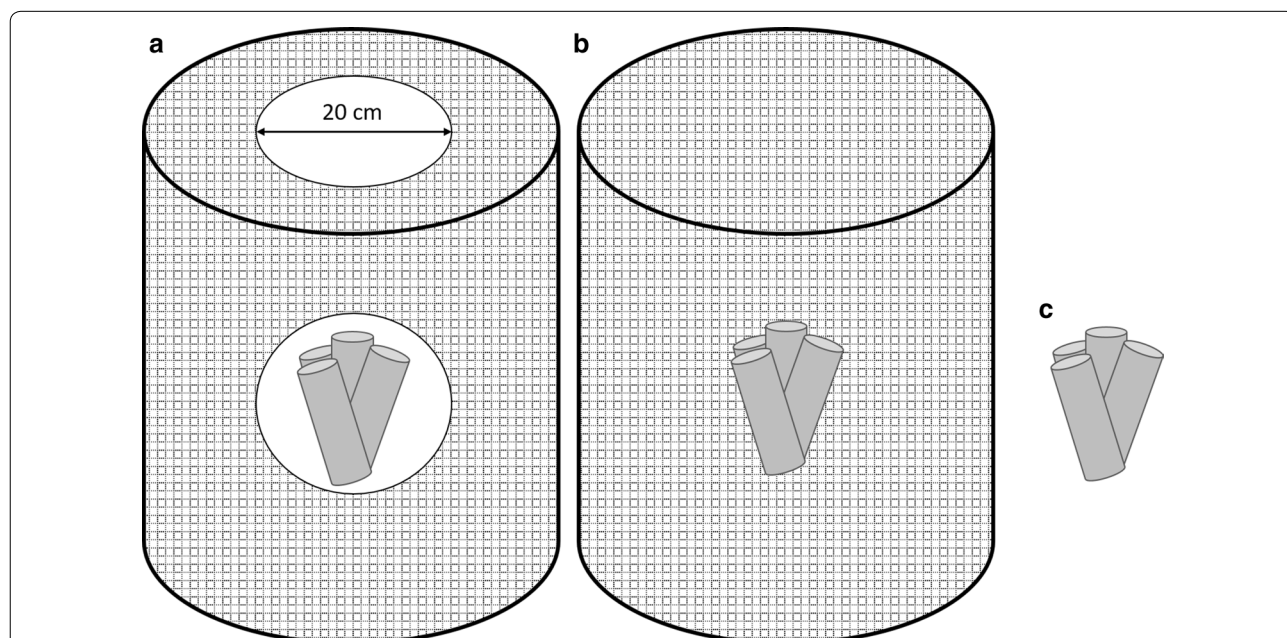


Fig. 2 Scheme of experimental cages: **a** Partial cage (procedural control) with 5 apertures (20 cm diameter), 4 on the side and 1 on the top; **b** total cage, without apertures; **c** corals without cages

in caged corals, they were more often associated with *M. braziliensis*. The most common Ostracoda taxa were Sigilliocopina 1, Podocopina 1 and Sigilliocopina 2, and they presented the same density trend among *Mussismilia* corals as was shown by copepods (Fig. 4).

Two-way ANOVA showed that the richness and density of crustaceans varied significantly with their associated *Mussismilia* species and cage treatment and that there was a highly significant interaction effect (Table 1).

For richness of associated crustaceans, a post hoc Tukey test found significant differences between *M. harttii* and *M. hispida*, and for *M. braziliensis* and *M. hispida*, while no significant differences were found between *M. harttii* and *M. braziliensis*. For density, all comparisons showed significant differences between *Mussismilia* corals. When we analysed the differences in richness between the cage treatments we found that total cage showed significant differences compared with partial cage and no cage treatments, and the same pattern was found for density. No significant differences were identified for partial cage and no cage treatments for richness or density (Table 2).

