Reduced Diversity and High Sponge Abundance on a Sedimented Indo-Pacific Reef System: Implications for Future Changes in Environmental Quality

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Abstract

Although coral reef health across the globe is declining as a result of anthropogenic impacts, relatively little is known of how environmental variability influences reef organisms other than corals and fish. Sponges are an important component of coral reef fauna that perform many important functional roles and changes in their abundance and diversity as a result of environmental change has the potential to affect overall reef ecosystem functioning. In this study, we examined patterns of sponge biodiversity and abundance across a range of environments to assess the potential key drivers of differences in benthic community structure. We found that sponge assemblages were significantly different across the study sites, but were dominated by one species Lamellodysidea herbacea (42% of all sponges patches recorded) and that the differential rate of sediment deposition was the most important variable driving differences in abundance patterns. Lamellodysidea herbacea abundance was positively associated with sedimentation rates, while total sponge abundance excluding Lamellodysidea herbacea was negatively associated with rates of sedimentation. Overall variation in sponge assemblage composition was correlated with a number of variables although each variable explained only a small amount of the overall variation. Although sponge abundance remained similar across environments, diversity was negatively affected by sedimentation, with the most sedimented sites being dominated by a single sponge species. Our study shows how some sponge species are able to tolerate high levels of sediment and that any transition of coral reefs to more sedimented states may result in a shift to a low diversity sponge dominated system, which is likely to have subsequent effects on ecosystem functioning.

Introduction

The plight of tropical coral reefs has been well reported with an estimated 60% of reefs being threatened by local-scale human activities, including coastal development, overexploitation, invasive species and pollution [1]. In addition, all coral reefs across the world face the threat of global warming and ocean acidification [2]. The Indo-Pacific region is a global hotspot of marine diversity for most major taxa [3] and encompasses 75% of the world’s coral reefs; however, this region has also experienced widespread degradation of its reefs. An analysis of 2667 surveys of Indo-Pacific coral reefs between 1968 and 2004 suggest that an average of 1% or 1,500 km² of hard coral cover has been lost per year over this period [4]. Despite high research effort, high public interest and the known societal importance of Indo-Pacific reefs, there is a paucity of information concerning the ecology of reef-associated fauna other than reef building corals and fish. Consequently, there is an urgent need for greater research effort focusing on the effects of environmental degradation on those fauna that play pivotal roles in driving the community structure of tropical reefs [5].

After corals, sponges are one of the most dominant benthic taxa inhabiting coral reefs [6] and play many important functional roles, particularly through their interactions with the water column, biogeochemical cycling, nutrient cycling, bioerosion, and their facilitation of primary production as a result of their symbiotic associations with microbes [7–9]. In addition, due to their competitive ability and well-documented interactions with other reef organisms [10], changes in the distribution, composition and abundance patterns of sponges are likely to affect overall reef ecosystem functioning (e.g. nutrient recycling and spatial interactions).

So called “phase shifts” have been widely associated with declining reef quality and reduced herbivore abundance [11] and most often reefs have changed from coral to algal-dominated states. However, there also appears to be the potential for coral-dominated systems to change to states dominated by sponges [12,13]. For example, increases in the bioeroding sponge Cliona

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The abundance and diversity of sponges were surveyed in situ using SCUBA in six 1 m² divided quadrats at each site (total n = 54). To identify a suitable sample size for the replication within each site, species accumulation curves based on surveys of 15 permanent monitoring quadrats (Bell unpublished data) were examined. Accumulation curves were produced using the statistical software package PRIMER for the observed number of species given the sample sizes ranging from 1–15 (figure S1). Six quadrats were surveyed at each site as this captured an average of 80% (46 of 58 species, with a 95% CI of 38 to 54 species) of the species captured in 15 quadrats and further quadrats provide limited returns in terms of the new species detected (3 quadrats: 50 species, 10 quadrats: 54 species), whilst significantly increasing the number of species captured.

