



# Effects of exposure, depth and aspect on sponge communities on a coral reef

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**ABSTRACT:** Coral reef benthic communities include a wide range of taxa, but most attention has been given to hard coral assemblages, and how their cover and composition vary over strong spatial gradients. Much less is known about the spatial distribution and composition of coral reef sponge communities, which may become increasingly important on reefs with declining coral cover. Here, we examined the effects of exposure, depth, aspect and location on the cover and composition of sponge assemblages on a coral reef in Kimbe Bay, Papua New Guinea. We quantified sponge cover and species composition along replicate line transects on 6 inshore reefs, sampling exposed (seaward) and sheltered (landward) sides of reefs at 5, 10 and 15 m depth, with reef aspect subdivided into slopes or walls along each transect. Although the substratum was generally dominated by corals and algae, sponges ranked 3rd, with an average of 13.1% cover, including 63 recognisable species. Morphologically there were 38 encrusting, 21 erect and 4 massive sponge species, with the encrusting sponges *Lamellodysidea* cf. *chlorea* and *Dysidea* sp1 exhibiting the highest cover. Sponge cover, species richness and species composition all exhibited complex interactions among depth, exposure and location. Sponge cover and species richness increased in transects with higher percentages of wall aspects, and assemblage structure differed between slopes and walls. Sponges are a diverse component of the benthos, with exposure, depth and reef aspect all contributing to explain spatial variation in assemblage structure.

**KEY WORDS:** Coral reefs · Sponges · Porifera · Depth · Exposure · Substrate inclination · Indo-Pacific

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## 1. INTRODUCTION

Coral reefs are complex tropical habitats composed of a diverse range of benthic organisms, most notably corals, which create the underlying reef substratum. However, coral reefs are also composed of other equally diverse taxa, including macroalgae, sponges, ascidians and other sessile invertebrates. The occurrence of these can vary along environmental gradients, leading to changes in the dominant benthic organisms inhabiting reef substratum (Kilar

& McLachlan 1989, Fabricius & De'ath 2001, Page-Albins et al. 2012, Bridge et al. 2013). Most attention has been given to the determinants of spatial patterns in cover and species composition of corals, and more recently, to macroalgae, as it becomes more prevalent on shallow inshore coral reefs (McCook et al. 2001, Jompa & McCook 2003, Przeslawski et al. 2015).

Coral and macroalgal assemblages vary along environmental gradients, including depth (Russ 2003, Fabricius et al. 2005, Roberts et al. 2015, Cooper et al. 2019) and wave exposure (Kilar & McLachlan 1989,

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Burt et al. 2010, Rattray et al. 2015). Additionally, reef aspect (substrate inclination) interacts with gradients of depth and wave exposure and can regulate coral and algal cover, with reefs composed of vertical walls and caves often exhibiting reduced coral and algal cover compared to more typical reef slopes (Battershill & Bergquist 1990, Jankowski et al. 2015). Less is known of the spatial patterns of other benthic assemblages, such as sponges, anemones, hydroids and ascidians when compared to corals, and our understanding of the influence of environmental gradients on the distribution cover and composition in these communities is still limited.

Distribution patterns of other benthic reef taxa are likely to become increasingly important, given the worldwide decline in coral cover and associated regime shifts towards algae and other benthic organisms (Gardner et al. 2003, Norström et al. 2009, Hoegh-Guldberg et al. 2017, Romero-Torres et al. 2020). Spatially structured sampling designs that focus on multiple environmental gradients can be useful to establish the relative importance of different physical drivers and their influence on sponge communities. Consequently, investigating some of the processes that determine spatial patterns in sponge communities will increase our understanding of the potential impacts of environmental change on future coral reef ecosystems.

Sponges can be abundant, species-rich and functionally relevant components of tropical coral reef benthos (Díaz & Rützler 2001, Van Soest et al. 2012, Wulff 2012, Maldonado et al. 2015, Bell et al. 2020). Their assemblages are highly variable within reef habitats and between reefs and regions (Kelly et al. 2003, Carballo et al. 2008). In some regions, sponges exceed the number of species of their hard-coral counterparts (Maldonado et al. 2015, Bell et al. 2020), and they can dominate the substratum either in terms of percentage of cover, numbers of individuals or volume (Plucer-Rosario 1987, Wulff 2012, Loh et al. 2015). Some sponges have increased in cover or abundance in degraded ecosystems (Rützler 2002, Carballo et al. 2013, Schönberg 2015a, Bell et al. 2017). In some cases, these changes appear to be irreversible and new sponge dominated regimes have been established (see Bell et al. 2013 for a review on sponges), although this may not be the case globally. Declining coral cover could open space for sponges to establish and ultimately replace corals (see Bell et al. 2013), but to evaluate this possibility, it is necessary to understand how sponges are distributed along natural environmental gradients.

Sponge cover varies along natural environmental gradients of depth and exposure (Bell & Barnes 2000a,

Williams et al. 2013, Schönberg 2021). Whether there are any general relationships between depth and sponge cover or diversity is still being debated (Lesser 2006, Scott & Pawlik 2019). Higher sponge diversity is associated with low hydrodynamic stress and light reduction in deeper areas (Suchanek et al. 1983, Alcolado & Gotera 1985, Bell 2007). To date, most of the studies regarding sponge cover and diversity have been conducted in the Caribbean (Pawlik et al. 2013, Bell et al. 2020). Less is known for the Indo-Pacific, where the patterns in diversity, distribution and abundance are still understudied (Van Soest et al. 2012, Rovellini et al. 2019). Although some changes in sponge cover and composition have been attributed to gradients of exposure, depth and location, the role of substrate profile and its interaction with those variables in regulating sponge communities has been barely studied in coral reefs (Bell 2007, Williams et al. 2013, Jankowski et al. 2015).

Most benthic coral reef surveys focus on coral cover alone and neglect the contribution of other taxa. Where sponges have been included, they are often aggregated into a single category, with little information on growth forms or species composition. Inventories of sponge diversity and species composition in most tropical regions are still poorly represented (Costello et al. 2010, Carballo et al. 2019, Rovellini et al. 2019, Bell et al. 2020). Species richness and composition are important metrics in describing sponge communities and in biodiversity evaluations for conservation and management (Bell et al. 2017). Sponges have diverse functional roles (e.g. Bell 2008), and increasing attention is needed to quantify and determine the responses of different sponge species and functional groups to natural gradients (Wulff 2017). Trends of reduction of coral cover on reefs around the world indicate that it is necessary to establish baselines (Gouezo et al. 2019), not just for the distribution and cover of sponges, but also for species representation to identify shifts in benthic community composition.

The aim of this study was to describe spatial patterns in the cover, species richness and species composition of sponges on the fringing coral reefs of Kimbe Bay, Papua New Guinea. Corals and reef fishes have been well studied in this area (Jones et al. 2004, Munday 2004), but information regarding sponges is limited, despite it being a potential hotspot for sponge biodiversity. Thus, we addressed gradients in relation to depth, exposure, location and the role of reef aspect (substrate inclination), ranging from gradual slopes to vertical drop-offs. The following specific questions are addressed: (1) How does

overall cover of sponges compare to that of other benthic reef organisms? (2) How do sponge cover and species richness vary in relation to exposure, depth and location? (3) How do sponge assemblages vary among exposure, depth and location? (4) Does reef aspect affect sponge cover, species richness and assemblage structure? Answers to these questions were sought to set a baseline for a more comprehensive understanding of the sponge communities in Kimbe Bay and a point of comparison for changes in reef ecosystem benthos in the future.

