



REPORT

Substratum selection in coral reef sponges and their interactions with other benthic organisms

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Received: 11 May 2022 / Accepted: 13 January 2023
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Abstract Substratum preferences and contact interactions among sessile organisms can be a major determinant of biotic gradients in the structure of benthic communities on coral reefs. Sponges are a substantial component of these communities, but their substratum requirements and interactions with other benthic taxa are poorly understood. Here, we quantified sponge substratum preferences and interactions from 838 randomly selected photo-quadrats across different depths (5, 10 and 15 m), exposure (sheltered and exposed), and substratum topography (horizontal, inclined and vertical surfaces) on coastal coral reefs in Kimbe Bay. A high proportion (55%) of sponge colonies were associated with dead coral, unconsolidated coral rubble (7%) and calcium carbonate rock (CaCO₃ rock) (7%),

even though they represented only 10%, 4% and 1% of the available substratum, respectively. Sponges interacted most frequently with algae (~34%), corals (~30%) and crustose coralline algae (CCA ~19%) that represented ~46%, ~18% and ~14% of the substratum cover, respectively. The microhabitat preferences of sponges and frequency of interactions with other taxa were mostly consistent across various exposure, depth and substratum topography conditions. Most interactions appeared to be “stand-offs” (71%) which are interactions with no clear winner or loser. However, when overgrowth occurred, sponges were usually winners, overgrowing corals (92%), CCA (81%) and macroalgae (65%). Three sponge species *Dysidea* sp1, *Lamellodysidea* cf. *chlorea* and *Lamellodysidea chlorea* accounted for 51% to 96% of the overgrowth of sponges over algae, corals and CCA, but there was no one species found to always win or lose. Our results suggest that sponges avoid other biological substrata by preferentially settling on dead coral, coral rubble and CaCO₃ rock, but when they do come into contact with algae and corals, they frequently overgrow their spacial competitors.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00338-023-02350-2>.

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Keywords Porifera · Overgrowth · Competition · Environmental conditions · Coral reefs

Introduction

Coral reefs are characterized by both high diversity and cover of sessile benthic organisms, with community structure determined by complex competitive interactions (Lang and Chornesky 1990; Connell et al. 2004; Vermeij and Sandin 2008). Benthic species must be able to establish on a substratum suitable for settlement and subsequently hold and increase space occupation through successful interactions

with other sedentary organisms. Selecting a favourable microhabitat to settle is crucial for a sessile organism, as this sets the environment it will experience throughout its life (Dayton 1971; Price 2010; Chadwick and Morrow 2011). Where a high proportion of the benthic habitat is occupied, finding substrata that offer optimal environmental conditions can be problematic. Once settled, benthic organisms grow and eventually share boundaries with other individuals, resulting in competitive interactions that may include stand-offs, advancing, or retreating (Aerts 2000). The outcomes of these interactions influence structure and functional dynamics of benthic communities on coral reefs (Chadwick and Morrow 2011; Glynn 2013). Theoretically, propagules of sedentary benthic species should settle where they are less likely to interact with superior competitors or where there is a better chance of interacting with inferior competitors. Understanding substratum preferences of benthic taxa and the consequences of any selectivity in settlement site can shed light on habitat preferences and competition dynamics for space in coral reefs systems.

Contact interactions and competition among scleractinian corals have received considerable attention (Connell 1976; Bak et al. 1982; Logan 1984; Lang and Chornesky 1990; Chornesky 1991; Connell et al. 2004; McCook et al. 2001; Schemske et al. 2009; Sandin and McNamara 2012; Álvarez-Noriega et al. 2018; George et al. 2021). There is much less information about interactions among other important benthic organism like algae (Bradbury and Young 1983; McCook et al. 2001), ascidians (Jackson 1977; Rodríguez-Martínez et al. 2012; Hieber et al. 2019) and sponges (Zea 1993; Meesters and Bak 1993; Tanner 1995; Aerts 2000; Schönberg and Wilkinson 2001; Engel and Pawlik 2005; Wulf 2006). The global decline in coral cover and increasing prevalence of macroalgae has reoriented attention to study coral-algae interactions and the mechanisms that favour algae prevalence via direct and indirect competition (Connell 1997; McCook et al. 2001; Jompa and McCook 2003; Brown et al. 2020). Sponges and other benthic dwellers have colonized vacant spaces previously occupied by corals (Aronson et al. 2002; Nagelkerken et al. 2005; Norström et al. 2009; González-Rivero et al. 2011; Marulanda Gómez et al. 2017; De Bakker et al. 2016; De Bakker et al. 2017; Bell et al. 2018a, b; Bell et al. 2022), but how these different taxa occupy, hold and expand is poorly understood.

Sponges are an increasingly important component of the benthic habitat on coral reefs (Rützler 2004; Wulff 2006; Bell 2020; Wolfe et al. 2021). Assessing how sponges occupy space and maintain themselves is critical to understanding their persistence and expansion (Jackson and Winston 1982; Wulff 2005; Bell 2015; Cárdenas et al. 2012). The sciophyllic nature of some sponges can be advantageous in environments with limited light. Sponges appear to have strong preferences for microhabitats, such

as caves and walls (Jackson 1977; Zea 1993; Van Soest 2009; Rützler et al. 2014; Jankowski et al. 2015; Wolfe et al. 2021), where they may have an advantage over other benthic organisms holding space by means of physical and chemical defences that weaken neighbouring organisms (Jackson and Buss 1975; Thacker et al. 2010; Kubanek et al. 2002; López-Victoria et al. 2006; Ashok et al. 2018). On exposed areas of reef, sponges tend to be less abundant probably as a result of heightened competitive interactions with other benthic dwellers (Cárdenas et al. 2012; Bell et al. 2020) or predation (Bjorndal 1990; Powell et al. 2015; Coppock et al. 2022). Few studies have described the interactions among sponges and corals at community scale (Suchanek et al. 1983; Aerts and Van Soest 1997; Aerts 1998; Pineda-Munive et al. 2017; Turicchia et al. 2018) or quantified contact interactions of sponges with other reef benthic taxa (Bell et al. 2020). Information of sponge interactions at community level in the Indo-Pacific biogeographical region and how the frequency of these interactions might be affected by environmental conditions is limited; and links between substratum choices and competitive interactions with other benthic organisms need to be evaluated.

Distribution and benthic cover of sponges have been related to gradients in depth, exposure and substratum topography (Bradbury and Young 1983; Valderrama and Zea 2003; Rützler 2004; Wulff 2005; Meesters et al. 1991; Williams et al. 2013; González-Murcia et al. 2022). Habitat preferences, as well as interaction frequency, may vary along these gradients in relation to changes in substratum type and availability (Suchanek et al. 1983; Aerts 2000; Lauer and Spacie 2004; De Voogd et al. 2004). In a rigid scheme of successional colonization, habitat preferences and sponge interactions might be predetermined (Choi 1984). According to this theory, sponges usually colonize the substratum only after other organisms have arrived and can be succeeded and outcompeted by specific benthic taxa such as solitary ascidians (Jackson 1977; Jackson and Winston 1982). However, there have been many deviations from these predictions (Greene and Schoener 1982; Greene et al. 1983). Sponges can be the most prevalent taxa on the substratum regardless the substrata and competitors involved (Meesters et al. 1991; Wolfe et al. 2021). Sponges might occur on multiple microhabitats, from optimal to marginal, each of them with associated benefits and costs that compromise their performance and persistence on coral reefs. The frequency and strength of competitive interactions between sponges and corals vary along depth gradients and below 10 m depth sponges are commonly aggressors and corals are regularly overgrown (Suchanek et al. 1983; De Voogd et al. 2004). The magnitude and outcome of sponge interactions with other benthic taxa are likely to be influenced by changes in wave exposure and substratum topography as well, but this alternative has not been explored.

The overall aim of this study was to quantify effective microhabitat selection by sponges and their frequency of interactions with other benthic taxa along conditions of exposure, depth and substratum topography, in Kimbe Bay Papua New Guinea. Here, sponges make up approximately 13% of the reef habitat (González-Murcia et al. 2022), although their cover varies and is particularly high on walls. The following specific questions were addressed: (1) Do sponges occur more frequently on a particular microhabitat substratum than others and how does this relate to substratum availability? (2) How does this substratum preference vary along conditions of exposure, depth or substratum topography? (3) Do sponges interact with some taxa more than others and how does this relate to patterns of distribution and cover? (4) Does the relative frequency of interactions of sponges with other benthic organisms change along depth, exposure and substratum topography conditions? (5) Are sponges competitive equals or competitive dominants

over other taxa, such as corals, algae and ascidians? (6) Are there some sponge species that are better than others in overgrowing other taxa?

Materials and methods

Study area and sampling design

Sampling was conducted from October to December 2018 in six inshore reefs located in Kimbe Bay, New Britain, Papua New Guinea ($5^{\circ}12.530$ S, $150^{\circ}22.801$ E; Fig. 1). Sampling on each reef was stratified according to exposure (landward and seaward side of the reef) and depth (5, 10 and 15 m), placing four 50 m length transects at each exposure and depth of the reef generating a total of 144 transects. On each transect, 20 to 33 quadrats of 0.5×0.5 m were randomly selected using the 100 random points on the 50 m transect measuring tape. In total, 838 quadrats were photographed,