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time spent performing the surveys. Quadrats were placed at random pre-selected positions along a 30 m transect tape, which was laid out following a 10 m depth contour on the reef slope. The location of the quadrats was determined using a random number generator (six random positions selected from 0–29 for each transect) prior to the surveys. If the pre-selected quadrat location happened to be an unsuitable location, such as a cave or overhang, the quadrat was moved to the nearest suitable reef slope/wall habitat location further along the tape. Sponge patches were counted if any part of the sponge was in the quadrat. We chose to measure the number of sponge patches rather than biomass or area occupied because: 1) the nature of the sponge assemblages in the region, which are dominated by small encrusting patches see [50]; 2) earlier studies in the region have shown a strong correlation between area occupied and number of patches, and similar multivariate assemblage patterns see [25]; 3) the topographic complexity of the study sites meaning it was not possible to estimate area occupied from photographs. All sponge species were assigned an ID code, which were considered Operational Taxonomic Units (OTUs) for the purposes of this study. To confirm the consistency and validity of these units, photographs were taken of each OTU, along with small samples that were used for spicule preparations and sections [51]. Habitat quality was defined by the percentage cover of hard coral, coralline algae, other algae (turf or macro), soft coral, rock, rubble, sand, and other (e.g. ascidians, bryozoans) calculated from photo-quadrats (n points = 100) using Coral Point Count [52]. Fish surveys were carried out between 10:00–15:00 along three 50×5 m transects on the reef slope (10 m) at each site using the time (15 mins) and distance restricted underwater visual census method see [53]. Spongivorous fish were classified as: a) those reported in the literature as having a diet of >5% sponge (from gut contents) [54–59] b) from a preliminary analysis of fish gut contents carried out as part of this study; and c) species observed feeding on sponges during this survey.

Environmental variables
Turidity, temperature and water column chlorophyll-a (as a proxy for food availability) were recorded using an RBR XR-420 data logger set to record every minute with no averaging. Water flow was measured with an impeller current meter (Valeport Model 106). The XR-420 data logger and flowmeter were deployed on reef slopes at a depth of 10 m for a minimum of three 24 hour periods at each study site. To quantify sedimentation levels, four sediment traps were deployed on the reef slope at a depth of 10 m for a minimum of 24 hours. The sediment samples were then weighed to obtain mean dry weight of sediment at each site. The angle of the reef surface within each quadrat was measured using a pivoted protractor mounted on a spirit level.

Statistical analyses
Statistical analyses were performed in the PRIMER-E v6 environment (Plymouth Routines In Multivariate Ecological Research) with the PERMANOVA add-on. Analyses were based on resemblance matrices calculated using Bray-Curtis similarity coefficients.
Benthic characteristics of the study sites

A one-factor permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in the benthic characteristics of the study sites with site as a fixed factor with nine levels. PERMANOVA was used as it is a permutation-based method and therefore makes no assumption about the distribution of the data. Site differences were represented graphically using unconstrained non-metric Multi Dimensional Scaling (MDS) and constrained Canonical Analysis of Principal Coordinates (CAP). Spearman rank correlations between individual benthic components and the resulting CAP axes were used to identify benthic groups that were characteristic of particular study sites.

Sponge abundance patterns

Differences in total sponge abundance among study sites was tested using a one factor PERMANOVA (PERMANOVA operating on univariate data is equivalent to a permutational ANOVA) with site as a fixed factor with nine levels. The associations between sponge abundance and biotic/environmental variables were investigated using distance-based multiple linear regression (DISTLM). DISTLM is a routine that can be used to model the relationship between a multivariate distance based dataset (whether the distances are calculated from multivariate assemblage data or between univariate data points), as described by a resemblance matrix, and a set of predictor variables [60]. Draftsman plots were used to check for skewness and multicollinearity in the predictor variables. Variables that were highly correlated with other variables were removed in order to maximise the parsimony of our models. Turbidity was excluded from the analysis as it was highly correlated (R²>0.9) with sediment levels. The following 10 variables were considered in the DISTLM analysis: substrate angle, temperature, sediment, flow rate, chlorophyll-a, hard coral cover, coralline algae, other non-coraline algae, soft coral and spongivorous fish abundance. Models incorporating all possible combinations of predictor variables were generated using the Best procedure within the DISTLM routine. We then used an information theoretic approach based on modified Akaike’s Information Criterion (AICc) to identify the best model. AICc values indicate the goodness of a model fit to the data, penalised for increasing the number of variables [61]. Models with the lowest AICc are considered the most parsimonious. We discuss the model with the lowest AICc value, but we also calculated the Akaike weights of all models with AICc values within five of the best model. The Akaike weight, \( w_i \), for a given model, denoted by subscript \( i \), is calculated as

\[
 w_i = \frac{e^{-\Delta_i/2}}{\sum_{j=1}^{R} e^{-\Delta_j/2}}
\]

where \( R \) is the number of candidate models and \( \Delta_i \) is the difference in AICc value between model \( i \) and the model with the lowest AICc value. The Akaike weight demonstrates the best model relative to others [62]. Assessing the Akaike weights therefore allows us to identify and quantify the uncertainty in model selection. The Akaike weights were also used to estimate the relative importance of each predictor variable [61]. For each predictor, the Akaike weights of all the models (with \( \Delta \text{AIC}_c \) less than 5) that contained that predictor were summed. The summed Akaike weights for each predictor can be interpreted as the relative importance of that predictor. Those predictors that consistently occur in the most likely models have an Akaike weight close to 1 whereas variables that are absent from or are only present in poorly fitting models (high AICc values) have an Akaike weight close to 0 [61].