## 2. MATERIALS AND METHODS

### 2.1. Study area description and sampling design

Sampling was conducted on coastal fringing reefs of Tamare-Kilu, in Kimbe Bay, Papua New Guinea (5° 12.530 S, 150° 22.801 E) (Fig. 1a–c), from October

to December 2018 on 6 inshore reefs used as the random factor 'location' (Fig. 1d). Benthic surveys at each reef were carried out using a stratified sampling design, with wave exposure assessed by sampling the landward and seaward sides of reefs, and water depth assessed by sampling at 5, 10 and 15 m depth. At each depth, 4 × 50 m transects were deployed along the depth contours of each reef surveyed. The combination of 6 locations × 2 levels of exposure × 3 depths × 4 replicate transects added to a total of 144 transects. In terms of the analysis, there were 3 orthogonal factors: exposure (fixed), depth (fixed) and location (random). Reef topography at the landward exposure was similar in the 6 reefs, with smooth slopes alternating with ridges, salients and scattered sandy patches. On the seaward exposure, the topography was similar for 5 reefs, with slopes and sandy patches separated by walls, ridges and overhangs with steep slope. Hanging Gardens was different because its topography consists of mainly

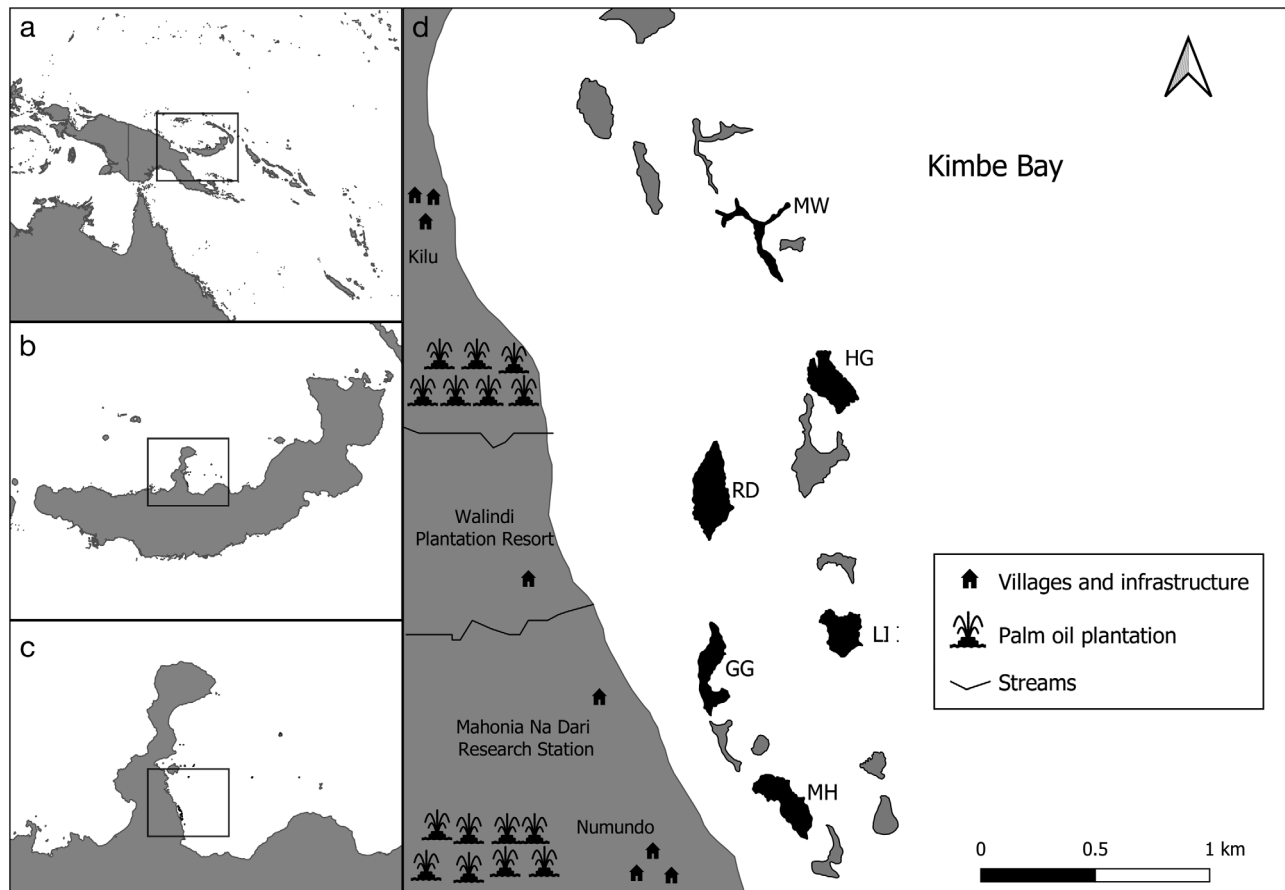


Fig. 1. Location of reefs studied in (a) Papua New Guinea (PNG), (b) New Britain, (c,d) Kimbe Bay, showing villages, palm oil plantations and streams in the area. Reefs where sponge cover and species richness were measured are highlighted in black (d), with other reefs in grey. MH: Matane Huva; GG: Gava Gava; LI: Limuka; RD: Rakaru Diri; HG: Hanging Gardens; MW: Matane Walindi

a wall and overhang gradients along the seaward exposure.

Video recordings were conducted along transects using the line point intercept (LPI) method to estimate the cover of different substrata and biota underneath 100 random points along a 50 m line transect (Hill & Wilkinson 2004). Thus, sponge percentage cover was equivalent to the number of points that occurred over sponges along the transect. Reef aspect (substrate inclination) was accounted for by quantifying the number of points in each transect according to whether they were along a 'wall' or 'slope', and the abundance and species richness of sponges in each aspect was recorded. Sponges were divided into 3 growth forms: encrusting, massive and erect (including branching and tubular forms). Other benthic categories included hard coral, soft coral, algae, sand, rubble, dead coral, hydroids, anemones, gorgonians, giant clams, and colonial and solitary ascidians. Operational taxonomic units (OTUs) were distinguished in field surveys to assess the effects of exposure, depth, location and substratum aspect on sponge species composition. Pictures of all sponges surveyed were taken and tissue samples were collected and preserved in 70% ethanol for identification. Sponges were later classified to genus (and species) level where possible (see Table S1 at [www.int-res.com/articles/suppl/m685p111\\_supp.xlsx](http://www.int-res.com/articles/suppl/m685p111_supp.xlsx)) using techniques as described by Hooper (2000).

## 2.2. Statistical analyses

Changes in sponge cover and sponge species richness in relation to exposure, depth and location were analysed using a Bayesian approach with the RStan package (Stan Development Team 2020). The model included percentage of cover of sponges as a response variable and exposure (fixed), depth (fixed), location (random) and their interactions as explanatory variables. To account for the variability among locations ('reefs'), this variable was considered a random factor since the magnitude of the effect of exposure and depth could change between locations ('reefs'). The model was adjusted to a Poisson negative binomial distribution to account for over-dispersion. A Markov chain Monte Carlo (MCMC) sampler was run for 5 chains and 20 000 iterations with a warm-up of 2000 for each chain. Thinning was set to 8, and the priors for the intercept were set to normal (0, 2.5), slope normal (0, 2.5), auxiliary (1) and covariance (1). Default priors were used since there is no information available that can be used for generating

priors of sponge cover and richness in the area; and their use provide the advantage of being wide and rather conservative. A homologous process was conducted to assess the relationship of species richness to the same set of predictors.

The MCMC diagnostics suggested that the chains were well mixed and converged on a stable posterior. There was no scale reduction or evidence of autocorrelation during the generation of the posterior, and the values of  $\hat{R} \leq 1.05$  indicated that thinning was appropriate to avoid autocorrelation in the sampling (McElreath 2016). The proportion of effective samples (ESS is a metric to measure the amount by which autocorrelation in samples increases uncertainty in comparison to an independent sample) indicated that the outcome of the variables in the analysis yielded a good proportion of unique samples (McElreath 2016). Patterns on the residuals were tested for normality, dispersion and variance homogeneity with the DHARMA package (residual diagnostics for hierarchical models; Hartig 2020). A similar process was applied to species richness as the response variable with the same set of predictors. The probability of the occurrence of given outcomes such as higher cover of sponges at exposed seaward sites compared to more sheltered landward sites, with water depths and substrate profiles, were estimated from the model outcomes using the estimated marginal means package (emmeans; Russell et al. 2020). Characteristics of the posterior distribution were summarized using intervals of defined boundaries and contrasts and effect sizes between levels of explanatory variables. Inferences were conducted using pairwise comparisons of the estimated values of the median as a measure of centrality and 95% confidence intervals of the highest probability density intervals (HPDIs), used as measurements of uncertainty. The exceedance p-value (the probability that a certain value will be exceeded in a predefined situation) was used as an indicator of the potential for some events to be observed (McElreath 2016).