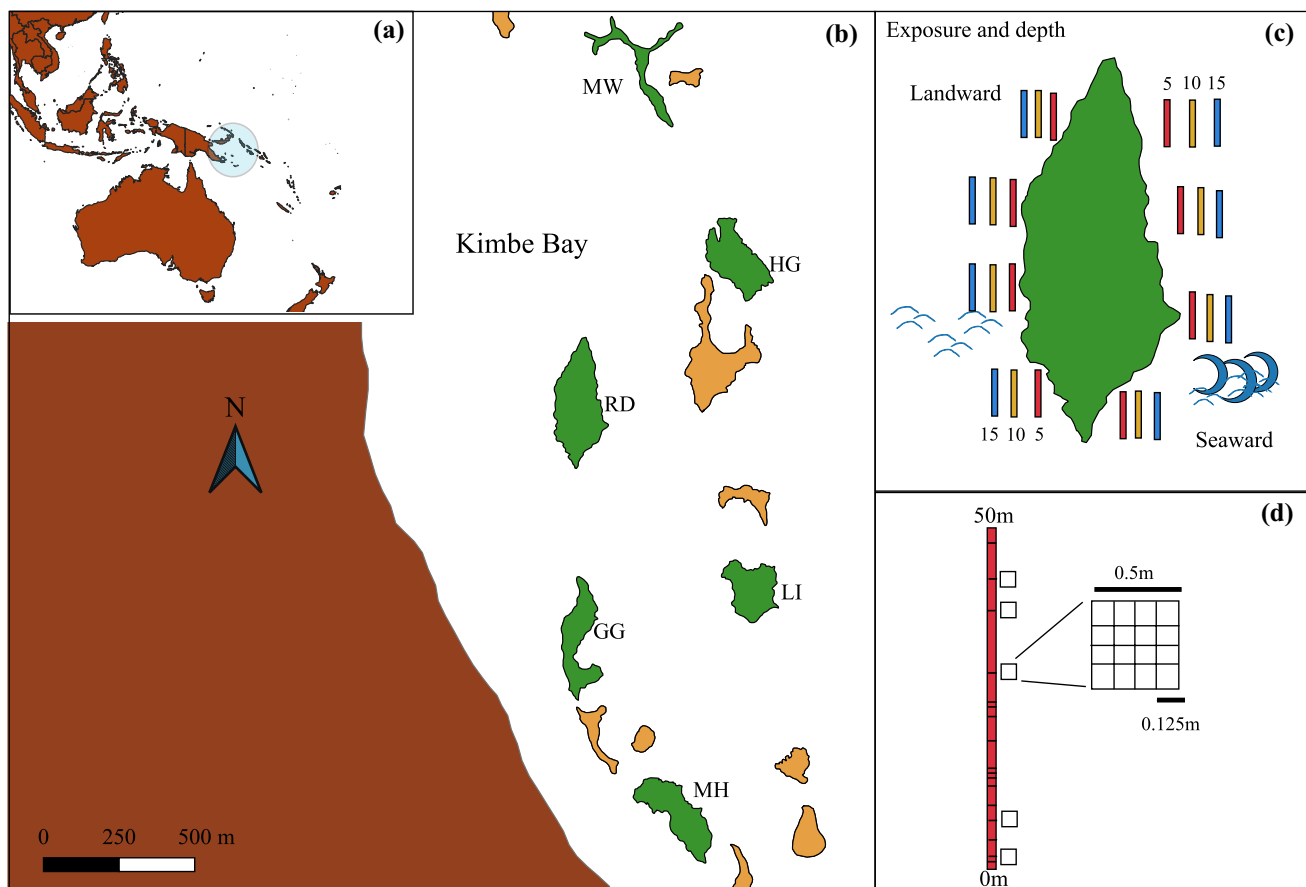


Fig. 1 Study area in Papua New Guinea, New Britain (inset A), Kimbe Bay highlighting the reefs where transects were deployed (green) and other reefs (yellow) (inset B). Transects of 50 m length were deployed at landward (sheltered) and seaward (exposed) sides at 5, 10 and 15 m depth (colour coded red, yellow, blue, respectively

(inset C), and 100 random points on the transect tape were used to randomly select the location of 4 to 9 quadrats of 0.5×0.5 m per transect, each quadrat had 16 sub-quadrats of 0.125×0.125 m (inset D). Abbreviations: MH: Matane Huva, GG: Gava Gava, LI: Limuka, RD: Rakuru Diri, HG: Hanging Gardens, MW: Matane Walindi

and substratum topography recorded considering the category Horizontal, when the substratum was flat or with mild slope, Vertical, when the substratum had approximately 90° slope and Inclined, whenever the slope in the substratum was approximately 45° degrees. Quadrats were divided with a rope in a grid with 16 sub-quadrats (0.125*0.125 cm), and a high-resolution photograph from each grid was obtained. Quadrats were considered the sample unit and 15 random points were overlayed and the substratum beneath each point was recorded to determine percentage of cover in the categories: calcium carbonate rock (CaCO₃ rock), dead coral, live coral, sand, rubble, sponge, algae, crustose coralline algae (CCA) ascidian, clams, anemone, other (gorgonians, hydroids, starfish, sea cucumber, barnacles) and NA when the substratum category could not be determined. The substratum where sponge colonies occurred was recorded to determine the occurrence of sponges per substratum category. Non-informative categories such as NA and substratum types in which sponges did not occur, were removed from further analysis.

Sponges and corals were identified to the lowest taxonomic level and Operational Taxonomic Units (OTU's) were used when sponges could not be identified. Hard corals were identified from digital images, based on previous molecular and morphological analysis on specimens collected from Kimbe Bay and housed in the Museum of Tropical Queensland. Due to the current upheaval in coral taxonomy and the additional uncertainties associated with identifying corals based on images, taxonomic names were assigned using the open nomenclature described by Cowman et al. (2020). Underwater photographs of the sponge specimens were taken considering the sponge colony, the sponge ectosome and endosome, then a piece of the sponge was collected and a picture of the sample out of the water was taken. Underwater pictures were taken using an Olympus TG-5 Camera, 18 mm focal length, underwater setting, macro and flash with exposure 1/200 s and vertical and horizontal resolution > 314 dpi. The sample of sponge tissue was collected and preserved in 70% ethanol for identification. Tissue preparations of the sponge specimens for light microscopy were made by cutting thin sections through the ectosome and endosome with a scalpel. These sections were then cleared in a xylene-phenol saturated solution for 12 h, dried, mounted on a microscope slide and fixed in DURCAPAN (Sigma-Aldrich co., St. Louis, USA) (see Hooper 2000). The spicules were prepared by cutting a small (3mm³) piece of sponge tissue, placing it in an Eppendorf tube with 2 ml of sodium hypochlorite (NaClO) and leaving it for 24 h until dissolved. Then, the samples were centrifuged at 10,000 rpm, and the supernatant removed. The precipitate was rinsed with water and ethanol 90% and centrifugated. This process was repeated three times to remove sodium hypochlorite (NaClO) traces. In some

situations, the samples were processed using a microscope slide, and then, dissolving the tissue in heated nitric acid after cooling, this was mounted with Canada Balsam. The microscope slides were examined using an Olympus BH2. Voucher specimens were deposited at the Invertebrate Collection of the Museum of Tropical Queensland under the codes G339460-339745. Taxonomic assignments were confirmed by Dr Merrick Ekins, Queensland Museum.

The frequency of interactions was quantified by documenting all contact interactions between sponges and other taxa, including anemones, ascidians, algae, coral, hydrozoan, other sponges and soft corals. Contact interactions among organisms were counted once among the same organism even though some individuals had multiple extensions in contact with the same organism in different areas. We accounted for all the interactions that a sponge colony had with other individuals from the same or different species. Contact interactions were scored whenever borders of the target organism were in direct contact with another organism, without distinction on the length of the contact of their borders. Thus, peripheral contacts and tissue contacts were included in the same category. Each interaction was classified as either (1) a “stand-off” or (2) an “overgrowth”. Stand-off is an interaction in which the borders of the organisms are in contact without evidence extensions or borders overgrowing one or the other. Even though there was no clear evidence of dominance in stand-offs, these interactions are not a stagnant process and may include early stages of sponge overgrowth or sponge being overgrow and are physiologically costly for the competitors. Overgrowth interactions were scored where there was clear evidence of the border of one organism overgrowing or covering the other, with clear damage to the individual being overgrown. In this case, the individual that extended its tissue over the other was recorded as the “winner”, and the overgrown individual, the “loser” in the interaction (SI 1). Situations, where multiple interaction points presented different interaction outcomes such as stand-offs and overgrowths of any of the competitors, were infrequent and when present, they were excluded from further analyses. It is acknowledged that this method represents a ‘snapshot’ of interactions in time, as we are sampling a dynamic process, however, on balance, we argue that over the scale of this campaign, we are representing a valid ‘composite’ outcome of the species interrelationships that are occurring.

Statistical analyses

The abundance of sponge colonies was tested using a Generalized Linear Mixed Effects Model (GLMM) with sponge abundance as the response variable and the fixed factors exposure, depth, substratum topography, reef, and percentage of cover of live and dead coral as explanatory

variables. Transect and quadrats within each transect were included as random factors to account for their variability. Percentage of cover of different substratum categories were not simultaneously included since these variables are not independent (e.g. more dead coral percentage associated with less live coral and other substrata). The model was fitted to a negative binomial Poisson distribution to adjust for the dispersion of the data. No deviations from the assumptions of goodness of fit, deviance, residual uniformity, overdispersion and zero-inflation were detected when tested using the DHARMA package (Hartig 2020). The same process was applied for other models with other percentages of cover. The best models included (a) the explanatory variables exposure, depth, substratum topography, reef and dead coral (%) or (b) same variables with live coral (%). Competing models were selected comparing Akaike Information Criteria (AIC). Interaction frequency was analysed following the same process and the best two models included (a) the explanatory variables exposure, depth, substratum topography, reef and live coral (%) or (b) same variables with algae (%).

Habitat preferences of sponge colonies were analysed using the percentage of cover of different substrata in each quadrat as measurement of substratum availability. The substrata sponges occupied were matched to the availability of the categories of substratum to determine the extent at which they preferred or avoided a given substratum. The categories were mutually exclusive, and any observation was assigned to only one substratum category. To determine the degree of microhabitat selectivity, Manly's resource selection ratios were calculated (Manly et al. 2007). Our sampling protocol followed the type I design (Thomas and Taylor 1990), and the habitat use and habitat availability were measured at population scale. The quadrats were selected randomly, and we recorded whether sponges occurred in them or not. Selection ratios (w_i) were calculated with the equation:

$$w_i = o_i / \pi_i$$

where o_i is the proportion of used resource units in category i and π_i is the proportion of available resource units in category i . Bonferroni-corrected confidence intervals were estimated for each selection ratio with the equation:

$$SE(w_i) = \sqrt{[o_i(1 - o_i)/(u_+ \pi_i^2)]}$$

where u_+ is the total number of used resource units. Values greater than 1 ($\pm 95\%$ CI) indicate that occurrence in that substratum is more than expected and values lower than 1 indicate that the substratum is used less than expected whenever 95% CI do not overlap with 1. Overlap of the values or 95% CI bars with 1 suggests that the substratum is used in accordance with its abundance. Manly's index

was used to determine if microhabitat selectivity varied in relation to exposure, depth and substratum topography as well. Manly's selection ratios were obtained using the adehabitatHS package (Calenge 2006).