Sponge diversity and assemblage patterns

Species diversity indices were calculated for each study site based on the OTUs. We measured the total number of species present (S), Shannon’s index (H’) and Pielou’s evenness index (J’). Species rank abundance curves were also generated to examine sponge assemblage structure at the different study sites. To examine the relationship between local abundance (within each site) and prevalence (among sites) we identified the maximum abundance and prevalence of each species [63]. The abundances

Figure 2. Benthic assemblage composition at the study sites. Canonical Analysis of Principal Coordinates (CAP) plot showing differences in benthic composition between study sites. Vectors are overlaid for benthic components that have a Spearman rank correlation greater than 0.4 with either of the resulting CAP axes. doi:10.1371/journal.pone.0085253.g002
for each species were summed across quadrats within each site and
the maximum of these summed site specific values (standardised to
abundance per m²) was taken as a measure of its local abundance.
These values were then plotted against its prevalence among sites
(= number of occupied sites/9). A log transformation was applied
to local abundance to control for extremely high values and to
achieve a relatively equal spread. A simple linear regression
(normal errors) was applied to the data to further examine the
relationship between abundance and occupancy and R² and
Pearson correlation coefficient values were calculated. These
analyses were performed in R version 3.0.2 [64].

The same PERMANOVA design was used as described above
to test for differences in the multivariate sponge assemblages at the
study sites. Prior to analysis a dispersion weighting transformation
was applied to the data to down-weight the importance of
numerically abundant species. This transformation was considered
appropriate as some sponges, particularly Lamellodysidea herbacea,
were highly abundant and also showed evidence of spatial
clustering [65]. Constrained analysis of principal coordinates

Table 1. Summary table of environmental and biological predictor variables.

| Variable             | Units       | Site                                |
|----------------------|-------------|-------------------------------------|
| Angle per site       | °           | Sampela 1: 46.67 (±31.09) Sampela 2: 50 (±16) Kaledupa: 52.67 (±20.7) Kaledupa Double Spur: 62.83 (±33.86) Buoy 1: 58.33 (±25.43) Buoy 3: 64.17 (±14.63) Buoy 4: 78 (±5.66) Pak Kasim’s Ridge 1: 66.67 (±19.92) Ridge 1: 65 (±21.68) |
| Temperature          | °C          | 27.73 (±0.12) 27.67 (±0.32) 28.12 (±0.18) 27.92 (±0.21) 27.37 (±0.13) 27.91 (±0.04) 27.82 (±0.37) 28.06 (±0.13) 27.66 (±0.13) |
| Turbidity            | Standard turbidity units | 3.88 (±0.16) 2.92 (±0.051) 0.26 (±0.019) 0.39 (±0.12) 0.26 (±0.019) 0.39 (±0.12) 0.39 (±0.12) 0.39 (±0.12) 0.39 (±0.12) |
| Chlorophyll-a        | µg/l        | 0.39 (±0.1) 0.39 (±0.12) 0.26 (±0.17) 0.26 (±0.08) 0.26 (±0.13) 0.26 (±0.14) 0.26 (±0.14) 0.26 (±0.14) 0.26 (±0.14) |
| Sediment             | g dry weight/day | 0.357 (±0.168) 0.322 (±0.051) 0.124 (±0.019) 0.124 (±0.019) 0.124 (±0.019) 0.124 (±0.019) 0.124 (±0.019) 0.124 (±0.019) 0.124 (±0.019) |
| Flow                 | m/s         | 0.063 (±0.044) 0.056 (±0.038) 0.014 (±0.02) 0.038 (±0.041) 0.02 (±0.024) 0.02 (±0.024) 0.02 (±0.024) 0.02 (±0.024) 0.02 (±0.024) |
| Hard coral % Cover   |             | 11.11 (±7) 7.73 (±5.43) 4.63 (±3.77) 27.49 (±14.86) 23.36 (±11.26) 31.45 (±16.74) 45.59 (±15.18) 57.05 (±13.83) 35.7 (±13.62) |
| Soft coral % Cover   |             | 6.39 (±5.44) 2.32 (±2.7) 22.13 (±10.15) 13.08 (±8.39) 4.96 (±3.03) 1.38 (±1.79) 3.88 (±5.76) 11.11 (±3.91) 17.34 (±16.96) |
| Coraline algae % Cover |         | 14.38 (±15.53) 14.12 (±7.79) 12.15 (±6.79) 27.43 (±11.75) 20.81 (±11.21) 27.34 (±24) 22.32 (±15.82) 15.12 (±6.72) 12.23 (±10.66) |
| Other non-coraline algae % Cover |     | 6.8 (±6.8) 1.12 (±4.83) 2.73 (±1.8) 2.97 (±2.44) 4.18 (±2.44) 4.16 (±2.44) 2.37 (±2.44) 2.27 (±1.75) 6.86 (±5.02) |
| Spongivorous fish Number/125 m² |     | 48 (±11.36) 37 (±8.33) 28 (±9.66) 37 (±8.08) 26 (±1.15) 19 (±4.16) 24 (±6.11) 23 (±7.81) 30 (±7.81) |
Figure 4. Distance based redundancy analysis (DbRDA) ordinations of fitted models. Distance based redundancy analysis (DbRDA) ordinations of models with the lowest AICc value of all competing models for: a) total sponge abundance; b) sponge abundance when Lamellodysidea herbacea was excluded; and c) Lamellodysidea herbacea abundance.