Species diversity and dominance were assessed applying the Shannon–Wiener and Simpson indexes, respectively. Similarities in sponge assemblages between exposures ('seaward' and 'landward'), depths (5, 10 and 15 m), 6 locations ('reefs') and their interactions were analysed using a non-metric dimensional scaling (nMDS) analysis. Sponge abundance from the 144 transects was transformed using Wisconsin double standardization to construct a similarity matrix based on the Bray–Curtis similarity index. A 'dummy species variable' containing the value 1 was added to the matrix to avoid problems in the estimation of the distances due to absences of records of

sponge cover in some transects (Clarke et al. 2006). The nMDS was constructed with a stable solution from random starts, setting the number of starts to 999 runs and basing the stress on monotonic (non-linear) regression. Stress, goodness-of-fit tests,  $R^2$  and Shepard plots were produced to assess goodness of fit between ordination distances and observed dissimilarity of the method.

The influence of exposure, depth and reef in sponge assemblages was tested using a multiple permutation ANOVA (Oksanen et al. 2019). This is a nonparametric test that uses the distance matrix and factors to define sample grouping. The significance tests were performed from permutations of the Wisconsin transformed data. The variables exposure, depth, reef and their interactions were included. We included the variable 'reef location' as a main term since it is not possible to incorporate random factors in multivariate tests. However, it allowed us to quantify the influence of location ('reef') in sponge assemblages between reefs. The contribution of species to the differences detected between depth, exposure and location ('reef'), and the extent to which some species were associated with those conditions, were tested with the indicator species analyses (De Cáceres & Legendre 2009). The analysis uses the point-biserial correlation method, which yields the combination where the difference between the observed and expected abundance/frequency of the species is the largest, or an indicator value index that provides the set of site-groups that best matches the observed distribution pattern of the species (De Cáceres et al. 2010). This method has the advantage of using multiple classifications of the same sites, increasing the amount of information resulting from the analysis and making it possible to distinguish sponges that are characteristic of the site. The groups that were tested corresponded to the main factors exposure, depth and location ('reef') and the categories for different levels of wall aspect. Influential sponge species were those that had a significance value of  $p < 0.05$ .

The possible relationships between the percentage of wall cover along each transect with sponge cover and species richness was evaluated using a generalized linear model following a Gaussian distribution under a Bayesian approach. The MCMC sampler was run for 5 chains and 20 000 iterations with a warm-up of 2000 for each chain. Thinning was set to 8, and the priors for the intercept were set to normal (0, 2.5), slope normal (0, 2.5), auxiliary (1) and covariance (1). The diagnostics and assumptions for this process followed the method described previ-

ously. To evaluate changes in sponge assemblages at different levels of wall aspect, an nMDS analysis was conducted. Transect scores were allocated in 5 categories representing different percentages of wall aspect; from low to high wall aspect, the categories were 0–20%, 21–40%, 41–60%, 61–80% and 81–100%. The data were square root transformed and the similarity metric was based on the Bray–Curtis similarity matrix. Diagnostics followed the previous methods. Observed differences were tested with the multiple permutation analyses of variance and characterization of sponge species defining each level of wall aspect was conducted with the indicator species analysis (De Cáceres & Legendre 2009). All analyses were performed in R 4.0.2 statistical software (R Core Team 2019).

### 3. RESULTS

#### 3.1. Relative cover of sponges, other biotic and abiotic substrata, and a checklist of species

Overall, sponges accounted for  $\sim 13 \pm 0.9\%$  (means are presented  $\pm$ SEM unless otherwise indicated) of the substratum, pooling all transects and the 3 growth forms (encrusting, erect and massive) (Fig. 2). This was similar for the overall cover of macroalgae ( $\sim 14 \pm 1.01\%$ ). The benthic community was dominated by corals ( $31.0 \pm 1.20\%$ ) and the remaining biotic categories (including ascidians) contributed less than  $0.42 \pm 0.18\%$  to the composition of the benthos (Fig. 2). Abiotic categories such as exposed dead coral, rock, rubble and sand represented together  $\sim 40\%$ , with sand ( $13.23 \pm 1.35\%$ ) and rubble ( $11.97 \pm 0.81\%$ ) exhibiting the highest values (Fig. 2).

Kimbe Bay sponge assemblages were diverse, with 63 sponge species recognized (Table S1). The most abundant sponge species were the encrusting sponges *Lamellodysidea* cf. *chlorea* ( $1.4 \pm 0.17$ ) and *Dysidea* sp1 ( $1.3 \pm 0.12$ ) (Fig. 3). The 20 most abundant species accounted for 10.3% of the sponge cover, with most accounting for less than 1% of the substratum (Fig. 3). These species were widely distributed according to exposure, depth and reef aspect (Table S1). The other 43 species had scattered distributions and were recorded at few locations, depths or exposure (Table S1). Morphologically, encrusting sponges were the most abundant and contributed with 38 species, followed by 21 sponges with erect morphology and 4 massive sponge species.

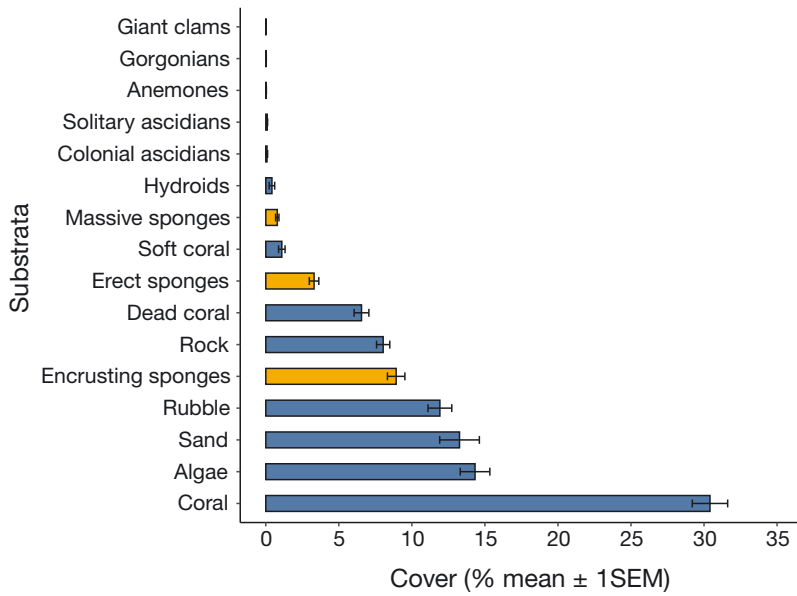


Fig. 2. Overall mean percentage of substratum cover on 6 inshore reefs in Kimbe Bay, Papua New Guinea, sampled at their seaward and landward sides, at 5, 10 and 15 m depth. Yellow bars represent sponges by morphological group (encrusting, massive and erect)

### 3.2. Effects of exposure, depth and reef on sponge cover

Sponge cover varied due to complex interactions between exposure and depth, and the extent of these changes was influenced by the location of the reefs ( $R^2 = 81\%$ ; Fig. 4, Table S2). Overall, wave exposure influenced sponge cover, and there were more sponges on the seaward exposure ( $15 \pm 1.36\%$ ) than on the landward exposure ( $12 \pm 0.89\%$ ). This trend was evident at Matane Huva, Matane Walindi and Hanging Gardens, where abrupt differences between exposures were recorded with 36% sponge cover at the seaward exposure compared to 13% on the landward exposure (Fig. 4, Table S2). The sponge cover on the seaward side of Hanging Gardens was 2.2 to 2.7 times higher than that at all the other reefs. On the contrary, Gava Gava, Limuka and Rakaru Diri had slightly higher values of sponge cover on the landward exposure.