When we compared the richness and density of uncaged corals, *M. harttii* showed higher values than *M. braziliensis* and *M. hispida*, while *M. braziliensis* had higher values than *M. hispida*. The same pattern was seen in the partial cage treatment. For total cage, there was an increase in the richness and density of crustaceans associated with *M. braziliensis* and *M. hispida*, compared with partial cage and no cage (Fig. 3).

For the most abundant decapod species (*Mithraculus forceps*, *Petrolisthes galathinus* and *Pachycheles monilifer*), higher densities were found in colonies of *M. harttii* in all treatments. For peracarids, the most abundant species presented different patterns: *Carpias* sp. and *Ceiriphotis megacheles* showed a similar pattern to the decapods, and *Ianiropsis* sp. did not present any clear pattern (Fig. 4).

Table 1 Results of two-way ANOVA of the effect of *Mussismilia* species (*M. harttii*, *M. braziliensis*, *M. hispida*) and cage treatment (total cage, partial cage, no cage) on the richness and density of associated crustaceans

Source	df	F	p
Richness			
<i>Mussismilia</i> species	2	18.595	< 0.001
Cage	2	5.683	0.007
<i>Mussismilia</i> species × cage	4	3.898	0.01
Density			
<i>Mussismilia</i> species	2	17.978	< 0.001
Cage	2	10.545	< 0.001
<i>Mussismilia</i> species × cage	4	3.511	0.016

Table 2 Results of post hoc Tukey test for comparisons of richness and density of crustaceans between *Mussismilia* species (*M. harttii*, *M. braziliensis*, *M. hispida*) and cage treatments (total cage, partial cage, no cage)

	Richness p value	Density p value
<i>M. harttii</i> × <i>M. braziliensis</i>	0.284	0.039
<i>M. harttii</i> × <i>M. hispida</i>	0.001	0.004
<i>M. braziliensis</i> × <i>M. hispida</i>	0.001	0.001
Total cage × Partial cage	0.016	0.002
Partial cage × no cage	0.999	0.879
Total cage × no cage	0.016	0.001

When we compared the composition of crustaceans associated with the corals, the SIMPER identified significant dissimilarities between all comparisons of cage treatments for *M. hispida*, with greater dissimilarities between partial cage vs. no cage, and the taxa that contributed most were Cyclopinidae 3 and Podocopina 2. *Mussismilia braziliensis* was second with high dissimilarity values for comparisons of all treatments, and a higher value was verified between total cage vs. no cage treatment, with *Halectinosoma* sp. 1 and *Idomene* sp.