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(CAP) was used to visualise the differences in the sponge assemblages and to identify species that were characteristic of the different study sites. Spearman rank correlations (>0.4) of individual species abundances with the CAP axes were used to determine which species were most characteristic of the study sites. The associations between sponge assemblage structure and the other variables were investigated using the same approach as our analysis of sponge abundance using permutational distance-based multivariate multiple regression (DISTLM).

**Results**

**Environmental variables and benthic characteristic of the study sites**

The environmental and biological parameters measured at each site are summarised in Table 1. Mean quadrat angle ranged from 78.66° ± 5.66° (±1 SD) at Buoy 4 to 46.67° ± 31.09° at Sampela 1. Chlorophyll-a also varied between sites with the highest mean value recorded at Kaledupa (0.42 ± 0.19 mg/l) and the lowest at Pak Kasim’s (0.14 ± 0.06 mg/l). There was little variation in the mean water temperatures recorded on the reef slopes at the study sites. Temperatures ranged from 28.12±0.18°C at Kaledupa to

**Table 2. Summary table of the results of the DISTLM analysis, results shown are for the model with the lowest AICc values for each response variable.**

| Response                          | AICc  | % total variability explained | Predictors               | % variability explained by each predictor | Pseudo-F | P-value | Relationship |
|-----------------------------------|-------|-------------------------------|--------------------------|------------------------------------------|----------|---------|--------------|
| Total sponge abundance            | 333.08| 13                            | Hard coral cover         | 0.47                                     | 0.57     | positive |
|                                   |       |                               | Sediment                 | 2.67                                     | 0.092    | positive |
|                                   |       |                               | Chlorophyll-a            | 0.96                                     | 0.34     | positive |
| Sponge abundance excluding        | 340.71| 34                            | Sediment                 | 12                                       | 1.21     | 0.0004  | negative    |
| L. herbacea                       | 390.85| 15                            | Quadrat Angle            | 12                                       | 7.64     | 0.0029  | positive    |
|                                   |       |                               | Hard coral cover         | 1                                        | 6.58     | 0.0064  | positive    |
|                                   |       |                               | Chlorophyll-a            | 4                                        | 2.38     | 0.12    | unclear     |
| Abundance of L. herbacea          |       |                               | Sediment                 | 15                                       | 9.2      | 0.0001  | positive    |
| Multivariate sponge assemblage    | 426.74| 26                            | Sediment                 | 8                                        | 5.06     | 0.0001  | NA          |
|                                   |       |                               | Chlorophyll-a            | 6                                        | 3.64     | 0.0001  | NA          |
|                                   |       |                               | Spongivorous fish        | 6                                        | 3.45     | 0.0001  | NA          |
|                                   |       |                               | Flow                     | 5                                        | 2.84     | 0.0001  | NA          |
|                                   |       |                               | Temperature              | 4                                        | 2.2014   | 0.001   | NA          |

**Figure 5. Sponge species relative abundance.** Dominance plot showing the percentage abundance of the 20 most abundant sponge species.

