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Sponge community composition in the Derawan Islands, NE Kalimantan, Indonesia

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Abstract

Coral reef ecosystems in Indonesia are among the most diverse in the world. Conservation, restoration and management of marine biodiversity hotspots such as Indonesia's coral reefs require accurate baseline knowledge of the constituent species and the environmental conditions under which these species thrive. Here we present a study on the habitat structure and diversity, composition and abundance of reef sponges in the Derawan Islands, East Kalimantan, Indonesia. Mean live coral cover across depths and sites was just under 30%, while the mean cover of rubble and dead coral exceeded 40%. The distribution of live coral cover was patchy; although lower inshore, some offshore sites had very low coral cover due to the effects of blast fishing. Rubble cover was highest inshore and beyond the barrier reef, whereas dead coral was most abundant in shallow-water and midshore reefs. A total of 168 sponge species or morphospecies were identified, of which *Stelletta clavosa*, *Lamellodysidea herbacea*, *Niphates* sp., *Ircinia ramosa* and *Petrosia nigricans* were the most common. Sponge composition varied in relation to distance from the Berau River and water visibility, in addition to sand cover and cover of encrusting corals. Importantly, sponges in the Derawan Islands appeared to thrive in inshore reefs that already had depauperate coral communities. This is in marked contrast to findings elsewhere in Indonesia (NW Java, SW Sulawesi) where inshore communities were depauperate for all taxa sampled.

Key words: Sponges • Coral reefs • Marine diversity • East Kalimantan • Berau

Introduction

Indonesian coral reefs are among the most diverse and threatened in the world. Proper conservation and management of Indonesia's coral reefs requires accurate baseline studies of the constituent taxa and environmental conditions (Mora et al. 2003). The acquisition of spatially explicit environmental data is essential to understand how spatial and environmental processes (including human-induced disturbance) interact to structure marine assemblages. Most reef surveys have tended to focus on charismatic groups such as corals or fishes and have generally taken place in areas which have already experienced massive losses in biodiversity and shifts in composition as a result of historical disturbances. In the Thousands Islands, NW Java, for example, historical coral collections were compared with recent reef surveys (van der Meij et al. 2009) and revealed that the diversity of corals has declined dramatically over a time span of only ca. 70 yr. Once diverse reefs close to the city of Jakarta had in fact virtually disappeared by 1995. Other studies, close to the city of Makassar (SW Sulawesi), reflected these findings in identifying a strong onshore–offshore gradient in composition with depauperate communities close to the city (Becking et al. 2006, Cleary et al. 2008). In addition to studying a wide array of coral reef taxa and using the limited historical data available to compare coral reef environments, it is also important to study the few remaining relatively undisturbed areas.

The Berau Delta and barrier reef system in East Kalimantan (Derawan Islands), Indonesia, is an intricate coastal system with a variety of coastal landforms and associated ecosystems. The Berau River basin and delta is composed of 2 major estuaries and is surrounded by mangrove forest. At the delta-front there is a barrier reef system that extends to the offshore islands of Kakaban and Maratua with oceanic reefs that border the Makassar Strait (Tomascik et al. 1997). Although the coastal region is reported to still have a number of relatively pristine characteristics, fish and shrimp ponds are gradually replacing the natural coastal vegetation and offshore reefs are becoming increasingly damaged by destructive, albeit illegal, fishing techniques such as blast fishing (Ismuranty 2003, Estradivari 2008). Furthermore, the Derawan Islands are unique and of global interest due to the presence of several marine lakes located within the islands of Kakaban and Maratua (Tomascik et al. 1997, Becking & Lim 2009, CHAPTERS 1, 3 & 4). In addition to the lakes, the Derawan chain contains Indonesia's largest nesting site of the endangered green sea turtle.

In the present study, we assessed the habitat structure (e.g. cover of branching coral, massive coral, sand or rubble), abiotic environmental variables (e.g. temperature, salinity, pH) and composition and abundance of larger reef sponges. Sponges have often been left out of biodiversity surveys because of difficulties in identifying taxa, even at higher taxonomic levels. They are, however, an important coral reef benthic group, and play a key role in nutrient cycling, water filtering, bioerosion, reef stabilization, spatial competition and as habitat for other reef invertebrates (Aerts & van Soest 1997, Skilleter et al. 2005, Wulff 2006, Bell 2008). The loss of sponge species could accelerate declines in coral reefs as they are fundamental in increasing water clarity, binding live corals to the reef frame and facilitating reef regeneration (Wulff 2006, Bell 2008). The aims of the present study were to: (1) assess to what extent the reefs of the Derawan Islands are undisturbed by quantifying the area of live coral cover and other structural components, including coral rubble and dead coral; (2) quantify spatial variation in sponge composition, abundance and species richness across a large spatial scale; and (3) quantify to what extent variation in composition can be explained by abiotic environmental variables, habitat structure variables or purely spatial variables.