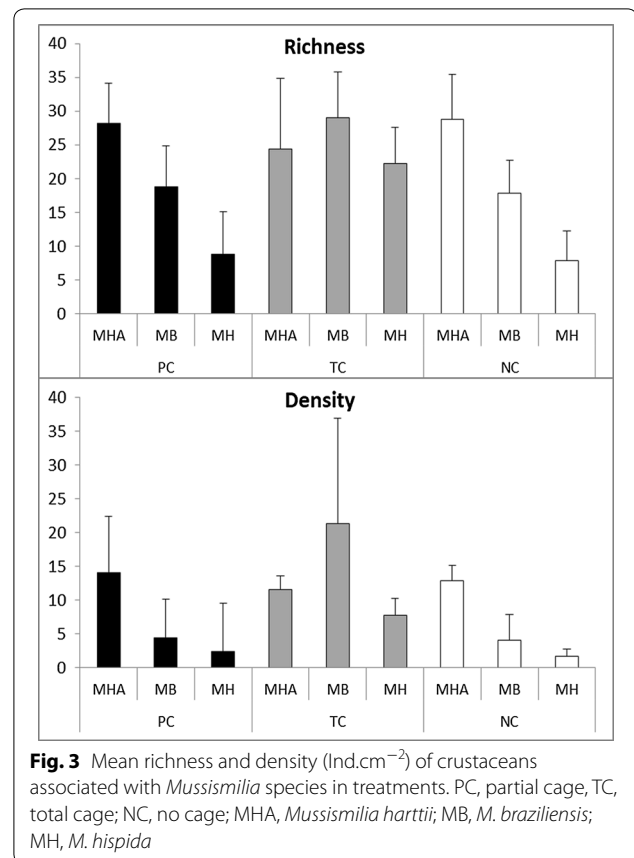
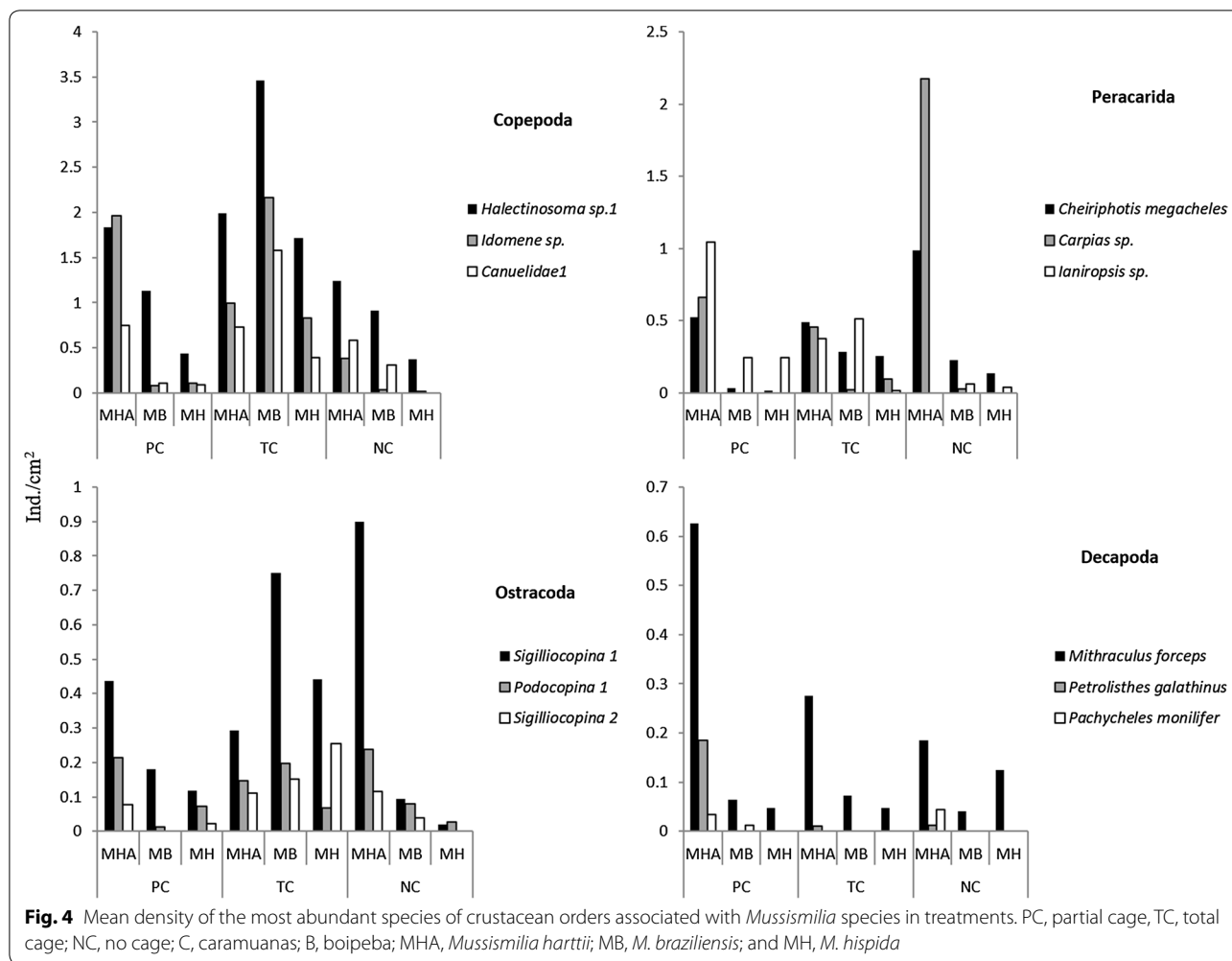