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37.37 ± 0.69°C at Buoy 1. The highest mean flow rate was recorded at Sampela 1 (0.063 ± 0.044 m/s) and the lowest was recorded at Buoy 1 (0.002 ± 0.0084 m/s). Mean spongivore fish abundance varied between 19 ± 4.16 per 250 m² transect at Buoy 3 to 40 ± 11.36 per 250 m² at Sampela 1. Benthic assemblage composition was significantly different between study sites (PERMANOVA, Pseudo-F = 5.6497, p = 0.0001). Overall allocation success from the CAP analysis was 40.74% (Fig. 2). The results of the CAP analysis of benthic characteristics (Fig. 2) showed that: Sampela 1 and Sampela 2 were characterized by sponges, sand and rubble; Kaledupa 1 was characterised by rock and soft corals; and Ridge 1, Pak Kasim’s, Buoy 1, Buoy 3, Buoy 4 and Kaledupa Double Spur were all characterized by hard coral.

Sponge abundance patterns

In total, we counted 3856 sponges across all the study sites with a mean density of 71 (±78) sponges per m². Total sponge abundance was significantly different between study sites (PERMANOVA, Pseudo-F = 2.6566, p = 0.0073). Sponge abundance was highest at Sampela 1 (103.67 sponges/250 m²) and lowest at Buoy 1 (0.0084 m/s). Mean spongivore fish abundance varied between 19 ± 4.16 per 250 m² transect at Buoy 3 to 40 ± 11.36 per 250 m² at Sampela 1. Benthic assemblage composition was significantly different between study sites (PERMANOVA, Pseudo-F = 5.6497, p = 0.0001). Overall allocation success from the CAP analysis was 40.74% (Fig. 2). The results of the CAP analysis of benthic characteristics (Fig. 2) showed that: Sampela 1 and Sampela 2 were characterized by sponges, sand and rubble; Kaledupa 1 was characterised by rock and soft corals; and Ridge 1, Pak Kasim’s, Buoy 1, Buoy 3, Buoy 4 and Kaledupa Double Spur were all characterized by hard coral.

Sponge diversity and assemblage patterns

The three sites with the highest total species richness were Ridge 1 (S = 43), Buoy 1 (S = 41) and Kaledupa Double Spur (S = 40) (Fig. 6). These sites also had the highest Shannon diversity and Pielou’s evenness. The sites with the lowest species richness were Sampela 1 (S = 19) and Sampela 2 (S = 28); these sites also had the lowest species diversity and evenness. Pielou’s evenness index showed that Sampela 1, and to a lesser extent Sampela 2, were

| Table 3. Table showing the summed Akaike weights for each parameter for all models within Δ AICc of five for each of the response variables. |

| Predictors                          | Total sponge abundance | Sponge abundance excluding L. herbacea | Abundance of L. herbacea | Multivariate sponge assemblage |
|-------------------------------------|------------------------|---------------------------------------|--------------------------|-------------------------------|
| Sediment                            | 0.47                   | 0.92                                  | 0.98                     | 0.72                          |
| Spongivorous fish                   | 0.2                    | 0.61                                  | 0.31                     | 0.53                          |
| Chlorophyll-α                       | 0.53                   | 0.53                                  | 0.16                     | 0.52                          |
| Temperature                         | 0.2                    | 0.42                                  | 0.23                     | 0.52                          |
| Flow                                | 0.26                   | 0.35                                  | 0.25                     | 0.49                          |
| Hard coral                          | 0.65                   | 0.62                                  | 0.19                     | 0.44                          |
| Quadrat angle                       | 0.19                   | 0.73                                  | 0.21                     | 0.38                          |
| Coralline algae                     | 0.28                   | 0.29                                  | 0.42                     | 0.37                          |
| Soft coral                          | 0.19                   | 0.23                                  | 0.29                     | 0.34                          |
| Other algae                         | 0.27                   | 0.16                                  | 0.29                     | 0.23                          |

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dominated by only a few species compared to the higher quality sites. This was also evident in the species abundance curves (figure S2). The sponge assemblages at Sampela 1 and to a lesser extent Sampela 2 were characterized by a skewed pattern with high abundances of one species. In contrast sponge assemblages at the other sites were more even with abundances more evenly distributed across more species. Plotting local abundance against prevalence revealed that the species that tended to be locally

Figure 6. Sponge species diversity. Species diversity measures: a) total number of species; b) Shannon-Wiener index ($H'$) c) Pielou's evenness index ($J'$).
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abundant were also widespread, whilst locally scarce species also tended to be present at fewer sites (Fig. 7). The relationship between local abundance and prevalence was highly significant (p-value < 0.001) with a Pearson correlation coefficient of 0.73 and an R² value of 0.53 from the linear model fit.