The frequency of sponge interactions with other taxa was compared to the proportional availability of the other taxa, measured in terms of overall percentage of cover. Sponge interaction frequencies in relation to availability of competitors were compared along conditions of exposure, depth and reef substratum topography using Manly's index. To evaluate the interaction outcomes such as "stand-offs" versus "overgrowth", and in the latter case, "winners" versus "losers" with other taxa (algae, coral or CCA), Chi-square tests of independence were conducted. To assess competitive dominance, we tested whether the proportion of sponges winning (overgrowing) and losing (being overgrown) differed from an expected 1:1 ratio. For the most common species involved in overgrowth interactions, a Chi-square test of independence was executed to evaluate if overgrowing (winning) or being overgrown (losing) depended on the species being involved in the interaction.

Results

1. Microhabitat preferences of sponges across environmental conditions of exposure, depth and substratum topography between reefs

We recorded the occurrence of 21,189 sponges from 82 species, identified at genus or species level (Table SI 2). Regardless of substrate choice, the most abundant sponges overall were *Dysidea* sp1 (23%), *Lamellodysidea chlorea* (21%) and *Lamellodysidea cf. chlorea* (18%). The most abundant 25 species are made up to 89% of the records of sponges. The sponges occurred on 10 substratum categories, with the majority (55%) found on dead coral. The next highest microhabitat occupied was live coral (14%), followed by CaCO₃ rock (7%), rubble (7%) and other live sponges (7%), with other substrata rarely occupied by sponges (Fig. 2a, b). Patterns of habitat use differed from patterns of habitat availability, with the substratum dominated by corals (39%). The use of dead coral, rubble and CaCO₃ rock by sponges is disproportionate, given that they make up only 10%, 4% and 1% of the substratum, respectively (Fig. 2b). The Manly's selection ratios showed that dead coral and CaCO₃ rock are the preferred benthic substrata, followed by rubble which was the only other substratum category used in a greater proportion than expected on the basis of availability (Fig. 3a). Live coral, algae other sponges and CCA were occupied less than expected based on their availability, indicating that sponges are generally avoiding other space occupying organisms (Fig. 3a).

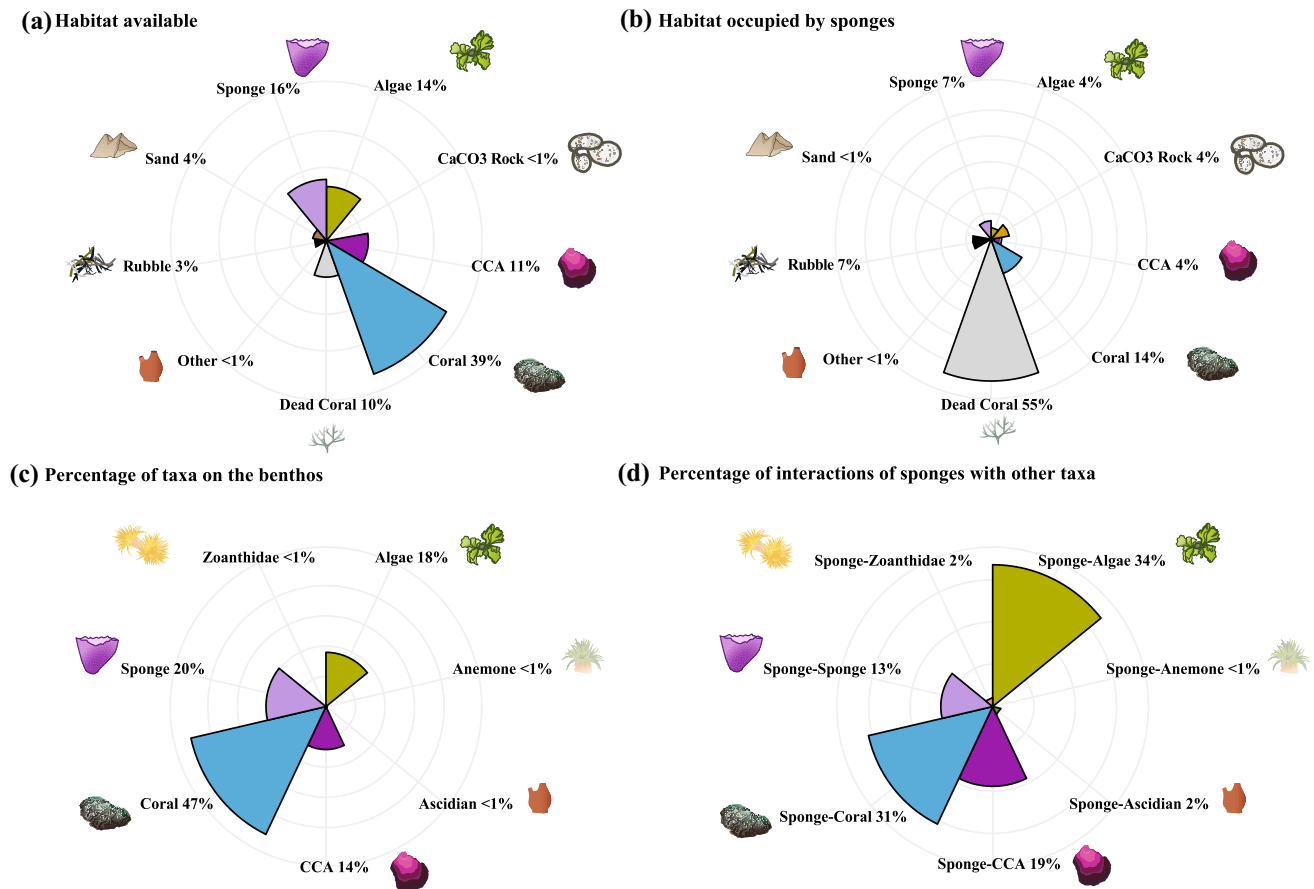


Fig. 2 Mean percentage of substratum availability in terms of % cover of nine substratum categories **a**, substratum occupied by sponges **b**, substratum covered by sessile taxa **c**, and sponge interactions **d** estimated on 838 quadrants in Kimbe Bay, Papua

New Guinea. Symbols courtesy of the Integration and Application Network modified by SGM. *The category “other” includes anemone, ascidians, bryozoans, gorgonians, clams, starfish, sea cucumbers, barnacles and zoanthids

Environmental factors did influence the abundance of sponges. Sponge abundance varied in response to different conditions of exposure, depth, substratum topography, reefs, dead coral and live coral cover. These environmental factors modified the abundance of sponge individuals with varying magnitude in each reef (Table 1). There were more sponges on the sheltered side of the reefs and usually sponges were more abundant at 10 m depth compared to 5 and 15 m that had similar number of sponges. The number of sponges was similar among most of the reefs, with the exception of Limuka that had lower sponge abundance than the other reefs. Strong differences in sponge abundance were associated to substratum topography with horizontal surfaces having almost 50% less sponges compared to inclined and vertical surfaces. The amount of exposed dead coral decreased with the occurrence of sponges and in areas with high number of sponges, the proportion of available dead coral substratum was low (Fig. 4a). This dynamic generated a negative trend

between sponges and dead coral substratum (Fig. 4a) that is interpreted as a replacement of exposed dead coral by sponges covering over dead coral. Conversely, in areas where sponge cover was low, there were large areas of dead coral exposed. The model including live coral cover (%) generated similar outcomes for the environmental variables (SI 3, 4) and sponge abundance was negatively associated to coral indicating that the number of sponges is higher in areas with low live coral cover (%) (Fig. 4b).

Changes in sponge abundance did not modify the occurrence preference of sponges on dead coral, CaCO₃ rock and rubble substrata that remain recurrent on landward and seaward exposures, at all depths and reef profiles (SI 6). Usually more than 50% of sponges occurred on dead coral regardless of the environmental gradient analysed (SI 6). The second microhabitat preferred by sponges was rubble, with few exceptions across survey sites at 15 m depth, and on vertical substratum topography where space was used in accordance with that substratum's

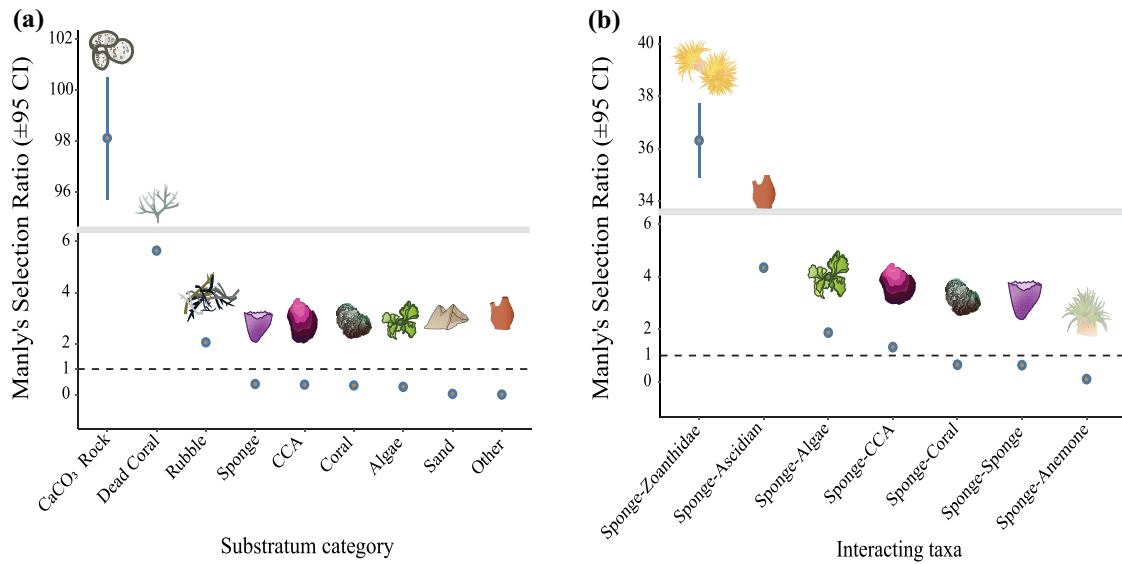


Fig. 3 Manly's selection ratios for sponges on the most abundant substratum types estimated **a** and interactions of sponges with other benthic taxa **b** estimated on 838 quadrats in Kimbe Bay, Papua New