Fig. 3 Mean richness and density (Ind.cm⁻²) of crustaceans associated with *Mussismilia* species in treatments. PC, partial cage; TC, total cage; NC, no cage; MHA, *Mussismilia harttii*; MB, *M. braziliensis*; MH, *M. hispida*



contributing more to these dissimilarities. Minor dissimilarities were identified for *M. harttii*; for these coral, higher dissimilarities were verified between partial cage vs. no cage treatments, with *Carpas sp.* and *Idomene sp.* contributing most to the dissimilarities (Table 3).

Discussion

Predation can be affected by habitat structure, e.g., by reducing the foraging efficiency of predators by providing refuge space [12]). Based on differences in the use of habitats as a refuge against predators, habitat structure may provide axes for niche diversification among prey, even if there is no competition for resources [9].

In coral reefs, crustaceans have been identified as the largest component of the most abundant reef fishes’ diet [13]. Hiatt and Strasburg [14] verified that crustaceans associated with corals are consumed by many species of reef fishes, especially when they move between coral colonies [24]. However, when crustaceans are protected

by a suitable refuge space within their coral host, fish are usually unable to predate them [22].

In the present study, the significant differences in richness and density patterns of crustaceans associated with *Mussismilia* corals between the treatments (total cage vs. partial cage, and total cage vs. no cage treatments) is evidence of the importance of predation in structuring the associated community. The absence of significant differences between partial cage and no cage treatments indicates there was no artefact influence of the structures used to construct exclusion cages. The exclusion of predators is known to impact communities by increasing their density and richness [4]. Our results also show that once predators were excluded in caged *M. braziliensis* and *M. hispida*, the richness and abundance of crustaceans grew to values close to those found in *M. harttii*, which is a species structurally more complex and provides additional refuge against predators.

Table 3 Average dissimilarities between cage treatments and correlations of the most important species contributing to the dissimilarities

	<i>M. harttii</i>	<i>M. braziliensis</i>	<i>M. hispida</i>
Total cage × partial cage			
Average dissimilarity	59.71	70.4	81.51
Species contribution	<i>Idomene</i> sp. 6.2	<i>Halectinosoma</i> sp. 1 9.5	Cyclopinidae 3 9.7
	<i>Halectinosoma</i> sp. 1 4.9	<i>Idomene</i> sp. 5.9	Podocopina 2 9.7
	<i>laniropsis</i> sp. 4.2	<i>laniropsis</i> sp. 4.5	<i>laniropsis</i> sp. 9.4
	Cyclopinidae 2 3.3	Canuelidae 1 4.2	<i>Asterocheres neptunei</i> 6.8
Total cage × no cage			
Average dissimilarity	60.76	77.96	81.45
Species contribution	<i>Carpias</i> sp. 6.6	<i>Halectinosoma</i> sp. 1 11.5	<i>Halectinosoma</i> sp. 1 14.2
	<i>Halectinosoma</i> sp. 1 4.3	<i>Idomene</i> sp. 6.2	<i>Quinquelaophonte</i> sp. 1 6.9
	Sigilliocopina 1 3.9	Canuelidae 1 4.4	<i>Idomene</i> sp. 6.1
	<i>Cheiriphotis megacheles</i> 3.5	<i>laniropsis</i> sp. 4.4	Sigilliocopina 1 4.2
Partial cage × no cage			
Average dissimilarity	65.42	72.12	83.79
Species contribution	<i>Carpias</i> sp. 6.5	<i>Halectinosoma</i> sp. 1 10.84	Cyclopinidae 3 10.5
	<i>Idomene</i> sp. 5.5	<i>Normanella</i> sp. 4.1	Podocopina 2 10.5
	<i>Halectinosoma</i> sp. 1 4.1	<i>Halectinosoma</i> sp. 2 3.4	<i>laniropsis</i> sp. 10.2
	<i>laniropsis</i> sp. 3.8	Canuelidae 1 3.7	<i>Asterocheres neptunei</i> 7