Changes in sponge cover were associated with water depth. Generally, sponge cover increased from 5 m ( $10 \pm 1.33\%$ ) to 10 m ( $14 \pm 1.29\%$ ) and 15 m

( $15 \pm 1.58\%$ ) depth. The increments in sponge cover from 5 to 15 m depth were constant at both exposures in Limuka reef, and the seaward exposure of Matane Huva, Matane Walindi and Hanging Gardens (Fig. 4). However, statistically significant differences in sponge cover at 15 m depth were detected only at Limuka and Hanging Gardens. At Limuka, sponge cover changed from 4 to 13 to 25% at 5, 10 and 15 m depth, respectively on the seaward exposure and from 8 to 18 and 20% on the landward exposure. At Hanging Gardens, sponge cover changed from 8 to 13 to 18% at 5, 10 and 15 m depth on the landward exposure, respectively; however, at the seaward exposure, sponge cover was similar among depths, ranging from 33 to 34 to 36% at 5, 10 and 15 m depth, respectively. No other significant changes in sponge cover were detected; nonetheless, in Matane Walindi, a reduction in sponge cover by depth was observed (Fig. 4, Table S2).

Trends in sponge cover changed by exposure and depth, but the direction of the trend and magnitude of those changes depended on the location (reef), generating synergistic or antagonistic effects (Fig. 4,

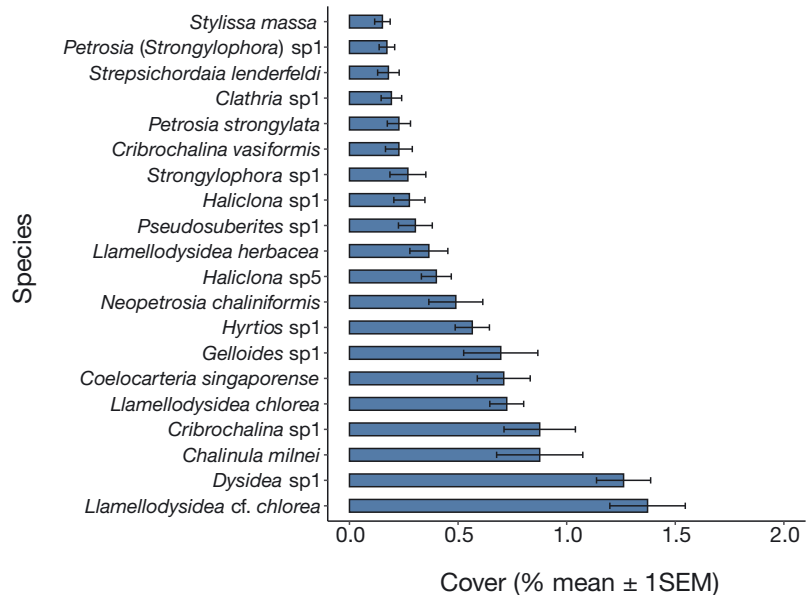


Fig. 3. Mean percentage cover for the 20 most abundant sponge species out of 63 recorded on 6 coral reefs of Kimbe Bay, Papua New Guinea, at the seaward and landward sides of the reefs, at 5, 10 and 15 m depth

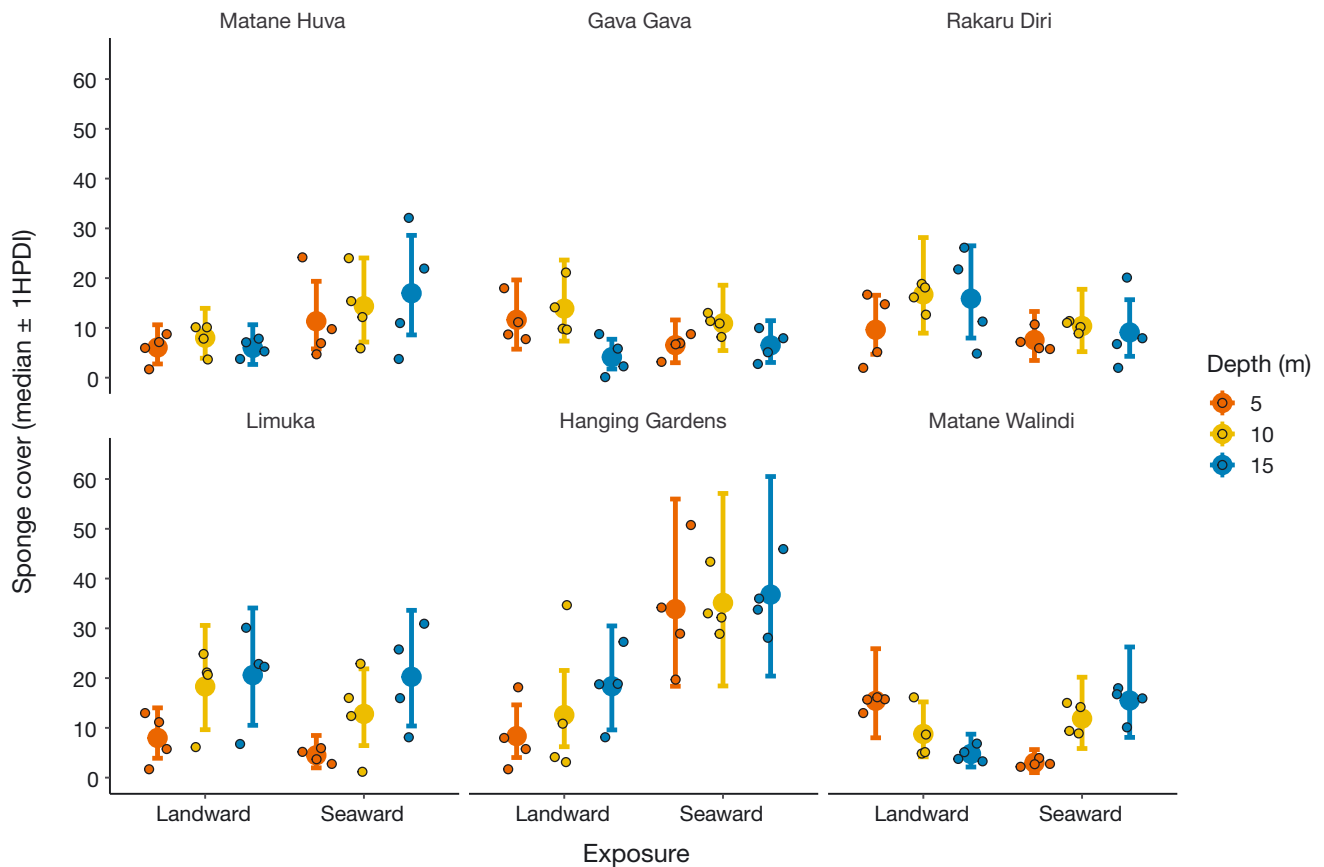


Fig. 4. Median percentage sponge cover in Kimbe Bay, Papua New Guinea. Error bars are highest probability density intervals (HPDIs) on 6 inshore reefs plotted with respect to exposure (seaward and landward sides) and depth (5, 10 and 15 m, colour coded). In groups that differed significantly, the bars for HPDI do not overlap. Small dots with black outlines represent values of sponge cover per individual transect

Table S2). For instance, distinctive sponge cover increments from 5 to 15 m depth were present at the seaward and landward exposure in Limuka. Similar trends were observed at the seaward exposure of Matane Huva, Matane Walindi and the landward exposure of Hanging Gardens and a decrease in sponge cover from 5 to 15 m was detected at the landward exposure of Matane Walindi.

### 3.3. Effects of location, exposure and depth on species richness

Sponge richness was related to exposure and depth, but the magnitude of these changes was influenced by the location of the reefs ( $R^2 = 82\%$ ; Fig. 5, Table S3).