Guinea. *Note that, the scale of the y axis has been interrupted to improve the visualization of extreme values. Symbols courtesy of the Integration and Application Network modified by SGM

Table 1 Abundance of sponge colonies between different levels of exposure, depth, substratum topography, reef and percentage of dead coral (a), and interaction frequency between different levels of

exposure, depth, substratum topography, reef and (b) estimated on 838 quadrants in Kimbe Bay, Papua New Guinea

	DF	Chi-square	Pr(> Chi-square)
<i>(a) Abundance fixed terms</i>			
Exposure	1	11.08	0.001
Depth	2	17.29	0.001
Reef	5	46.29	0.001
Substratum topography	2	51.29	0.001
Dead coral (%)	1	5.30	0.021
<i>Random terms</i>			
	Variance	Standard deviation	
Transect	0.00684	0.08	
Quadrat	0.02382	0.15	
<i>(b) Interaction's frequency fixed terms</i>			
Exposure	1	11.44	0.001
Depth	2	17.34	0.001
Reef	5	198.18	0.001
Substratum topography	2	35.68	0.001
Coral (%)	1	62.77	0.001
<i>Random terms</i>			
	Variance	Standard deviation	
Transect	0.00147	0.12	
Quadrat	0.02742	0.17	

availability. Live coral was the second highest used substratum by sponges along all the environmental conditions considered. However, the use of live coral was less than expected based on the abundance of this habitat

suggesting that sponges avoid live coral substratum. Other substratum categories, including biotic and abiotic substrata, were barely occupied by sponges, and usually "avoided" as habitat.

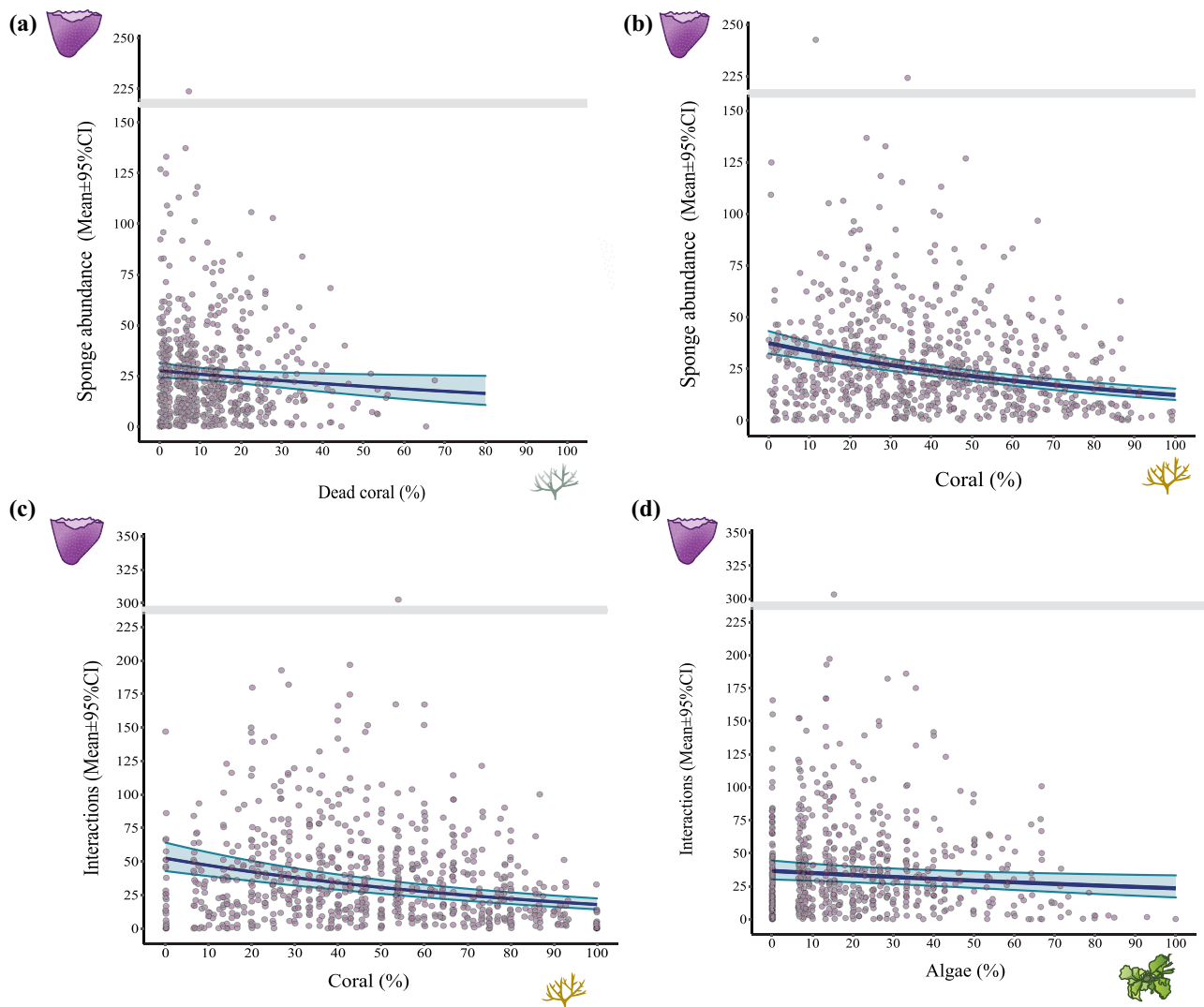


Fig. 4 Sponge abundance in relation to dead coral **a** and live coral cover **b**, the full model included variables exposure, depth, substratum topography and reef (see methods) and sponge interaction frequency in relation to live coral **c** and algae cover **d**, the full model included variables exposure, depth, substratum topography and reef

(see methods) that were estimated from 838 quadrats in Kimbe Bay, Papua New Guinea. *Note that, the scale of the y axis has been interrupted to improve the visualization of extreme values. Symbols courtesy of the Integration and Application Network modified by SGM

2. Frequency of interactions of sponges with other benthic taxa across environmental conditions of exposure, depth and substratum topography between reefs.

We recorded 30,040 interactions between sponges and eight major benthic groups. Only 2,759 (~13%) sponges were not in contact with any other taxa. Sponges had higher proportions of interactions with algae (~34%), corals (~30%), CCA (~19%) and other sponges (~13%), respectively, with interactions with other benthic taxa relatively rare (<2%) (Fig. 2 c, d). These patterns diverged from that which might be expected on the basis of the percentage of cover of the different taxa. Even though sponges had a high proportion of interactions with corals,

the Manly's selection ratio revealed that this was less than expected based on the cover of corals (46%) (Fig. 3b). Similarly, sponges appeared to be avoiding interacting with other sponges and anemones. On the other hand, the lower number of sponge interactions with algae, CCA, zoanthids and ascidians was higher than expected, given their relatively low covers of 18% and 14% and less than 1%, respectively. There were 79 sponges identified at genera or species level involved in interactions with other benthic dwellers. The 25 most abundant sponge species represented 88% (26,529) and the species *Dysidea* sp1, *Lamellodysidea* cf. *chlorea* and *Lamellodysidea chlorea* constituted 63% of all the interactions with 27%, 20% and 16%, respectively.

The number of interactions of sponges was strongly associated with sponge abundance ($r^2 = 0.85$, 5 CI = 0.83–0.87, $p < 0.0001$) having on average 1.4 interactions per sponge (SI 5). Interaction frequency changed along environmental factors of exposure, depth, substratum topography, reefs, dead coral and live coral cover. There were more sponge interactions recorded on the sheltered side of the reefs and at 10 m depth compared to 5 m and 15 m. Sponge interaction frequency was similar between most of the reefs, but Limuka that had fewer sponge interactions compared to the other reefs. Abrupt changes in interaction frequency were observed between levels of substratum topography with sponges on horizontal surfaces having almost 45% less interactions compared with inclined and vertical surfaces. The frequency of sponge interactions decreased ~60% when the percentage of coral cover increased from 0 to 80% (Fig. 4c). The model including algae cover produced similar estimates of interaction frequency for the environmental variables (SI 7, 8), and algae cover was associated to a ~31% reduction in interaction frequency when algae changed from 0 to 80% (Fig. 4d).

The interaction preferences of sponges with other benthic taxa were generally unaltered between levels of the environmental factors studied. The proportions of sponge interactions with other taxa were very similar across the two different exposures, the three depths and three reef levels of substratum topography in all reefs. Sponges regularly interacted more than expected with algae and CCA, and when present with zoanthids and ascidians. Sponges often tended to avoid interactions with corals, other sponges and other organisms (SI 9). Sponge interactions on horizontal and inclined areas were similar to the general pattern, interacting mainly with algae, CCA, zoanthids and ascidians. However, on vertical substrata, sponges were the dominant substratum category, followed by algae, corals and CCA. On vertical substratum sponge-coral and sponge-CCA interactions occurred in a similar proportion from what was expected, based on their proportion of availability.