Of the three *Mussismilia* species, *M. harttii* has been previously identified to harbour the richest and most abundant fauna [23]. This result was confirmed in the present study by comparison of *Mussismilia* species in uncaged and partial cage treatments: there was a significant difference in the richness and abundance of associated carcinofauna among species of *Mussismilia* corals.

Higher richness and densities associated with *M. harttii* in uncaged and partial cage treatments, compared with *M. braziliensis* and *M. hispida*, indicates that the partial cages allowed the predators to freely access the colonies. Nogueira et al. [23] identified the space among corallites, an exclusive feature of *M. harttii*, as the most important factor influencing the richness and abundance of associated fauna. The space among corallites acts as a refuge against predators, which is confirmed by the results obtained from caged corals, in which no statistical difference was observed for richness and density once the predators had been excluded.

Our results for the most abundant copepods and ostracods showed higher mean values of density in caged colonies of *M. braziliensis*. This indicates that copepods and ostracods associated with uncaged colonies and partial cages of *M. braziliensis* were affected by predators feeding preferentially on the most abundant species, reducing their population size. The habitat structure of *M. braziliensis* may provide other benefits beyond protection against predators, e.g., easier access to resources, allowing the growth of populations of small animals like copepods

and ostracods. In normal conditions (uncaged), those benefits are suppressed by the harshness of predation.

For decapods, we found higher densities associated with caged *M. harttii*, compared with caged *M. braziliensis* and *M. hispida*. As found by Nogueira et al. [23], *Mithraculus forceps* was the most abundant decapod species, with higher values associated with *M. harttii*. The association of this crab with corals was described as mutualistic by Stachowicz and Hay [25]. According to these authors, the crab obtains food and protection by living among the coral branches and benefits the coral host by preventing the overgrowth of algae.

The most abundant medium-sized species (2–10 mm), the peracarids *Cheiriphotis megacheles* and *Carpias* sp. [26], displayed the same pattern as the most abundant decapods, however, this could be due to cage artefacts. The mesh size used to construct cage artefacts are much smaller than most crabs species, thus, once cages were placed around coral species, crabs associated with the corals remained confined and others could not access the cage interiors. Consequently, the number of species and individuals associated with corals remained the same as at the beginning of the experiment. This is corroborated by the higher values recorded for small crustaceans, e.g., copepods (0.1–1.2 mm) [27] of caged *M. braziliensis* colonies.

Results of SIMPER showed high dissimilarities in the crustacean assemblage between exclusion cage treatments for all three *Mussismilia* species; even with differences in richness and density among cage treatments, the

composition of crustaceans was very variable, which may have produced the high dissimilarities found.

Conclusions

The present study indicates the high importance of predation in structuring the assemblage of crustaceans associated with the endemic coral species of the genus *Mussismilia*. We have confirmed the results of Nogueira et al. [23], who concluded that differences in the richness and abundance of associated fauna among the *Mussismilia* species are a result of the different habitat structures provided by each species, with *M. harttii* being the species that harbours the richest and most abundant associated fauna.

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Authors' contributions

MMN collected and identified material studied, performed data analyses, interpreted the results, and wrote the manuscript. EN and RJ collected and supervised animals identification, provided resources and helped with the interpretation of the results. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article. Datasets are available from the corresponding author on request.

Ethics approval and consent to participate

This study does not involve human participants, animals followed all applicable international and national guidelines for use of animals in research.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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