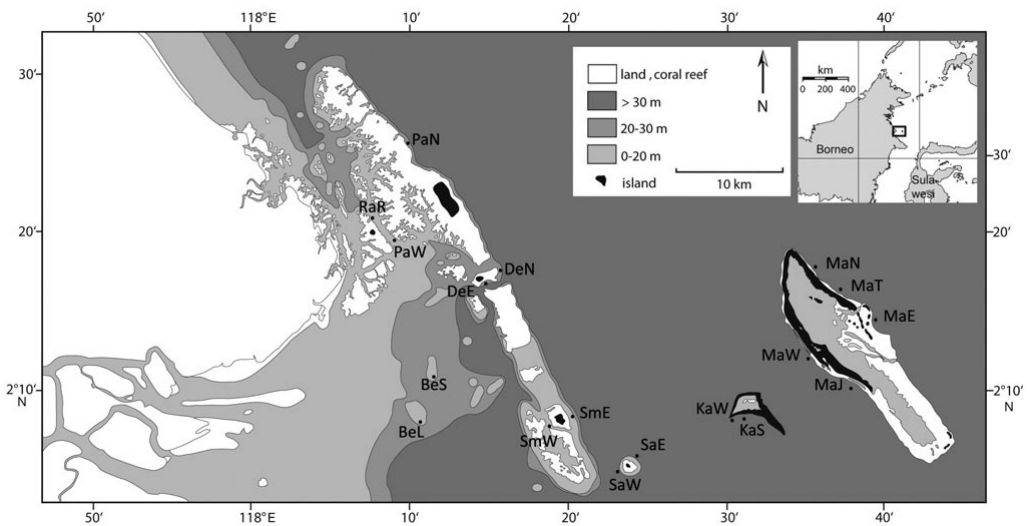


Figure 1. Derawan Islands, East Kalimantan, Indonesia. BeL: Berau 'Lighthouse'; BeS: Berau South; DeE: Derawan 'Jetty Point'; DeN: Derawan 'Coral Garden'; KaS: Kakaban Southwest; KaW: Kakaban West; MaN: Maratua Northwest; MaE: Maratua 'Midnight Snapper'; MaW: Maratua 'Traffic'; MaT: Maratua 'Parade'; MaJ: Maratua 'Johnny's Reef'; PaW: Panjang West; PaN: Panjang Northeast; RaR: Rabu Rabu; SmE: Samama East; SmW: Samama West; SaE: Sangalaki East; SaW: Sangalaki West. Site information provided in Table 1. Map adapted from Renema (2006a) with permission.

Materials & Methods

Study area. Research for the present study took place in the Derawan Islands, NE Kalimantan, Indonesia. Coral reefs in this area are found across a water gradient from fluvially influenced to fully oceanic, separated by a barrier reef. The reefs inside the barrier reef are under direct influence of the Berau River, and the river plume can extend 15 to 30 km from the mainland during the rainy season. The depth of the coral reefs inside the barrier reef varies from 10 m close to the river mouth to more than 150 m close to the barrier. Inshore reefs have a relatively low coral cover, with high densities of filter feeders such as sponges, soft corals and crinoids, and the rubble is covered by fine mud and silt (Renema 2006a). The outside barrier is comprised of diverse reef types, dominated by dense stands of corals and coarse sand. The annual rainfall in Berau is approximately 2000 mm with no particular rainy season, though there is less rainfall June–September (average 110–125 mm per month) compared to the rest of the year (average 150–200 mm per month) and an increase of strong winds from the North between December–March (Tomascik et al. 1997, Mantel 2001, Renema 2006).

Sponges. Sampling took place using SCUBA diving from 10 to 23 August 2008. Surveys were made at 2 depths (5 and 10 m) at 18 different sites (Fig. 1, Table 1). Sponge species and their abundance were noted in 1 m² quadrats laid every 1 m along a 30 m line-transect. Smaller (cryptic, boring and thinly encrusting) sponge specimens were excluded from the present study. Species were visually identified in the field, and fragments of all species were collected for closer examination and identification to species level by N. J. de Voogd. ethyl alcohol and deposited in the Porifera collection of Naturalis Biodiversity Center (RMNH POR.).

Environmental variables. Vertical water visibility, temperature, pH, salinity and depth were assessed as local abiotic environmental variables. Vertical water visibility was measured using a Secchi disc following English et al. (1994) at around 12:00 h near the surveyed sites. Depth was measured using a computerized depth meter (Suunto). Geographic coordinates were recorded at each transect with a handheld GPS device (Garmin GPS 60). Temperature, salinity and pH were measured with an YSI Model 63 handheld pH, conductivity, salinity and temperature system. In addition to these variables, we also include the distance of each site to the mouth of the Berau River. We assumed this was a proxy of processes including sedimentation and land-based contamination, as the Berau River is the main conduit of these factors into the research area.