3. Are sponges competitive equals or competitive dominants?

Most of the interactions between sponges and other taxa, including the main biotic components algae, corals and CCA, were stand-offs (71% of 30,040 interactions) (Fig. 5). Where overgrowth was observed (29% of interactions), more often than not it was the sponge overgrowing other taxa (Fig. 5). The interaction outcome depended on whether algae, corals or CCA were involved in the interaction with the sponge ($\text{Chi}^2 = 2322.1$, $\text{df} = 4$, $p \text{ value} < 0.0001$). In sponge-algae interactions, stand-offs were the most common outcome with 77% (7,733) of the total, followed by sponges overgrowing algae (15%) (1,512) and algae overgrowing sponges in less

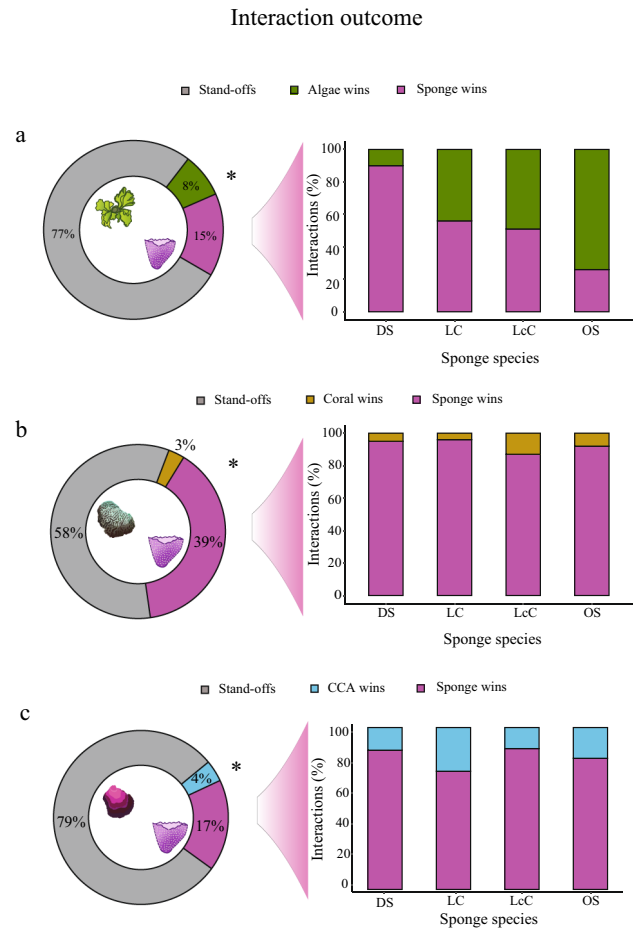


Fig. 5 Percentage of interactions of sponges with algae (a); corals b and CCA c classified as stand-offs, sponges overgrowing the competitor and overgrown by its competitor, respectively, and subsets of aggressive interactions for the three most common species *Dysidea* sp1 (DS), *Lamellodysidea chlorea* (LC), *Lamellodysidea cf. chlorea* (LcC) and other sponges (OS) estimated on 838 quadrats in Kimbe Bay, Papua New Guinea. Symbols courtesy of the Integration and Application Network, Sponge by Caroline Donovan, Algae by Tracey Saxby and CCA by Kim Kraeer and Lucy Van Essen-Fishman modified by SGM

extent (8%) (803) ($\text{Chi}^2 = 10,459$, $\text{df} = 2$, $p \text{ value} < 0.0001$) (Fig. 5a). The higher percentage of sponges overgrowing algae (65%) versus algae overgrowing sponges (35%) indicated that sponges are usually winners in interactions with algae ($\text{Chi}^2 = 63.023$, $\text{df} = 1$, $p \text{ value} < 0.0001$). There were 41 sponge species involved in overgrowth interactions with algae but most of them (91%) involved the sponges *Dysidea* sp1 (69%), *Lamellodysidea chlorea* (12%), *Lamellodysidea cf. chlorea* (10%). There were 35 sponges identified to species level and 14 sponge OTU's being overgrown by 37 algae OTU's. The most common sponges being overgrown by algae were *Dysidea* sp1 (14%), *Lamellodysidea cf. chlorea* (17%), *Lamellodysidea chlorea* (17%) and *Coelocarteria singaporensis* (13%) (Fig. 5).

In sponge-coral interactions, stand-offs were also the most frequent, comprising 58% (5,376) of the interactions followed by overgrowth interactions of sponge on corals with 39% (3,565), and only 3% (298) represented overgrowth of corals over sponges (Fig. 5b) ($\text{Chi}^2 = 4379.2$, $\text{df} = 2$, p value < 0.0001). When considering overgrowth, sponges were clearly most likely to win, overgrowing corals in 92% of cases, as opposed to corals overgrowing sponges in only 8% of cases. There were 66 sponge species, and 53 coral genera involved in overgrowth sponge-coral interactions. Sponge species with higher number of overgrowth interactions with corals were *Dysidea* sp1 (25%), *Lamellodysidea* cf. *chlorea* (20%), *Lamellodysidea chlorea* (17%) that together represented 62% of all sponges overgrowing corals. Corals of the genera *Porites* spp (41%), *Psammacora* spp (23%), *Coscinaraea* (3%), *Leptastrea* (2%), *Pavona* spp (5%), *Pachyseris* spp (2%), *Anacropora* spp (2%) and *Acropora* spp (2%) were affected the most. There were 32 sponge species overgrown by corals, most of them colonies of *Lamellodysidea* cf. *chlorea* (31%), *Lamellodysidea chlorea* (15%) and *Dysidea* sp1 (10%) representing 56% of all the overgrowths. Encrusting coral forms of the genus *Porites* spp overgrew sponges (winners) in 36% of the overgrowth sponge-coral interactions.

In sponge interactions with CCA, stand-offs were also the most common interaction accounting for 79%, (4,440) of all interactions, followed by sponges overgrowing CCA in 17% (987) and CCA growing on sponges in 4% (222) of the interactions ($\text{Chi}^2 = 453.92$, $\text{df} = 2$, p value < 0.0001) (Fig. 5c). Sponges were the most likely to be winners, with sponges overgrowing CCA in 81% of the interactions and CCA overgrowing sponges in only 19% of the interactions. There were 67 sponge species recorded overgrowing 5 CCA OTU's. The sponges that accounted for most of the overgrowth were *Lamellodysidea* cf. *chlorea* (20%), *Lamellodysidea chlorea* (9%), *Dysidea* sp1 (8%) that pooled together accounted for 37% of the aggressive interactions of sponges over CCA. Moreover, 34% of the overgrowth occurred over *Lamellodysidea* cf. *chlorea* (15%), *Lamellodysidea chlorea* (14%), *Dysidea* sp1 (5%) and 66% on other sponges. Thus, sponge interactions with algae, corals and CCA involve a great diversity of species of each taxon. Most of the interactions involve the encrusting sponges *Lamellodysidea* cf. *chlorea*, *Lamellodysidea chlorea* and *Dysidea* sp1 but there is no one sponge that always wins or losses (Fig. 5c).

Discussion

Our study indicates that encrusting sponge species of inshore reefs in Kimbe Bay show strong preferences in habitat use for non-living substrata, most notably for dead

coral, CaCO_3 rock and rubble. Sponges tended to avoid other living substrata such as hard corals and algae, which take up 53% of the available space. The strong selectivity of sponges towards non-living substrata suggests there is a premium on settling in the right place and avoiding contact with other organisms as much as possible, at least in the early stages of development and growth. This pattern was consistent across different depths, reef exposure and reef substratum topography, with dead coral always the most preferred substrata. Despite preferring non-living substrata, 87% of the sponges were in contact with other taxa, most notably hard corals, algae and CCA. These interactions were not random, with interactions with corals less than expected, and interactions with CCA and algae more than expected, given their relative cover. Seventy-one percent of the interactions were “stand-offs”, with no clear winners, and where overgrowth occurred, sponges were usually the winners, especially over CCA, which may explain why they appear to prefer interacting with this taxon. The sponge species involved in interactions were diverse, but were dominated by three encrusting species *Dysidea* sp1, *Lamellodysidea chlorea*, and *Lamellodysidea* cf. *chlorea*. Winners and losers in interactions varied depending on the competitor with no one sponge always succeeding on overgrowing another. Our results suggest that sponges have successful strategies for occupying and persisting in the face of competition for space on these reefs and could readily outperform other taxa if other factors lead to a decline in coral cover.

The preference for dead coral, CaCO_3 rock and rubble could enable sponges to become established for a period before having to face interactions with other benthic taxa. It also indicates the high level of specialization that some sponges have to sciophyllic microhabitats such as those created by rubble deposition (for a review see Wolfe et al. 2021). Sponge occurrence on dead coral, CaCO_3 rock and rubble could be expected if sponge larvae or propagules are competitively inferior. Settling near fully developed adults of the same species or other taxa could have detrimental impacts on their survival and development through direct aggressive interactions (Uriz et al. 1998; Vermeij and Sandin 2008). Experiments on settlement success in sponges, coral, algae, crustose coralline algae (CCA) and turf algae indicate that recruitment was largely enhanced in areas of low competition (Battershill and Bergquist 1990; Uriz 1998; Fabricius and De'ath 2001; Vermeij and Sandin 2008; Fabricius et al. 2005; Bergquist and Sinclair 2010; Brandt 2019) and the preference for non-living substratum is merely the reflection of sponge larvae avoiding agonistic interactions with other benthic organisms.

Sponge preferences for dead coral, CaCO_3 rock and rubble could also be associated with the ecological requirements of some sponges, since many species are bioeroders degrading calcium carbonate (Pari et al 2002;

Schönberg and Suwa 2007; Schönberg 2015). Indirect evidence of sponge preferences for dead coral, CaCO_3 rock and rubble is supported by increases in sponge colonization of coral skeletons after severe coral declines (Rützler 2002; López-Victoria and Zea 2004; Schönberg and Ortiz 2008; Carballo et al. 2013; Wolfe et al. 2021). In the Indo-Pacific region, bio-eroding sponges can occupy on average ~9% of available dead substratum and changes in community structure are primarily attributed to differences in the availability of CaCO_3 rock from dead coral (Marlow et al. 2018).

Environmental conditions generally did not restrict or modify the microhabitat selection of sponges for dead coral, CaCO_3 rock and rubble. The only conditions where sponges exclusively occupied dead coral were at 15 m depth and on vertical surfaces. This indicates that environmental variables associated with depth, exposure or substratum topography might have a secondary role on determining sponge microhabitat occupation. We suspect that changes in environmental variables along the gradients of depth and exposure that were analysed did not exert enough pressure for most of the sponges to shift habitat preferences towards other substratum types. Alternatively, these assemblages are well adapted to the range of conditions in the area. As suggested by Wulff (2005), probably at finer scale, environmental factors can act as filters excluding some species from a habitat, but when their effect is negligible, biological interactions like competition and predation could be reshaping sponge communities.