The number of species detected ranged from 0 to 25 across all 144 transects. Overall patterns in sponge richness were observed between the seaward and landward exposure of Hanging Gardens,

but not at other locations (Fig. 5, Table S3). The seaward exposure of Hanging Gardens had on average 16 sponge species per transect. This was 2.5 times higher than the average number of species recorded for other reefs and the landward exposure of Hanging Gardens reef itself.

Sponge species richness was slightly lower at 5 m depth ( $6 \pm 0.62$ ) compared to 10 ( $8 \pm 0.61$ ) and 15 m ( $8 \pm 0.66$ ) depth. Increments in species richness along the depth gradient were observed at 10 and 15 m depth at Limuka (Fig. 5, Table S3). The number of species detected changed from 1 at 5 m depth to 11 at 15 m depth on the seaward exposure, and from 3 at 5 m depth to 11 at 15 m depth at the landward exposure, respectively. No additional significant effects on species richness were detected, in spite of some slight trends detected by depth at the landward exposure of Hanging Gardens and at both exposures in Matane Walindi (Fig. 5, Table S3). The interaction of depth and exposure associated with a high variability between locations indicated that

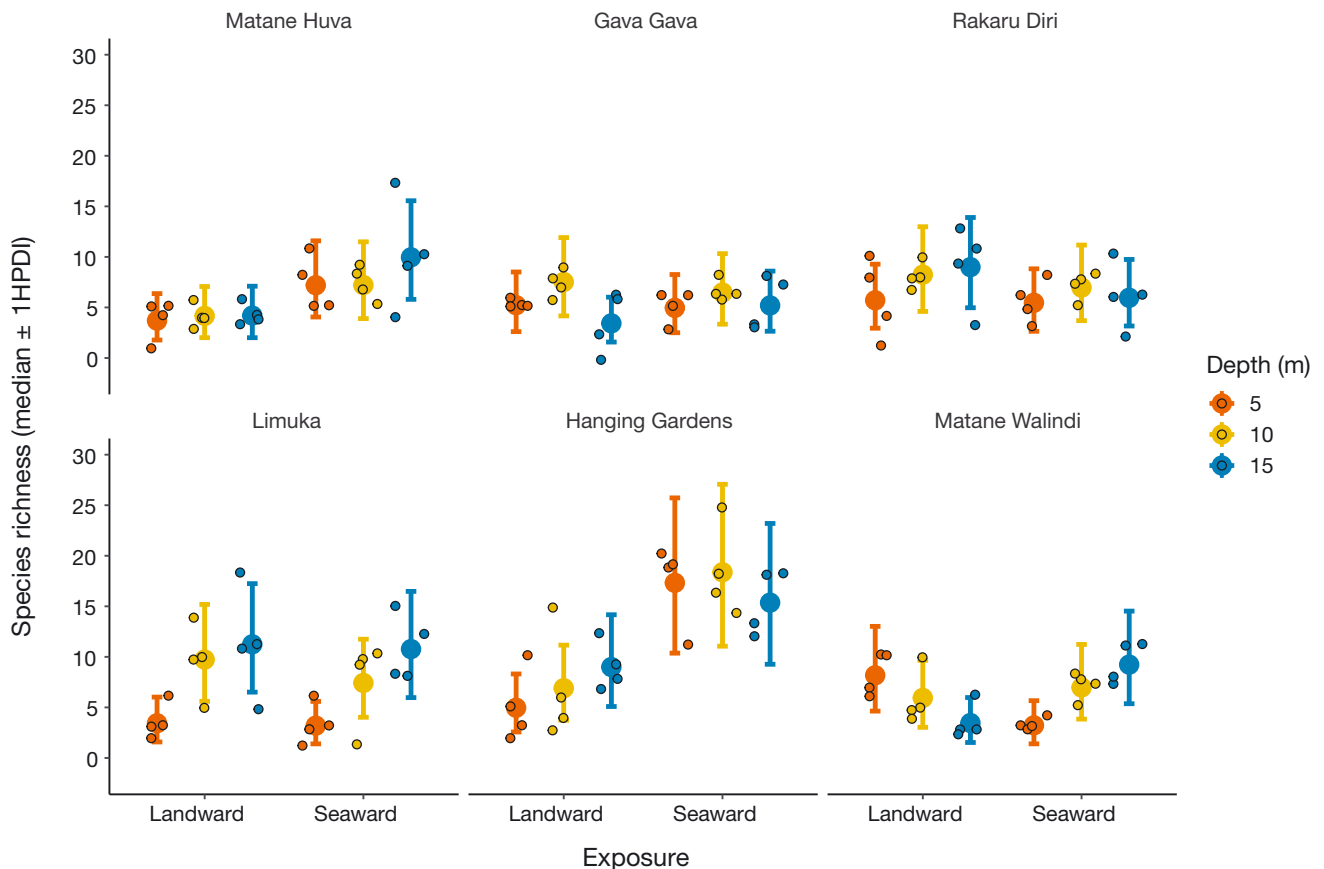


Fig. 5. Median species richness of sponges in Kimbe Bay, Papua New Guinea. Error bars are highest probability density intervals (HPDIs) on 6 inshore reefs plotted with respect to exposure (seaward and landward sides) and depth (5, 10 and 15 m, colour coded). In groups that differed significantly, the bars for HPDI do not overlap. Small dots with black outlines represent values of sponge species richness per individual transect

changes in species richness between depths and exposures occur, but their trend and magnitude depend on the reef.

### 3.4. Effects of location, exposure and depth on sponge assemblages

The structure of sponge assemblages differed significantly according to exposure, depth, location and the interaction among these factors, indicating that the amount of change was determined by simultaneous changes in these conditions ( $R^2 = 38\%$ ; Fig. 6a–c and Table 1). Differences between assemblages due to exposure, depth and reef were largely explained by changes in cover of 13 sponge species (Table 2, Table S4). Seven species characterized sponge assemblages at different exposure levels: *Hyrtios* sp1, *Coelocarteria singaporensis* and *Neopetrosia chaliniformis* were more associated with the landward exposures of the studied reefs, and *Cribochalina* sp1, *Hal-*

*iclona* sp1, *Gelloides* sp1 and *Chalinula milnei* were commonly found at the seaward exposures (Table 2). There were 4 species that characterized sponge assemblages by depth. The species *Cribochalina* sp1 and *Petrosia strongylata* characterized depths from 10 to 15 m and *C. milnei* and *Strongylophora* sp1 were predominantly found at 15 m depth, but there were not distinctive species for the 5 m depth (Table 2). Sponge assemblages varied between reefs, and led to changes in cover of combinations of 8 species. Hanging Gardens was typified by the presence of 6 species from which 3, *Chalinula milnei*, *Haliclona* sp1 and *Gelliodes* sp1, were not shared with other reefs. Similarly, Matane Walindi was characterized by the occurrence of *Pseudosuberites* sp1, and *Lamellodysidea chlorea* was the distinctive species for Matane Walindi and Rakaru Diri reefs. The common species that characterized Matane Huva and Gava Gava reef was the encrusting sponge *Dysidea* sp1. *Cribochalina* sp1 and *Strepsichordaia lendenfeldi* were characteristic species of Limuka reef (Table 2).