PERMANOVA tests revealed that there was a significant difference between the sponge assemblages at the study sites (pseudo-F = 3.12, p < 0.001). Sponge assemblages at Sampela 1 and Sampela 2 were similar, and characterised by high abundance of Lamellodysidea herbacea (Fig. 8). Sponge assemblages at Kaledupa, Buoy 1 and Ridge 1 were characterised by Stelleta clavosa,
Callyspongia (Euplacella) biru and Cinachyrella c.f. australiensis Pak Kasim’s and Kaledupa Double Spur, were characterised by Clathria (Microciona) mona, Dysidea sp. 12, and Haplosclerina sp. Finally, Buoy 3 and Buoy 4 were characterised by Chelonaplysilla sp 5.

The best model identified using DISTLM explained 26% of the variation in sponge assemblages between quadrats and contained five variables: sediment (8%), chlorophyll-a (6%), spongivorous fish abundance (6%), flow rate (5%), and temperature (4%) (Fig. 9). The Akaike weights of all the predictor variables ranged from 0.72 to 0.23 (Table 4). Spongivorous fish abundance, chlorophyll-a and temperature had Akaike weights greater than 0.5 providing some support for these variables being correlated with sponge assemblage structure, but the major contributor was sediment with an Akaike weight of 0.72.

Discussion

Sponges play key functional roles in coral reef ecosystems and identifying the variables that influence their distribution, abundance and diversity patterns is important for our understanding and predictions of the effects of anthropogenic impacts on coral reefs. Earlier studies of sponge distribution and abundance patterns have identified a number of important abiotic and biological variables, however, few studies have examined the effects of multiple variables and their relative importance concurrently. We aimed to determine the variables correlated with the distribution and abundance patterns of sponges on an Indonesian reef system, and to determine the direction of these relationships. Initially, we found that by modeling overall sponge abundance we were unable to explain most of the variation across the study sites. However, further analysis demonstrated that this was most likely due to contrasting responses to sedimentation of the most abundant species in the study, Lamellodysidea herbacea, compared to all the other sponge species. In contrast to abundance patterns, sponge assemblage patterns were explained by a larger number of variables with no single dominant driver. Importantly, we also found that sites with the lowest coral cover and highest sedimentation rates were characterized by sponges rather than by any other group of benthic organisms. Although sponge diversity at these sites was lower, overall sponge abundance was just as high as at sites with high levels of coral cover. Given the low coral cover at the high sediment sites, that have previously had much higher levels of coral cover (30–35% in 2002) [66], we propose that some sponge species have the potential dominate sites where environmental quality has declined. It has been proposed that many coral reefs may become sponge reefs in the future in response to ocean warming and acidification [13]. Our study further supports this hypothesis in that further reductions in environmental quality through increases in sedimentation may also favor sponge-dominated reefs; however, they will likely be low diversity systems.