Sponges predominantly interacted with corals, but tended to avoid those interactions, and preferred to interact with CCA and algae. Corals are strong competitors and might reduce sponge survival, inflicting damage by abrasion or chemical defence (Schönberg and Wilkinson 2001). Algae and CCA were not the dominant benthic group suggesting that the frequency of interactions among these taxa is not by chance and follows patterns of competition for similar habitats. Algae and some sponges are opportunistic groups that undergo outbreaks and establish on dead coral skeletons, sometimes becoming dominant in alternative states (Zea 1993; Norström et al. 2009; González-Rivero et al. 2011; Ferrari et al. 2012). Both taxa are characterized by rapid reproduction and growth and can be resilient to environmental stress when compared to corals. We suspect that the frequency of sponge-CCA and sponge-algae interactions is the result of rapid colonization on dead coral and CaCO_3 rock. Dead coral and CaCO_3 rock might represent the ideal substratum for these taxa, whose recruits grow and expand rapidly to monopolize it, as it has been described by Pineda-Munive (2017) in recently dead branching *Acropora* spp. corals and other benthic invertebrates like ascidians (Tebbett et al. 2019). Even though some sponge species interact and colonize other live organisms and

benefit from them (see Lauer and Spacie 2004; Bergquist 2010), we consider that the interactions of sponge-algae and sponge-CCA that we documented are competitive interactions caused by similar habitat requirements rather than cooperation. Sponges might prefer interacting with CCA and algae because some sponges such as *Dysidea* sp1 could be competitively superior to these taxa and are likely to overgrow them.

Microtopographic differences can facilitate the colonization of some surfaces by sponge assemblages (Choi 1984; Winston and Jackson 1984; Jackson 1977; Meesters 1991). For sponges, vertical substratum topography bolstered patterns of habitat preference and interactions with other benthic counterparts. Substratum topography can be linked to changes in environmental conditions including differences in sediment deposition, light incidence and surge exposure offering advantages to benthic organisms that cannot cope with sediments and do not possess solid skeletons (McGehee 1994). Changes in communities determined by substratum topography have been observed in corals and sponges with encrusting and plating forms being more abundant on walls meanwhile branching and massive species dominate slopes (Jackson 1977; Jankowski et al. 2015; González-Murcia et al. 2022). As the substratum topography changes, communities of benthic dwellers get replaced by representatives that can maximize their performance on those conditions, increasing the number of other competitors (Jackson 1977). Sponges might prefer to inhabit inclined and vertical areas since sediment deposition is reduced and their performance can be maximized, probably accelerating growth rates and resulting in multiple contact interactions with surrounding individuals.

Most of the interactions between sponges and other organisms were “stand-offs”, with no obvious winner or loser. Despite the lack of direct physical evidence of aggression, stand-off interactions may require continued allocation of energetic resources to maintain the status quo (Aerts 2000). Stand-offs can represent a prelude to overgrowth or involve alternative strategies of aggression and competition that are not generally acknowledged. Stand-off interactions are connected to concomitant changes in both counterparts that can include continuous growth adjacent to one another border, accumulation, and relocation of resources on the borders and simultaneous retreat-overgrowth from both counterparts (Jackson and Winston 1982; Aerts 2000). Consequently, a substantial proportion of stand-off interactions observed could represent a transition towards a shift in dominance of one of the parts involved, and the strategy utilized in each of these interactions is very likely to be species specific.

Sponges usually overgrew corals and CCA indicating some dominance over species of these taxa, while there was a more equal outcome when interacting with algae. Sponge

competitive success over other many sessile taxa has also been documented on the under surface of foliose corals (Jackson and Winston 1982). Thus, we suspect that if the CaCO_3 rock substratum availability increases because of coral (or other taxa) mortality, sponges are likely to colonize vacant substratum whenever they can cope with the new environmental conditions and overtake space from corals or opportunist taxa such as algae, CCA and ascidians. The apparent preference of sponges for interacting with algae and CCA has been previously noted by Jackson and Winston (1982) and Pineda-Munive (2017). We do not have evidence of space saturation and the occurrence of some sponge species on corals and other live organisms might reflect competitive superiority of some species or precipitated settlement due to inter or intraspecific factors that lead some individuals to recruit in marginal and suboptimal habitats. These alternatives offer interesting research avenues that could be explored in future investigations.

Sponges generally overgrew other main benthic competitors, but in spite of this dominance, it is interesting to question why sponges are not dominant in cover and abundance on exposed surfaces in the coral reef benthos. Highly aggressive sponges such *Terpios hoshinota* (Elliott et al 2016) and *Chalinula nematifera* (Turicchia et al 2018) are known to proliferate in coral-dominated environments in the Indo-Pacific, including in Kimbe Bay (Ekins et al. 2017), although the factors that triggered these outbreaks are unknown. Interactions among benthic organisms can offer insights of potential mechanisms of subordinate species driving substratum cover in coral reefs but the trends are less predictable for aggressive species. One alternative can be that substratum monopolization by dominant species can be curtailed in environments that are patchy and discontinuous, favouring diversity at different scales (Wulff 2005). Coral reefs contain a mosaic of substrata generating discontinuous sections composed of sand, CaCO_3 rock, rubble and biotic substratum that could generate enough disjunctions to avoid that dominant species monopolize the benthos. Top-down control might determine sponge abundance since predators like fish (Randall and Hartmann 1968; Wulff 1994; for a review see Coppock et al. 2022), turtles (Meylan et al. 1988; Bjorndal 1990; von Brandis 2014) and other invertebrates (Powell et al. 2015) consume significant amounts of sponges.

We cannot distinguish whether the occurrence of sponges overgrowing corals was the result of sponge colonization on healthy corals, or colonization on corals previously affected by diseases or having lesions and subsequently colonized by sponges. Energy investment on recovery from drastic environmental changes and diseases might impair coral fitness to endure competitive interactions (Meesters and Bak 1993), and we suspect that this might facilitate sponge overgrowth on corals.

At a larger scale, bleaching events have reshaped coral assemblages and size structures towards coral colonies of small or intermediate size (Dietzel et al. 2020), and the competitive fitness of the current hard coral communities to withstand benthic dwellers and monopolize spaces might be compromised (George 2021). Mild but pervasive disruptions such as coral diseases are more prevalent in coral reefs (Harvell et al 2007), and coral colonies partially affected by diseases might be more prone to be colonized by sponges than healthy corals (Aerts 2000). Our results support the alternative that sponges do preferentially colonize calcium carbonate vacant space and that increments in their abundance might involve a process of substitution of dead corals after bleaching rather than competitive dominance, at least for those species that could display opportunist strategies.

Conclusions

Encrusting sponges are employing strategies to maximize their success in space occupation that involve preferences for substrata and interactions with particular taxa. Most notably, sponges prefer to be attached to non-living substrata (CaCO_3 rock and rubble) and to interact with non-coral organisms (CCA, algae, zoanthids and ascidians). They do attach to corals, and they do appear to be able to overgrow them, but this does not seem to be the preferred option. Selection of dead coral, CaCO_3 rock and rubble apparently is the most favourable option to maximize settlement and experience low competition during settlement; nonetheless, other taxa can follow similar strategies and mechanisms for space competition used by sponges, and this needs to be assessed. Sponges are one of the main components of the benthos and are often overgrowth winners. We presented detailed information of the current benthic interaction dynamic of sponges with insights on sponges' dominance that could lead to sponge-dominated reefs in the Anthropocene. Future experiments can provide insights on the potential of sponges to colonize living substrata, dead coral and CaCO_3 rock to investigate the effect of multispecies interactions versus interactions with single organisms. Interacting preferentially with algae, CCA, zoanthids and ascidians might be based on competitive superiority of sponges over these taxa, or a circumstantial result based on similar microhabitat preferences since both groups appear to be opportunist. In a dynamic, competitive and structured system such as coral reefs, stand-off interactions could be a transitory stage rather than a fixed condition. Future work is necessary to assess the progression and outcomes of interactions when in contact with different taxa to understand the prevalence of species in contact

competition or mechanisms that determine stand-offs and overgrowth.

Acknowledgements The authors appreciate the support of the staff at Mahonia Na Dari Research and Conservation Centre and Walindi Plantation Resort. We acknowledge the traditional owners of the Tamare-Kilu reefs in Kimbe Bay, and we are thankful to them for allowing us to undertake this research. A collaboration with Amy Coppock on the distribution and abundance of sponges facilitated data collection for this project. This research was supported by core funding to G. P. Jones from the ARC Centre of Excellence for Coral Reef Studies (CE140100020) and funds from the Small Grant Program of The Rufford Foundation to Saúl González-Murcia (SGM). Data collection was conducted with the approval of the James Cook University Ethics Review Committee (Approval number A2583). The data presented are part of the doctoral research thesis of SGM at James Cook University. Symbols for graphs courtesy of the Integration and Application Network, sponge by Caroline Donovan, CaCO₃ rock, coral, sand, algae, ascidian, anemone, zoanthid by Tracey Saxby, CCA by Kim Kraeer and Lucy Van Essen-Fishman, dead coral and rubble by Catherine Collier are modified by SGM.