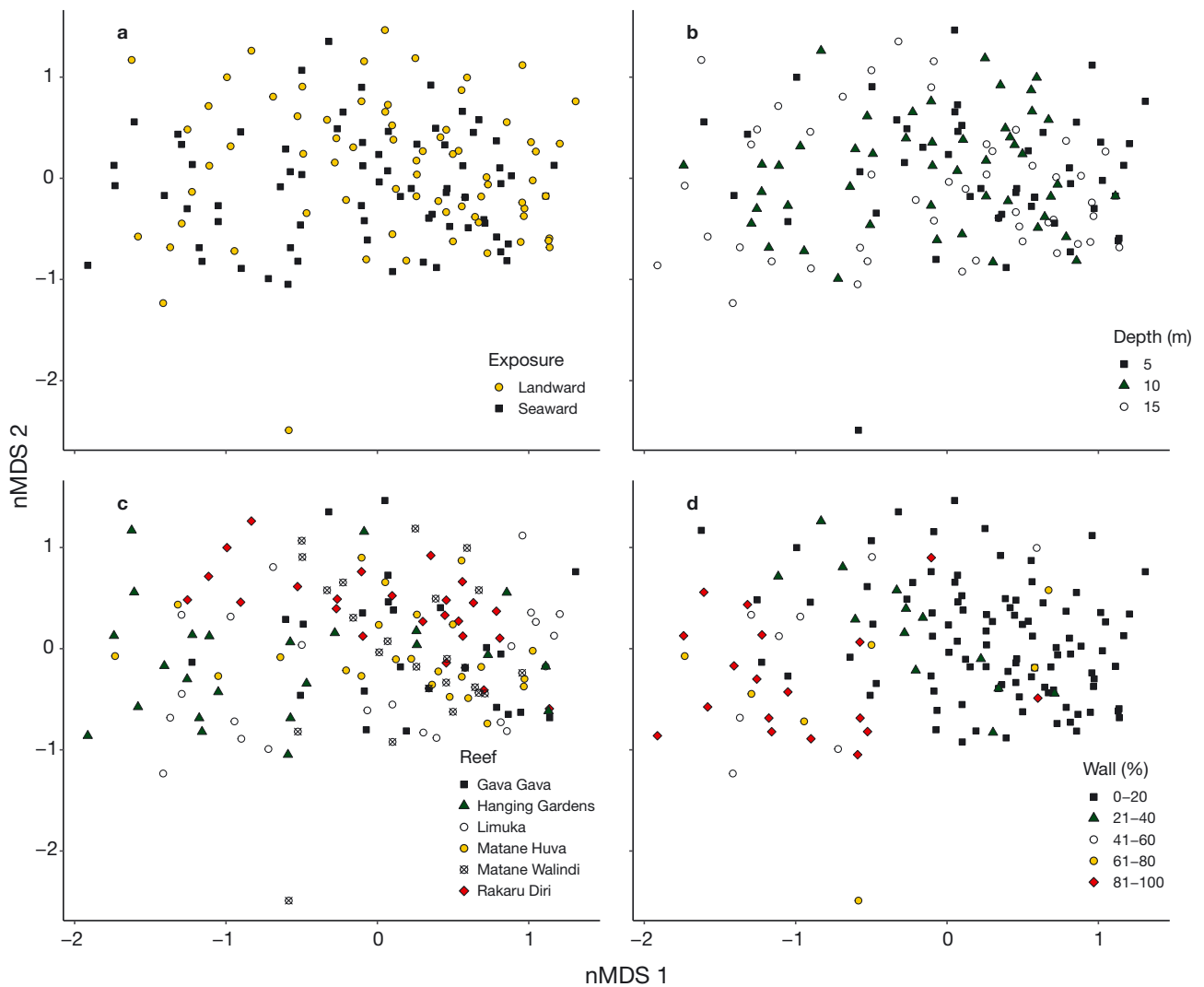


Fig. 6. Non-metric multidimensional scaling (nMDS) plots for sponge assemblages from 144 transects in inshore coral reef habitats of Kimbe Bay, Papua New Guinea. Four grouping factors were chosen: (a) exposure (seaward and landward side per reef), (b) water depth (5, 10, 15 meters), (c) individual location (reef,  $n = 6$ ) and (d) reef aspect (% wall). Data were transformed applying Wisconsin transformation on all species, and similarity is based on Bray–Curtis similarity distance. Stress value = 0.24

Table 1. Statistical results of multiple permutation ANOVA assessing types of substrate cover at seaward and landward exposures at 5, 10 and 15 m water depth on 6 inshore reefs in Kimbe Bay, Papua New Guinea. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

	df	Sum of squares	Mean of squares	$F$	$R^2$	Pr(> $F$ )
Exposure	1	0.51	0.51	2.57	0.01	0.004**
Depth	2	1.19	0.59	3.03	0.03	0.001**
Reef	5	3.77	0.75	3.83	0.11	0.0001***
Exposure $\times$ Depth	2	0.51	0.25	1.28	0.01	0.197
Exposure $\times$ Reef	5	1.93	0.38	1.96	0.05	0.001**
Depth $\times$ Reef	10	2.29	0.22	1.16	0.07	0.091
Exposure $\times$ Depth $\times$ Reef	10	2.38	0.23	1.21	0.07	0.047*
Residuals	108	21.22	0.19		0.62	
Total	143	33.79			1.00	

Table 2. Statistical results explaining the suitability of indicator species that distinguish or characterize sponge assemblages and are grouped by exposure (seaward and landward), water depth (5, 10 and 15 m) and location (6 reefs) in inshore Kimbe Bay, Papua New Guinea. r.g.: group-equalized phi coefficient of association. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; ND: not determined. Species names in **bold** highlight species that were detected as relevant in more than one level

Factor	Species	r.g. stat	p
Exposure			
Landward	<i>Hyrtios</i> sp1	0.21	0.0153*
	<i>Coelocarteria singaporensis</i>	0.24	0.0096**
	<i>Neopetrosia chaliniformis</i>	0.16	0.0411*
Seaward	<i>Cribrochalina</i> sp1	0.27	0.0010**
	<i>Haliclona</i> sp1	0.21	0.0073**
	<i>Gelliodes</i> sp1	0.19	0.0144*
	<i>Chalinula milnei</i>	0.18	0.0259*
Depth (m)			
5	No species detected	ND	ND
10–15	<i>Cribrochalina</i> sp1	0.27	0.0037**
	<i>Petrosia strongylata</i>	0.23	0.0201*
15	<i>Chalinula milnei</i>	0.25	0.0037**
	<i>Strongylophora</i> sp1	<b>0.21</b>	<b>0.0302*</b>
Location			
Gava Gava	<b><i>Dysidea</i> sp1</b>	<b>0.26</b>	<b>0.0280*</b>
Haging Gardens	<i>Chalinula milnei</i>	0.52	0.0001***
	<i>Gelliodes</i> sp1	0.33	0.0027**
	<i>Haliclona</i> sp1	0.33	0.0021**
	<b><i>Dysidea</i> sp1</b>	<b>0.26</b>	<b>0.0280*</b>
	<b><i>Cribrochalina</i> sp1</b>	<b>0.41</b>	<b>0.0001***</b>
	<b><i>Strepsichordaia lendenfeldi</i></b>	<b>0.28</b>	<b>0.0191*</b>
Limuka	<b><i>Cribrochalina</i> sp1</b>	<b>0.41</b>	<b>0.0001***</b>
	<b><i>Strepsichordaia lendenfeldi</i></b>	<b>0.28</b>	<b>0.0191*</b>
Matane Huva	<b><i>Dysidea</i> sp1</b>	<b>0.26</b>	<b>0.0280*</b>
Matane Walindi	<i>Pseudosuberites</i> sp1	0.41	0.0001***
	<b><i>Lamellodysidea chlorea</i></b>	<b>0.42</b>	<b>0.0001***</b>
	<b><i>Dysidea</i> sp1</b>	<b>0.26</b>	<b>0.0280*</b>
Rakaru Diri	<b><i>Lamellodysidea chlorea</i></b>	<b>0.42</b>	<b>0.0001***</b>
	<b><i>Dysidea</i> sp1</b>	<b>0.26</b>	<b>0.0280*</b>

### 3.5. Effect of reef aspect on sponge cover and species richness

Sponge cover and species richness generally increased in transects with a larger wall area (Table 3, Fig. 7a,b). The percentage of wall cover explained 54% of the variability in overall sponge cover. The average sponge cover in transects without walls was equal to 8.23%, and increased by 0.22% sponge cover for every 1% increment in wall aspect on the transect (HPDI = 0.19–0.25; Table 3, Fig. 7a). Wall aspect correlated with increments in sponge cover with a magnitude of change of almost 2.7 times more sponges on walls than on slopes (exceedance  $p = 1$ ). Thus, on

average, the percentage of sponge cover changed from 8.23% in areas without walls to 30.23% in areas with 100% wall aspect. Increments in sponge cover larger than 50% were likely to occur when the wall aspect increased from 0 to 25% (exceedance  $p = 1$ ).