Habitat structure. The habitat structure was assessed during the line intercept transect (LIT) method for surveys (English et al. 1994, Edinger & Risk 2000). In the present study, the cover of 28 life forms (see English et al. 1994) was assessed along two 30 m line transects located at 5 and 10 m depth in each site. The life forms (including non-living substrate) were hard dead coral (dead coral, dead coral with algae), *Acropora* corals (branching, encrusting, submassive, digitate, tabular), non-*Acropora* corals (branching, encrusting, foliose, massive, submassive, mushroom, *Heliopora*, *Millepora*, *Tubipora*); other fauna (soft corals, sponges, zoanthids and other invertebrate taxa); algae (algal assemblages, coralline algae, *Halimeda*, macroalgae, turf algae); and abiotic (sand, rubble, rock). The LIT method was used to estimate the cover of a life form and non-living substrate, in this case along a 30 m transect. The cover or percentage was calculated by the fraction of the length of the line that was intercepted by the life form in question.

Analytical framework. All analyses were performed and figures were made using R (www.r-project.org). For rarefaction and estimation of species richness using the Chao1 and Chao2 richness estimators, we used the *vegan* and *fossil* packages, respectively. Two ordination techniques were used to analyse the species: environmental and spatial data matrices. Principal components analysis (PCA) was used as an unconstrained ordination technique to explore the major axes of variation in the species $\times$ sites data matrix. Redundancy analysis (RDA) was used as a constrained ordination technique to relate sponge species to environmental variables (Legendre & Gallagher 2001). Input for the PCA and RDA consisted of $\log_e(x + 1)$ species abundance data that were first transformed using the *decostand* function in the *vegan* package. Through this transformation, the species abundance data were adjusted so that the PCA and RDA preserved the chosen distance among objects (sample sites). In the present case, the Hellinger distance was used, as recommended by Legendre & Gallagher (2001).

Spatial variation in the study area was modelled using principal coordinates of neighbor matrices (PCNM). PCNM is a novel method for quantifying spatial trends across a range of scales and is based on eigenvalue decomposition of a truncated matrix of geographic distances among sampling sites (Borcard & Legendre 2002). For a detailed description of PCNM, see Borcard & Legendre (2002) and Dray et al. (2006). Significant PCNM eigenvectors were selected using the *quickPCNM* function with 999 permutations. Significant environmental and habitat structure variables were selected using the *forward.sel* function in the *packfor* package with 999 permutations. (Both *quickPCNM* in the PCNM library and *packfor* are available at the website of Pierre Legendre, www.bio.umontreal.ca/legendre/indexEn.html). The forward selection test used was based on a novel forward selection procedure that corrects for the inflated Type I error and overestimation of explained variance associated with classical forward selection (Blanchet et al. 2008). All significant PCNM, environmental and spatial variables were used in an RDA using the *rda-Test* function (www.bio.umontreal.ca/legendre/indexEn.html). Finally, we used variance partitioning (with the *varpart* function in *vegan*) to partition the variance explained by spatial, environmental and habitat structure variables.

Table 1. Characteristics of all transects sampled during the course of this study. Distance river: distance from the mouth of the River Berau, Lat: latitude in decimal degrees, Long: longitude in decimal degrees. Abundance: number of individual sponges sampled, Richness: rarefied number of species observed based on the minimum number of individuals sampled on a transect (n = 35). Life form data representing the percentage cover of coralline algae, turf algae, dead corals, rubble, sand, sponges and all live corals combined are also presented.