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References

- Aerts LAM (1998) Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. *Mar Ecol Progr Ser* 175:241–249. <https://doi.org/10.3354/meps175241>
- Aerts LAM (2000) Dynamics behind standoff interactions in three reef sponge species and the coral *Montastraea cavernosa*. *Mar Ecol* 21:191–204. <https://doi.org/10.1046/j.1439-0485.2000.00685.x>
- Aerts LAM, Van Soest RWM (1997) Quantification of sponge coral interactions in a physically stressed reef community, NE Colombia. *Mar Ecol Progr Ser* 148:125–134. <https://doi.org/10.3354/meps148125>
- Álvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Connolly SR (2018) Negligible effect of competition on coral colony growth. *Ecology* 99:1347–1356. <https://doi.org/10.1002/ecy.2222>
- Aronson R, Precht W, Toscano WT, Koltz K (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Mar Biol* 141:435–447. <https://doi.org/10.1007/s00227-002-0842-5>
- Ashok AM, Schönberg CHL, Raj KD, Bhoopathi M, Bharath MS, Patterson EJK (2018) A sponge of the *Cliona viridis* complex invades and excavates corals of the Gulf of Mannar, south-eastern India. *Mar Freshw Res* 69:874–882. <https://doi.org/10.1071/MF17247>
- Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: Influence of time, location of interaction and epifauna. *Mar Biol* 69:215–222. <https://doi.org/10.1007/BF00396901>
- Battershill N, Bergquist PR (1990) The influence of storms on asexual reproduction, recruitment, and survivorship of sponges. In: Rützler K (ed) *New perspectives in sponge biology*. Smithsonian Institution Press, Washington DC, pp 497–403
- Bell JJ, Rovellini A, Davy SK, Taylor MW, Fulton EA, Dunn MR, Bennett HM, Kandler NM, Luter HM, Webster NS (2018a) Climate change alterations to ecosystem dominance: how might sponge-dominated reefs function? *Ecology* 99:1920–1931. <https://doi.org/10.1002/ecy.2446>
- Bell JJ, Bennett HM, Rovellini A, Webster NS (2018b) Sponges to be winners under near-future climate scenarios. *Bioscience* 68:955–968. <https://doi.org/10.1093/biosci/biy142>
- Bell JJ, McGrath E, Kandler NM, Marlow J, Beepat SS, Bachtiar R, Carballo JL (2020) Interocean patterns in shallow water sponge assemblage structure and function. *Biol Rev Camb Philos Soc* 95:1720–1758. <https://doi.org/10.1111/brv.12637>
- Bell JJ, Micaroni V, Strano F (2022) Regime shifts on tropical coral reef ecosystems: future trajectories to animal-dominated states in response to anthropogenic stressors. *Emerg Top Life Sci* 146(1):95–106. <https://doi.org/10.1042/ETLS20210231>
- Bergquist PR, Sinclair ME (2010) The morphology and behaviour of larvae of some intertidal sponges. *N Z J Mar Freshw Res* 2(3):426–437. <https://doi.org/10.1080/00288330.1968.9515247>
- Bjorndal KA (1990) Digestibility of the sponge *Chondrilla nucula* in the green turtle, *Chelonia mydas*. *B Mar Sci* 47:S67–S70
- Bradbury RH, Young PC (1983) Coral interactions and community structure: an analysis of spatial pattern. *Mar Ecol Progr Ser* 11:265–271. <https://doi.org/10.3354/MEPS011265>
- Brandt ME, Olinger LK, Chaves-Fonnegra A, Olson JB, Gochfeld DJ (2019) Coral recruitment is impacted by the presence of a sponge community. *Mar Biol*. <https://doi.org/10.1007/s00227-019-3493-5>
- Brown KT, Bender-Champ D, Hoegh-Guldberg O, Dove S (2020) Seasonal shifts in the competitive ability of macroalgae influence the outcomes of coral–algal competition. *R. Soc Open Sci* 7:201797. <https://doi.org/10.1098/rsos.201797>
- Calenge C (2006) The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Carballo JL, Bautista E, Nava H, Cruz-Barraza JA, Chavez JA (2013) Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecol Evol* 3:872–886. <https://doi.org/10.1002/ece3.452>
- Cárdenas CA, Davy SK, Bell JJ (2012) Correlations between algal abundance, environmental variables and sponge distribution patterns on southern hemisphere temperate rocky reefs. *Aquat Biol* 16:229–239. <https://doi.org/10.3354/ab00449>
- Chadwick NE, Morrow KM (2011) Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N (eds) *Coral Reefs: An Ecosystem in Transition*. Springer Netherlands, Dordrecht, pp 347–371. https://doi.org/10.1007/978-94-007-0114-4_20
- Choi DR (1984) Ecological succession of reef cavity-dwellers (coelobites) in coral rubble. *B Mar Sci* 35:72–79. <https://doi.org/10.1007/BF00336773>
- Chornesky EA (1991) The ties that bind: Inter-clonal cooperation may help a fragile coral dominate shallow high-energy reefs. *Mar Biol* 109:41–51. <https://doi.org/10.1007/BF01320230>
- Connell JH (1976) Competitive interactions and the species diversity of corals. In: Mackie GO (ed) *Coelenterate Ecology and Behavior*. Springer US, Boston, MA, pp 51–58. https://doi.org/10.1007/978-1-4757-9724-4_6

- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16:101–113. <https://doi.org/10.1007/s003380050246>
- Connell JH, Hughes TP, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity in corals. *Ecol Monogr* 74:179–210. <https://doi.org/10.1890/02-4043>
- Coppock AG, Kingsford MJ, Battershill C, Jones GP (2022) Significance of fish–sponge interactions in coral reef ecosystems. *Coral Reefs* 41:1285–1308. <https://doi.org/10.1007/s00338-022-02253-8>
- Cowman PF, Quattrini AM, Bridge TCL, Watkins-Colwell GJ, Fadli N, Grinblat M, Roberts TE, McFadden CS, Miller DJ, Baird AH (2020) An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. *Mol Phylogenet Evol* 153:106944. <https://doi.org/10.1016/j.ympev.2020.106944>
- Dayton PK (1971) Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 41:351–389. <https://doi.org/10.2307/1948498>
- De Bakker DM, Meesters EH, Bak RPM, Nieuwland G, Van Duyl FC (2016) Long-term shifts in coral communities on shallow to deep reef slopes of Curaçao and Bonaire: are there any winners? *Front Mar Sci*. <https://doi.org/10.3389/fmars.2016.00247>
- De Bakker DM, van Duyl FC, Bak RPM, Nugues MM, Nieuwland G, Meesters EH (2017) 40 Years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats. *Coral Reefs* 36:355–367. <https://doi.org/10.1007/s00338-016-1534-9>
- De Voogd NJ, Becking LE, Hoeksema BW, Noor A, Van Soest RWM (2004) Sponge interactions with spatial competitors in the Spermonde Archipelago. *Boll Mus Ist Biol Univ Genova* 68:253–261
- Dietzel A, Bode M, Connolly SR, Hughes TP (2020) Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. *Proc Biol Sci*. <https://doi.org/10.1098/rspb.2020.1432>
- Ekins M, Willis B, Bridge T, Srinivasan M, Rowley S, Hooper J (2017) The coral killing sponge *Terpios hoshinota* in Kimbe Bay, Papua New Guinea. *Mem Queensl Mus* 60, 174–175. <https://doi.org/10.17082/j.2204-1478.60.2017.2017-02>
- Elliott J, Patterson M, Summers N, Miternique C, Montocchio E, Vitry E (2016) How does the proliferation of the coral-killing sponge *Terpios hoshinota* affect benthic community structure on coral reefs? *Coral Reefs* 35:1083–1095. <https://doi.org/10.1007/s00338-016-1434-z>
- Engel S, Pawlik JR (2005) Interactions among Florida sponges. I. Reef Habitats *Mar Ecol Progr Ser* 303:133–144. <https://doi.org/10.3354/meps303133>
- Fabricius K, De'ath G, (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19:303–309. <https://doi.org/10.1007/s003380000120>
- Fabricius K, De'ath G, McCook L, Turak E, Williams DM, (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar Pollut Bull* 51:384–398. <https://doi.org/10.1016/j.marpolbul.2004.10.041>
- Ferrari R, González-Rivero M, Mumby PJ (2012) Size matters in competition between corals and macroalgae. *Mar Ecol Progr Ser* 467:77–88. <https://doi.org/10.3354/meps09953>
- George EE, Mullinix JA, Meng F, Edwards C, Felts B, Haas HAC, Mueller B, Roach TNF, Salomon P, Silveira C, Vermeij MJ, Rohwer F, Luque A (2021) Space-filling and benthic competition on coral reefs. *PeerJ*. <https://doi.org/10.7717/peerj.11213>
- Glynn PW (2013) Fine-scale interspecific interactions on coral reefs: functional roles of small and cryptic metazoans. In: Lang MA, Marinelli RL, Roberts SJ, Taylor PR (eds) *Research and discoveries: The revolution of science through scuba*. Smithsonian Institution Scholarly Press, Washington DC, pp 229–248
- González-Murcia S, Coppock AG, Ekins M, Battershill CN, Jones GP (2022) Effects of exposure, bathymetry (depth) and aspect on sponge communities on a coral reef. *Mar Ecol Progr Ser* 685:11–126. <https://doi.org/10.3354/meps13981>
- González-Rivero M, Yakob L, Mumby PJ (2011) The role of sponge competition on coral reef alternative steady states. *Ecol Modell* 222(11):1847–1853. <https://doi.org/10.1016/j.ecolmodel.2011.03.020>
- Greene CH, Schoener A (1982) Succession on marine hard substrata: a fixed lottery. *Oecologia* 55:289–297. <https://doi.org/10.1007/BF00376914>
- Greene CH, Schoener A, Corets E (1983) Succession on marine hard substrata: the adaptive significance of solitary and colonial strategies in temperate fouling communities. *Mar Ecol Progr Ser* 13:121–129. <https://doi.org/10.3354/MEPS013121>
- Harvell D, Jordán-Dahlgren E, Merkel S, Rosenberg E, Raymundo L, Smith S, Willis B (2007) Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography* 20:172–195. <https://doi.org/10.5670/oceanog.2007.91>
- Hiebert LS, Vieira EA, Dias GM, Tiozzo S, Brown FD (2019) Colonial ascidians strongly preyed upon, yet dominate the substrate in a subtropical fouling community. *Proc R Soc B* 286:20190396. <https://doi.org/10.1098/rspb.2019.0396>
- Hooper JNA (2000) *Sponguide: guide to sponge collection and identification*. Queensland Museum, South Brisbane. <https://www.qm.qld.gov.au/~media/Documents/Find+out+about/Animals+of+Queensland/Sea+life/sponguide-2003.pdf>
- Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am Nat* 111:743–767. <https://doi.org/10.1086/283203>
- Jackson JBC, Buss L (1975) Allelopathy and spatial competition among coral reef invertebrates. *Proc Nat Acad Sci USA* 72:5160–5163. <https://doi.org/10.1073/pnas.72.12.5160>
- Jackson JBC, Winston JE (1982) Ecology of cryptic coral-reef communities. I. distribution and abundance of major groups of encrusting organisms. *J Exp Mar Biol Ecol* 57:135–147. [https://doi.org/10.1016/0022-0981\(82\)90188-5](https://doi.org/10.1016/0022-0981(82)90188-5)
- Jankowski MW, Gardiner NR, Jones GP (2015) Depth and reef profile: effects on the distribution and abundance of coral reef fishes. *Environ Biol Fishes* 98:1373–1386. <https://doi.org/10.1007/s10641-014-0365-1>
- Jompa J, McCook L (2003) Coral-algal competition: macroalgae with different properties have different effects on corals. *Mar Ecol Progr Ser* 258:87–95. <https://doi.org/10.3354/meps258087>
- Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals—a review of mechanisms and effects. In: *Ecosystems of the world*. Elsevier, Amsterdam pp 209–252.
- Lauer TE, Spacie A (2004) An association between freshwater sponges and the zebra mussel in a southern lake Michigan Harbor. *J Freshw Ecol* 19(4):631–637. <https://doi.org/10.1080/02705060.2004.9664744>
- Logan A (1984) Interspecific aggression in hermatypic corals from Bermuda. *Coral Reefs* 3:131–138. <https://doi.org/10.1007/BF00301957>
- López-Victoria M, Zea S (2004) Storm-mediated coral colonization by an excavating Caribbean sponge. *Clim Res* 26:251–256. <https://doi.org/10.3354/cr026251>
- López-Victoria M, Zea S, Weil E (2006) Competition for space between encrusting excavating Caribbean sponges and other coral reef