The percentage of wall habitat along transects accounted for 49% of the variation in sponge species richness. Sponge species richness increased from ~5 species in transects with no wall to 22 species in transects completely on walls (Table 3, Fig. 7b). The increase in species richness was larger than 35% when the percentage of wall aspect increased from 0 to 25% (exceedance  $p = 0.95$ ), and it grew by at least another 25% when the aspect changed from 25 to 50% (exceedance  $p = 0.98$ ). Increments in species richness in transects with wall aspect larger than 50% were less likely to occur. Transects with wall aspect between 50 and 100% were likely to have only 15% increase in species richness (exceedance  $p = 1$ ).

The composition of sponge assemblages also differed between transects with different levels of wall aspect cover (Fig. 6d, Table 4). Percentage of wall aspect explained 14% of the variance among assemblages (Table 4). There were no particular species or groups that characterized sponge assemblages with wall aspect between 0 and 40%, indicating high variability in transects with this amount of wall aspect (Table 5). However, on tran-

sects with wall aspect between 41 and 100%, rare sponge species were seemingly restricted to walls. For example, *Cribrochalina* sp1 was associated with transects comprising >60% of wall, and *Chalinula milnei*, *Gelliodes* sp1 and *Haliclona* sp1 in areas of 80–100% wall aspect (Table 5).

## 4. DISCUSSION

Sponge assemblages are a significant and diverse element of the benthos in coral reef systems in Kimbe Bay. Together, our results suggest that while gradients of exposure and depth have an important influ-

Table 3. Statistical results assessing relationships of sponge cover and sponge species richness with availability of vertical (walls) substrate in 144 transects on inshore reefs in Kimbe Bay, Papua New Guinea. Estimate: median; SE: standard error; low HPDI: low high probability density interval; high HPDI: high high probability density interval;  $\hat{R}$ : convergence diagnostic for between and within chains estimates for model parameters; ESS: estimated sample size; PPD: posterior predictive distribution

Term	Estimate	SE	Low HPDI	High HPDI	$\hat{R}$	ESS
Sponge cover						
Intercept	8.23	0.70	6.90	9.65	1.00	18100
Percentage of wall	0.22	0.02	0.19	0.25	1.00	18008
Sigma	6.98	0.42	6.22	7.84	1.00	17789
Mean PPD	13.33	0.84	11.70	14.96	1.00	18006
Log-posterior	-490.06	1.25	-492.83	-488.87	1.00	17903
Sponge species richness						
Intercept	5.25	0.33	4.60	5.88	1.00	17939
Percentage of wall	0.09	0.01	0.08	0.11	1.00	18049
Sigma	3.22	0.19	2.84	3.59	1.00	18456
Mean PPD	7.37	0.38	6.60	8.09	1.00	17999
Log-posterior	-377.67	1.24	-380.45	-376.49	1.00	17670

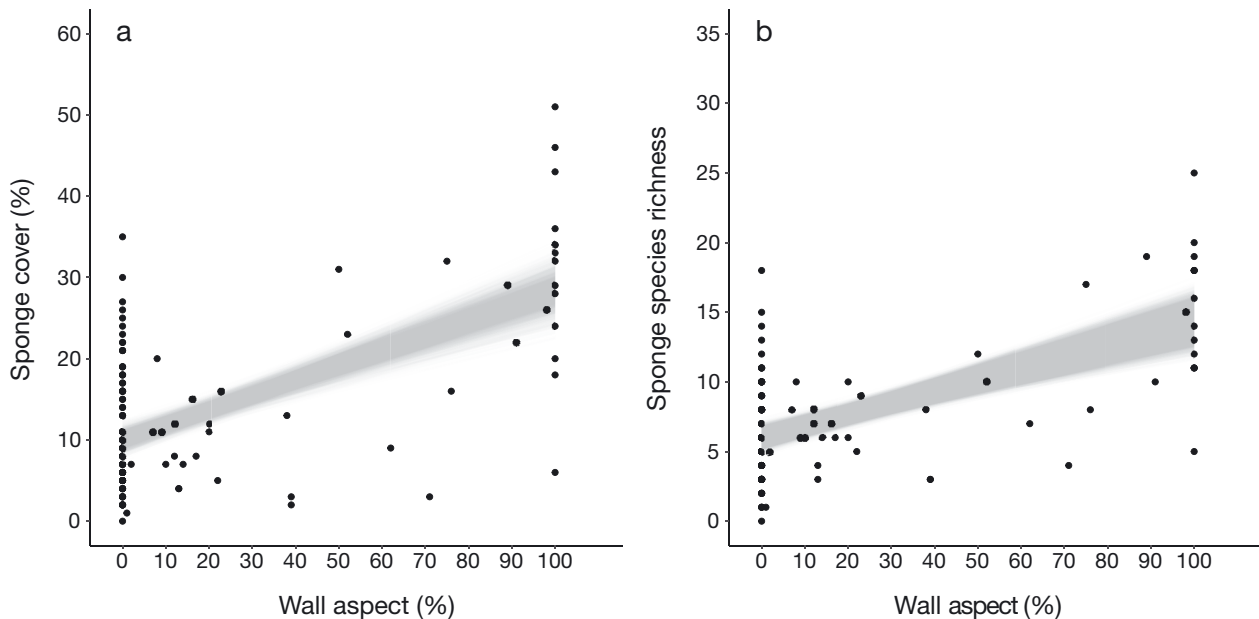


Fig. 7. Sponge cover (a) and sponge species richness (b) in relation to availability of vertical substrate (wall aspect) per transect recorded for 144 transects on 6 inshore reefs in Kimbe Bay, Papua New Guinea. Shaded area represents the frequency distribution of potential values of the slope determined from the model

ence on sponge assemblages, many patterns are being largely driven by the unique characteristics of individual reefs. Sponge cover in Kimbe Bay is similar to that on other reefs in the Central Indo-Pacific biogeographical region, but exceeds the sponge cover reported for regions such as the Central Pacific and Tropical West Atlantic (for reviews, see Rovellini et al. 2019, Bell et al. 2020). Beyond quantification of sponge assemblages, comparisons of sponge cover and sponge species richness in relation to other ben-

thic categories are limited (Williams et al. 2013, Bell et al. 2017, Schönberg 2021). However, such comparisons are necessary to evaluate the significance of sponges to the overall structure of reef systems. In our study, sponge cover was almost comparable to algae cover, the second most important biotic category after corals. This suggests that sponges might be important space competitors and play a significant role in benthic ecological processes on Kimbe Bay reefs.

Table 4. Multiple permutation ANOVA results for sponge assemblages on inshore reefs of Kimbe Bay, Papua New Guinea, testing availability of vertical substrate per transect in 144 transects, 5 categories of substrate cover at seaward and landward sides of the reefs and at 5, 10 and 15 m depth at 6 reefs. \*\*p < 0.01

	df	Sum of squares	Mean of squares	F	R <sup>2</sup>	Pr(>F)
% Wall aspect	4	2.8081	0.70202	5.6766	0.14042	0.001**
Residuals	139	17.1899	1.12367		0.85958	
Total	143	19.998			1	

Table 5. Indicator species analyses on sponge assemblages grouped by percentage of wall aspect in 144 transects in 6 inshore reefs in Kimbe Bay. \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001; ND: not determined. Species names in **bold** highlight species that were detected as relevant in more than one level

Wall aspect (%)	Species	Correlation	p
0–20	No species detected	ND	ND
20–40	No species detected	ND	ND
41–60	<i>Gelloides</i> sp1	0.39	0.021*
	<b><i>Cribochalina</i> sp1</b>	<b>0.51</b>	<b>0.0001**</b>
61–80	<b><i>Cribochalina</i> sp1</b>	<b>0.51</b>	<b>0.0001**</b>
81–100	<i>Chalinula milnei</i>	0.56	0.0002***
	<i>Haliclona</i> sp1	0.38	0.0269*
	<i>Gelliodes</i> sp1	0.39	0.0210*
	<b><i>Cribochalina</i> sp1</b>	<b>0.51</b>	<b>0.0001**</b>