Our study is consistent with earlier studies in tropical systems that have found that sponge abundance and diversity are strongly correlated with sedimentation levels including an earlier study in the Wakatobi [18,23,25,67,68]. There are a number of potential ways in which sedimentation could affect sponge abundance and diversity. Increasing sedimentation levels in aquaria has been shown to reduce the pumping rate of a tropical sponge [69], which is likely to have negative effects on sponge physiology. There is also evidence that, under conditions of dispersed flow with silt deposition, sponges in experimental aquaria crawled significantly longer distances on the substratum than their control counterparts, most likely to locate microhabitats with lower exposure to silt [70]. Artificially increasing the sediment levels settling on sponges in situ can also have a negative effect on sponge growth rates and reproductive status with sponges subjected to increased silt levels containing lower numbers of spermatozoa than those in control treatments [71]. In a field experiment on a Mediterranean sponge species, exposure to sediment significantly reduced the longevity and success of young sponge recruits [72]. However, in contrast to these reports of the negative effects of sedimentation on sponges, a number of studies have reported high levels of sponge species richness and abundance in sedimented environments [24,29], suggesting many species are tolerant to sedimentation. In addition, sedimentation has also been implicated in mediating competition effects between sponges and other benthic organisms, whereby negative effects of sediment on sponge competitors can enhance the success of sponges [24]. We propose that increased sedimentation rates have the potential to benefit some sponge species and may even have the potential to drive changes to sponge-dominated reef communities, especially when Lamellodysidea herbacea is present. When we examined the abundance patterns of the most common sponge in our study, L. herbacea, we found that it was positively correlated with sedimentation. This species was present at all the sites we surveyed, but was very abundant at Sampela 2, the sites with the lowest levels of coral cover and considered the most degraded. Interestingly, L. herbacea was also reported to be the most abundant sponge species at Derawan Islands, also in Indonesia [73]. The reason for the success of this species at highly sedimented sites is unclear and perhaps surprising since it is phototrophic, however, sedimentation rates at Sampela show considerable seasonal variability, with the highest sediments during June-October [48]. Therefore it is possible that this species may be able to tolerate sediment since it does not experience warming and acidification [13]. Our study further supports this hypothesis in that further reductions in environmental quality has declined. It has been proposed that many coral reefs may become sponge reefs in the future in response to ocean warming and acidification [13]. Our study further supports this hypothesis in that further reductions in environmental quality through increases in sedimentation may also favor sponge-dominated reefs; however, they will likely be low diversity systems.

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Figure 9. Factors associated with observed variation in sponge assemblages at the study sites. Distance based redundancy ordination (DbRDA) of the model with the lowest AICc value for the multivariate sponge assemblage data. doi:10.1371/journal.pone.0085253.g009
The role of mucous in the prevention of sediment build up on tropical sponges has not been fully explored. However, the role of mucous in the prevention of sediment build up on tropical sponges has not been fully explored. The other important variables that we found associated with sponge abundance were substrate angle and spongivorous fish abundance. In general, we found a positive relationship between surface angle and sponge abundance, which is consistent with an earlier smaller scale study in the Wakatobi [25]. The effect of substrate angle on sponges is most likely to be indirect through its interaction with sedimentation, light availability and the differential effect of these variables on other organisms affecting the rate and potential outcome of spatial competition between these organisms and sponges. Finally, sponge abundance excluding Lamellodysidea herbacea was negatively correlated with spongivorous organisms and sponges. The species occupancy-abundance plot shows that the species that were the most abundant were also widespread. The most common species Lamellodysidea herbacea was present at every site not just the Sampela sites so appears to be a generalist species able to tolerate a wide range of conditions. Our best model explaining differences in sponge assemblage composition among quadrats included sedimentation, chlorophyll-a, fish spongivore abundance, flow and temperature. However, unlike our model of sponge abundance, no single variable explained much more variation than the others and we were able to explain less variation in overall sponge assemblage structure than in the overall patterns of sponge abundance. One of the reasons for this is the exceptionally high sponge diversity in this area [50,51] that inevitably leads to high variability in sponge assemblages between quadrats. Given that our results show that sponge assemblage variation is related to a number of variables and that each variable explained only a small amount of variation in sponge assemblages, it may be difficult to predict how specific anthropogenic changes will affect overall sponge assemblage structure. Other variables that might account for the unexplained variation in sponge assemblage structure include light levels, wave exposure, competition, and nutrient and food availability (although we did measure Chl-a as a proxy for food availability) as these have all been associated with changes in sponge abundance in other studies [23,24,76].

Table 4. List of spongivorous fish and the percentage sponge found in gut contents.