- organisms. *Mar Ecol Progr Ser* 312:113–121. <https://doi.org/10.3354/meps312113>
- Manly BF, McDonald L, Thomas DL, McDonald TL, Erickson WP (2007) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*: Springer, Netherlands
- Marlow J, Schönberg CHL, Davy SK, Haris A, Jompa J, Bell JJ (2018) Bioeroding sponge assemblages: the importance of substrate availability and sediment. *J Mar Biol Assoc* 99:343–358. <https://doi.org/10.1017/s0025315418000164>
- Marulanda-Gómez Á, López-Victoria M, Zea S (2017) Current status of coral takeover by an encrusting excavating sponge in a Caribbean reef. *Mar Ecol* 38:e12379. <https://doi.org/10.1111/maec.12379>
- McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417. <https://doi.org/10.1007/s003380000129>
- McGehee AM (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Progr Ser* 105:243–255. <https://doi.org/10.3354/meps105243>
- Meesters EH, Bak RPM (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar Ecol Progr Ser* 96:189–198. <https://doi.org/10.3354/meps096189>
- Meesters E, Knijn R, Willemsen P, Pennartz R, Roelbers G, Vansoest RWM (1991) Sub-rubble communities of Curacao and Bonaire coral reefs. *Coral Reefs* 10:189–197
- Meylan A (1988) Spongivory in hawksbill turtles: a diet of glass. *Science* 239:393–395. <https://doi.org/10.1126/science.239.4838.393>
- Nagelkerken I, Vermonden K, Moraes OCC, Debrot AO, Nagelkerken WP (2005) Changes in coral reef communities and an associated reef fish species, *Cephalopholis cruentata* (Lacépède), after 30 years on Curaçao (Netherlands Antilles). *Hydrobiologia* 549:145–154. <https://doi.org/10.1007/s10750-005-5448-8>
- Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Mar Ecol Progr Ser* 376:295–306. <https://doi.org/10.3354/meps07815>
- Pari N, Peyrot-Clausade M, Hutchings PA (2002) Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. *J Exp Mar Biol Ecol* 276:109–127. [https://doi.org/10.1016/S0022-0981\(02\)00243-5](https://doi.org/10.1016/S0022-0981(02)00243-5)
- Pineda-Munive EM, García-Urueña RDP, Zea S (2017) Acropora coral colonies as microhabitats for sponges in Tayrona National Natural Park, Colombian Caribbean. *Mar Ecol* 38:1–12. <https://doi.org/10.1111/maec.12380>
- Powell A, Jones T, Smith DJ, Jompa J, Bell JJ (2015) Spongivory in the Wakatobi Marine National Park, Southeast Sulawesi, Indonesia. *Pac Sci* 69:487–508. <https://doi.org/10.2984/69.4.5>
- Price N (2010) Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia* 163:747–758. <https://doi.org/10.1007/s00442-010-1578->
- Randall JE, Hartman WD (1968) Sponge-feeding fishes of the West Indies. *Marine Biol* 1:216–225. <https://doi.org/10.1007/BF00347115>
- Rodríguez-Martínez RE, Jordán-Garza AG, Baker DM, Jordán-Dahlgren E (2012) Competitive interactions between corals and *Trididemnum solidum* on Mexican Caribbean reefs. *Coral Reefs* 31:571–577. <https://doi.org/10.1007/s00338-011-0871-y>
- Rützler K (2002) Impact of crustose clionid sponges on Caribbean reef corals. *Acta Geol Hisp* 37:61–72
- Rützler K (2004) Sponges on coral reefs: a community shaped by competitive cooperation. *Boll Musei Ist Biol Univ Genova* 68:85–148
- Rützler K, Piantoni C, van Soest RWM, Diaz MC (2014) Diversity of sponges (Porifera) from cryptic habitats on the Belize barrier reef near Carrie Bow Cay. *Zootaxa* 3805:1–129. <https://doi.org/10.11646/zootaxa.3805.1.1>
- Sandin SA, McNamara DE (2012) Spatial dynamics of benthic competition on coral reefs. *Oecologia* 168:1079–1090. <https://doi.org/10.1007/s00442-011-2156-0>
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions. *Annu Rev Ecol Syst* 40:245–269. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173430>
- Schönberg CHL (2015) Monitoring bioeroding sponges: using rubble, quadrat, or intercept surveys? *Biol Bull* 228:137–155. <https://doi.org/10.1086/BBLv228n2p137>
- Schönberg CHL, Wilkinson C (2001) Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69–76. <https://doi.org/10.1007/s003380100143>
- Schönberg CHL, Suwa R (2007) Why bioeroding sponges may be better hosts for symbiotic dinoflagellates than many corals. *Porifera Research: Biodiversity, Innovation and Sustainability*, Rio de Janeiro
- Schönberg CHL, Ortiz J (2008) Is sponge bioerosion increasing? *International Coral Reef Symposium*, Florida
- Suchanek TH, Carpenter RC, Witman JD, Harvell CD (1983) Sponges as important space competitors in deep Caribbean coral reef communities. *The Ecology of deep and shallow coral reefs*. Rockville
- Tanner JE (1995) Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *J Exp Mar Biol Ecol* 190:151–168. [https://doi.org/10.1016/0022-0981\(95\)00027-0](https://doi.org/10.1016/0022-0981(95)00027-0)
- Tebbett SB, Streit RP, Bellwood DR (2019) Expansion of a colonial ascidian following consecutive mass coral bleaching at Lizard Island, Australia. *Mar Environ Res* 144:125–129. <https://doi.org/10.1016/j.marenvres.2019.01.007>
- Thacker RW, Cristina Díaz M, de Voogd NJ, van Soest RWM, Freeman CJ, Mobley AS, LaPietra J, Cope K, McKenna S (2010) Preliminary assessment of sponge biodiversity on Saba Bank, Netherlands Antilles. *PLoS ONE* 5(5):e9622. <https://doi.org/10.1371/journal.pone.0009622>
- Thomas D, Taylor E (1990) Study designs and tests for comparing resource use and availability. *J Wildl Manag* 54:322–330. [https://doi.org/10.2193/0022-541X\(2006\)70\[324:SDATFC\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[324:SDATFC]2.0.CO;2)
- Turicchia E, Hoeksema BW, Ponti M (2018) The coral-killing sponge *Chalinula nematifera* as a common substrate generalist in Komodo National Park, Indonesia. *Mar Biol Res* 14:827–833. <https://doi.org/10.1080/17451000.2018.1544420>
- Uriz MJ, Maldonado M, Turon X, Martí R (1998) How do reproductive output, larval behaviour, and recruitment contribute to adult spatial patterns in Mediterranean encrusting sponges? *Mar Ecol Progr Ser* 167:137–148. <https://doi.org/10.3354/meps167137>
- Valderrama D, Zea S (2003) Esquemas de distribución de esponjas arrecifales (Porifera) del Noroccidente del Golfo de Urabá, Caribe Sur, Colombia. *Bol Invest Mar Cos* 32:37–56
- Van Soest RWM (2009) New sciophilous sponges from the Caribbean (Porifera: Demospongiae). *Zootaxa* 2107(1):1–40. <https://doi.org/10.5281/zenodo.187789>
- Vermeij MJ, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology* 89:1994–2004. <https://doi.org/10.1890/07-1296.1>
- von Brandis RG, Mortimer J, Reilly B, van Soest R, Branch G (2014) Taxonomic composition of the diet of hawksbill turtles (*Eretmochelys imbricata*) in the Republic of Seychelles. *West Indian Ocean J Mar Sci* 13:81–91
- Williams GJ, Smith JE, Conklin EJ, Gove JM, Sala E, Sandin SA (2013) Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave energy gradients on spatial patterns. *PeerJ* 1:e81. <https://doi.org/10.7717/peerj.81>

- Winston JE, Jackson JBC (1984) Ecology of cryptic coral reef communities. 4. community development and life histories of encrusting cheilostome Bryozoa. *J Exp Mar Biol Ecol* 76:1–21. [https://doi.org/10.1016/0022-0981\(84\)90013-3](https://doi.org/10.1016/0022-0981(84)90013-3)
- Wolfe K, Kenyon TM, Mumby PJ (2021) The biology and ecology of coral rubble and implications for the future of coral reefs. *Coral Reefs* 40:1769–1806. <https://doi.org/10.1007/s00338-021-02185-9>
- Wulff JL (1994) Sponge feeding by Caribbean angelfishes, trunkfishes, and filefishes. In: van Soest R, van Kempen T, Braekman JC (eds) *Sponges in time and space*. Balkema, Rotterdam, pp 265–271
- Wulff JL (2005) Trade-offs in resistance to competitors and predators, and their effects on the diversity of tropical marine sponges. *J Anim Ecol* 74:313–321. <https://doi.org/10.1111/j.1365-2656.2005.00925.x>
- Wulff JL (2006) Ecological interactions of marine sponges. *Can J Zool* 84:146–166. <https://doi.org/10.1139/z06-019>
- Zea S (1993) Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. *Caribb J Sci* 29:75–88

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