Sponge morphology can be used as a proxy of species richness and functional diversity (Bell 2007) and inform reef environmental condition (Schönberg & Lim 2019, Schönberg 2021). In Kimbe Bay, sponges with encrusting morphologies were more abundant and species rich than massive and erect morphologies. Encrusting sponges appear to be extremely versatile, and are often characteristic of areas of hydrodynamic regimes with strong turbulent flow, as well as flow-reduced, nutrient-poor habitats with intermediate sediment size (Schönberg 2021). Inshore reefs in Kimbe Bay are sheltered with limited turbulent flow, the tides are characterized as small (<1 m) slow and less vigorous than other semidiurnal tides (Steinberg et al. 2006), but the monsoon season (November to March) can raise some turbulence and sediments (S. González-Murcia pers. obs.). Thus, the dominance of encrusting morphologies might indicate a compromise of species adapted to flow-reduced habitats and tolerant to sediments to some extent. Dominance of encrusting morphologies is a recurring pattern in other tropical reefs in the Central Indo-Pacific region (Farnham & Bell

2018), with few exceptions (Bell 2007, Hadi et al. 2015). Hence, our results contribute to filling gaps in our knowledge of sponge assemblages compared to other benthic organisms, and provide information to support and complement records of morphological diversity in sponge assemblages of tropical reefs in the Central Indo-Pacific region and the Eastern Coral Triangle province (sensu Spalding et al. 2007).

Reef exposure influenced sponge assemblages, resulting in lower sponge cover and species richness on the calmer landward compared to the more exposed seaward sites in inshore reefs of Kimbe Bay. The landward exposure was characterized by *C. singaporensis*, a fistular endopsammic (growing within sand or sediments) sponge that inhabits sites with low current to stagnant waters and tolerates high sediment environments (Schönberg 2016, 2021, Schönberg & Lim 2019). This indicates that at the landward side, hydrodynamic conditions and sediments might be influencing the structure of sponge assemblages in Kimbe Bay. The seaward exposure was distinguished by sponges with divergent morphologies. Encrusting shapes such as *Haliclona* sp1 and *Chalinula milnei* and thickly branching species such as *Cribochalina* sp1 and *Gelliodes* sp1 occur in areas with turbulent currents and less sediment or sediments of larger sizes (Bell et al. 2002, Schönberg 2016, 2021). Seaward areas are more exposed to currents and thus can benefit filter-feeding organisms, enhancing food supply and reducing sediment accumulation along with its associated physiological costs (Schönberg 2015b, Pineda et al. 2016, Strehlow et al. 2017, Abdul Wahab et al. 2019).

On coastal coral reefs, exposure to terrestrial runoff, sediment resuspension and deposition can have negative impacts on sponges via abrasion, energy cost and maintenance needs due to shading and clogging (Alcolado 1979, 1994, Wilkinson & Cheshire 1990, Aerts & Van Soest 1997). In one case, this reduced sponge diversity by 50% (Bell & Barnes 2003). Sedimentation rates can select for more tolerant sponge species adapted to turbid environments and exclude less tolerant sponges, which occur in areas with lower sediment rates (Bell et al. 2002, Powell et al. 2010, 2014). Our results suggest that differences in sponge assemblages between landward and seaward exposures are largely driven by currents, and this may also be linked to sediment

dynamics. Whether differences in cover and richness observed between exposure at landward and seaward sites represent permanent or transitory stages is still to be assessed. Likewise, differential impacts of currents and sediment deposition in sponge assemblages and selection pressure over sponges, morphologies or traits requires further investigation.

Sponge assemblages varied over the 5 to 15 m depth range examined in this study, suggesting that a range of environmental factors that covary with depth may be important (Bell & Barnes 2000a,b, Bell 2007). The diverse and sometimes divergent environmental requirements of sponge species do not allow us to rank these environmental factors from most to least important, since responses are likely to be species specific. In other studies, hydrodynamic regime and sedimentation have been suggested as the 'strongest drivers' (e.g. Schönberg 2021). Water turbulence, wave action and other types of stress have a strong impact on shallow areas (Huston 1985, Bridge et al. 2013), but their intensity attenuates with depth (Page-Albins et al. 2012, Frade et al. 2018). This may explain the interaction between depth and exposure that was detected on the Kimbe Bay reefs. Abrupt transitions of sponge communities along depth gradients have suggested the existence of a 'critical depth' (sensu Alcolado & Gotera 1985) from shallow to deep waters, usually between 5 and 10 m depth (Alcolado & Gotera 1985, Guzmán & Guevara 1998). Sponge communities above this limit are chaotic and less stable than assemblages below the critical depth (Battershill & Bergquist 1990, Alcolado 1994), which could explain the absence of characteristic sponge species in our 5 m depth stratum.

We consider that water turbulence could play a relevant role in regulating changes in sponge communities along the depth gradient in Kimbe Bay, since the distinctive species at the 10 and 15 m depth strata were encrusting and erect forms that are adapted to harsh hydrodynamics. However, this does not rule out other factors in explaining depth distributions, such as light attenuation, with different photosymbiotic organisms affecting the depth range of different sponge species. As multiple environmental factors such as temperature, wave action, light irradiance, pressure and sediment suspension covary with depth, together with the additional effects of biological interactions such as competition and recruitment (see Bell & Barnes 2000a, Bell 2007, Schönberg 2021 and references therein), it will be a complex task to isolate the effect of depth alone in explaining changes in abundance, species richness and species composition along depth gradients.

Reef aspect influenced sponge cover, richness and the species composition of sponge assemblages in Kimbe Bay. In line with our expectations, sponge cover and diversity were higher at sites with more vertical walls, especially on transects that had at least 25% or more wall habitat. The wall on the seaward side of Hanging Gardens reef had the highest values of cover and richness, with similar values from 5 to 15 m depth. Differences in reef aspect can determine the accumulation of sediment particles and wave exposure (Bell & Barnes 2000b), as well as predation (Durán et al. 2018). Our results reinforce the conclusions of Janowski et al. (2015), who found higher sponge cover on walls compared to slopes and more abrupt changes in sponge cover along walls in Kimbe Bay.

Sponges that characterized gentle slopes were mainly encrusting and massive forms such as *Dysidea* sp1, *L. cf. chlorea* and *C. singaporensis*, which are well adapted to places with high sediment rates. These species actively and selectively incorporate sediments and coarse particles in their skeleton, saving the physiological costs of producing them (for a review, see Schönberg 2016). In walls, erect sponge morphologies were conspicuous and the species *Cribrochalina* sp1, *Gelloides* sp1 and *Haliclona* sp1 were often present. Walls are less likely to accumulate sediments, and the morphology of these species minimizes surface area thus reducing sediment deposition (Bell et al. 2002). Thus, aspect influenced sponge assemblages at different scales and modified gradients of sponge cover and species richness that were determined by depth and exposure in other reefs.

Sponges represent a significant and diverse component of the benthic habitat in Kimbe Bay, although reefs are still coral dominated at the depths sampled. Sponge diversity and assemblage structure were influenced by the location-specific patterns of depth, exposure and reef aspect. As modification of coastal environments has strong repercussions in shallow inshore systems, documenting distribution patterns of benthic communities, and particularly sponges, is essential to identify potential changes generated by anthropogenic disruptions. Biodiversity loss and homogenization could represent a threat to the highly diverse sponge assemblage inhabiting Kimbe Bay reef systems. In conclusion, this paper provides a baseline for studying benthic dynamics and ecological drivers in change in sponge communities in Kimbe Bay. Exposure, depth and reef aspect play important roles in explaining spatial variation in cover, species richness and species composition of sponges; nonetheless, the relevance of these variables will be different in each reef.

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