| Family         | Species                    | % Gut Contents | Location          | Reference                       |
|----------------|----------------------------|----------------|-------------------|---------------------------------|
| Acanthuridae   | Ctenochaetus binotatus      |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Acanthuridae   | Acanthurus pyroferus        |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Balistidae     | Sufflamen bursa             | 5.88           | Hawaii, USA       | Hobson, E. S., 1974             |
| Bleniidae      | Ecsenius pictus             |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Chaetodontidae | Chaetodon bennetti          | 13             | Kalimantan, Indonesia | Nagelkerken et al 2009          |
| Chaetodontidae | Chaetodon kleinii           | 8              | Kalimantan, Indonesia | Nagelkerken et al 2009          |
| Chaetodontidae | Chaetodon lunulatus         | 5              | Kalimantan, Indonesia | Nagelkerken et al 2009          |
| Chaetodontidae | Chaetodon unimaculatus      | 17.49          | Hawaii, USA       | Hobson, E.S. 1974               |
| Chaetodontidae | Forcipiger flavissimus      |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Chaetodontidae | Heniochus varius           | 6              | Ryukyu Islands, Japan | Sano, M., 1989                 |
| Pomacanthidae  | Centropyge vrolikii        | 40             | Papua New Guinea | Eagle, J.V., & Jones, G. P., 2004 |
| Pomacanthidae  | Pomacanthus imperator       | >50            | Maldives          | Anderson, C. & Hafiz, A., 1987  |
| Pomacanthidae  | Pomacanthus xanthometopon   | >50            | Maldives          | Anderson, C. & Hafiz, A., 1987  |
| Pomacanthidae  | Pygoplites diacanthus       | >50            | Maldives          | Masuda, H. & Allen G.R., 1993   |
| Pomacanthidae  | Centropyge bicolar         |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Pomacanthidae  | Centropyge tibicen          |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Pomacentridae  | Chrysiptera rex             |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Labridae       | Halichoeres poroseon       |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Nemipteridae   | Scolopsis bilineata         |                | Sulawesi, Indonesia | Personal observation of feeding behavior |
| Zanclidae      | Zanclus cornutus            | 84             | Hawaii, USA       | Hobson, E. S., 1974             |

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A limitation of this study is that the data were collected over a relatively short time period. Biological assemblages are influenced by long-term changes in the local environment and thus our surveys, which were carried out in 2010, only provide a ‘snapshot’ of the predictor variables measured. There is some evidence from other studies in the WMNP carried out over the last ten years that the environmental characteristics that we measured were representative of the spatial variation between the sites. For example, sedimentation rates measured in 2002 were approximately 3 times higher at Sampela 1 than at Kaledupa and 3 times higher than at Buoy 3 [77], which is similar to our findings (sedimentation at Sampela was 3 times higher than Kaledupa and 1.5 times higher than at Buoy 3). Furthermore, monitoring data collected from six of the sites included in this study (S1, K, KDS, B3, PK, R1) by the Indonesian Institute of Marine Sciences (LIPI) and Operation Wallacea show that in 2007 mean hard coral cover was lowest at Kaledupa, followed by Sampela 1, with higher coral cover at the other sites [46]. Therefore, while further sampling of the explanatory variables would be advantageous, particularly as they are likely to vary temporally, we are confident that the data we have collected identifies the relevant spatial variation between sites.

Overall, we found that the degraded sites at Sampela supported as many sponges as the higher quality reefs, although this assemblage had low evenness and was effectively dominated by a single sponge species. Interestingly, despite a major decline in coral cover from 35–40% to currently less than 10% over the last decade, and large declines in herbivorous fish abundance [78], there does not appear to have been any phase shift to an algal-dominated system, which might have been predicted [11]. It is also interesting to note that, sponge densities at Sampela recorded in 2004 were lower (between 60–80 sponges m⁻²), than the present study, suggesting potential increases in sponge abundance over the last decade as coral cover has declined [25]. The fact that the Sampela sites have seen major declines in coral abundance (from >30% to 8–11%) [66] and that sponge abundance appears to have increased provides evidence that the system might be moving to a more sponge-dominated state. Alternatively, sponges may have always been abundant at these sites and persisted as corals have declined in response to environmental degradation, although this explanation seems unlikely given overall sponge abundance was similar at degraded and high quality reefs, yet diversity was much reduced at the degraded site and dominated by one, apparently sediment tolerant species. Based on our study, and from increasing evidence in the literature e.g. [18,19], sponge-dominated systems should be considered as a credible future trajectory for some coral reefs [13], and particularly those experiencing heavy sedimentation.

Supporting Information

Figure S1 Species accumulation curve. Species accumulation curve showing the expected mean number of observed species (plus 95% CI) for sample sizes ranging from 1–15 quadrats. For each sample size the means and 95% CI of the species count are obtained from the species observed in 10000 random selections of that samples size from the original 15 quadrats. The dashed line shows the total number of species across the 15 quadrats (n = 58) and the dotted line illustrates the species count for six quadrats. (TIF)

Figure S2 Species abundance curves. Species abundance curves for each study site showing the abundances of all the species observed at each study site ranked from highest to lowest abundance. (TIF)

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Author Contributions

Conceived and designed the experiments: ALP [JB DJS LHJ]. Performed the experiments: ALP [JB]. Analyzed the data: ALP [TJ]. Contributed reagents/materials/analysis tools: ALP [DJS JB]. Wrote the paper: ALP [JB DJS TJ]. Sponge sample identification: JB.

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