Site code	Location	Depth (m)	Visibility (m)	pH	T (°C)	Salinity (ppt)	Distance river (km)	Lat
BeL	Berau 'Lighthouse'	5	6.5	8.24	28.8	33	9.66	2.16
BeL	Berau 'Lighthouse'	10	6.5	8.21	28.9	33.55	9.66	2.16
RaR	Rabu-Rabu	5	7.5	8.25	28.85	33.8	11.02	2.35
RaR	Rabu-Rabu	10	7.5	8.215	28.9	33.8	11.02	2.35
BeS	Berau 'South'	5	8	8.24	28.95	32.95	12.43	2.20
BeS	Berau 'South'	10	8	8.195	28.85	33.35	12.43	2.20
PaW	West Panjang	5	11	8.235	28.75	33.6	13.86	2.33
PaW	West Panjang	10	11	8.18	28.6	33.6	13.86	2.33
PaN	Northeast Panjang	5	21	8.285	28.9	33.95	16.66	2.43
PaN	Northeast Panjang	10	21	8.255	28.95	33.9	16.66	2.43
DeE	Derawan 'Jetty Point'	5	21.5	8.29	28.6	34	19.40	2.28
DeE	Derawan 'Jetty Point'	10	21.5	8.25	28.6	34	19.40	2.28
DeN	Derawan 'Coral Garden'	5	26	8.295	29.4	34.1	21.00	2.30
DeN	Derawan, Coral Garden	10	26	8.26	28.9	34.05	21.00	2.30
SmW	West Samama	5	13	8.225	28.75	33.6	26.18	2.13
SmW	West Samama	10	13	8.185	28.65	33.8	26.18	2.13
SmE	East Samama	5	24.5	8.26	28.85	33.9	28.86	2.13
SmE	East Samama	10	24.5	8.21	28.8	33.75	28.86	2.13
SaW	West Sangalaki	5	25	8.23	28.65	34	34.49	2.09
SaW	West Sangalaki	10	25	8.195	28.7	34.05	34.49	2.09
SaE	East Sangalaki	5	28.5	8.26	28.7	33.15	35.89	2.09
SaE	East Sangalaki	10	28.5	8.21	28.75	34.1	35.89	2.09
KaS	Southwest Kakaban	5	41.5	8.25	28.45	34.15	47.11	2.14
KaS	Southwest Kakaban	10	41.5	8.205	28.25	34.05	47.11	2.14
KaW	West Kakaban	5	40	8.27	28.15	34.15	48.02	2.14
KaW	West Kakaban	10	40	8.24	28.05	34.1	48.02	2.14
MaW	West Maratua 'Turtle traffic'	5	45.5	8.265	28.8	33.95	56.69	2.20
MaW	West Maratua 'Turtle traffic'	10	45.5	8.24	28.8	33.75	56.69	2.20
MaJ	Southwest Maratua 'Johnny's Reef'	5	41	8.29	28.8	34	61.88	2.17
MaJ	Southwest Maratua 'Johnny's Reef'	10	41	8.245	28.2	34.1	61.88	2.17
MaN	Northeast Maratua 'Macronesia'	5	42.5	8.245	28.9	33.65	56.87	2.29
MaN	Northeast Maratua 'Macronesia'	10	42.5	8.225	28.9	33.45	56.87	2.29
MaT	East Maratua 'Turtle parade'	5	46.5	8.295	29	33.9	60.57	2.26
MaT	East Maratua 'Turtle parade'	10	46.5	8.255	29	33.9	60.57	2.26
MaE	Southeast Maratua 'Midnight snapper'	5	27.5	8.225	29.3	33.6	63.63	2.24
MaE	Southeast Maratua 'Midnight snapper'	10	27.5	8.22	29.05	33.65	63.63	2.24

Long	Abundance	Richness	Coraline algae (%)	Turf algae (%)	Dead coral (%)	Rubble (%)	Sand (%)	Sponge (%)	Total coral (%)
118.17	161.00	14.79	0.00	3.00	6.00	5.33	8.00	16.00	25.67
118.17	231.00	18.29	1.17	0.50	0.00	38.50	7.17	16.33	4.50
118.13	163.00	19.48	0.00	2.00	9.67	24.33	9.00	9.67	34.67
118.13	205.00	21.05	1.50	8.00	5.67	33.50	10.83	3.50	30.00
118.19	321.00	18.54	1.00	0.33	5.70	19.50	17.00	12.47	22.67
118.19	270.00	13.13	2.67	0.00	1.83	11.00	10.33	10.63	53.37
118.18	224.00	15.54	0.00	0.00	8.33	18.00	9.00	11.50	41.00
118.18	141.00	20.85	0.00	0.67	1.00	57.00	7.33	3.17	22.83
118.16	100.00	14.60	4.97	0.00	10.47	47.67	4.27	1.27	23.73
118.16	283.00	15.52	3.27	2.27	4.10	36.60	2.60	6.27	16.17
118.25	106.00	15.45	0.00	0.00	19.33	54.33	11.17	0.67	9.00
118.25	132.00	13.13	5.77	0.20	12.70	33.10	17.50	2.40	27.33
118.26	110.00	14.48	3.00	0.00	24.67	9.33	9.33	4.33	35.33
118.26	312.00	18.41	8.20	0.00	17.67	16.33	3.00	3.80	33.50
118.32	174.00	13.49	0.00	0.33	19.33	8.33	6.33	3.80	51.83
118.32	135.00	15.26	4.50	0.00	8.00	23.00	20.00	1.33	34.50
118.34	122.00	16.40	2.33	1.83	11.17	11.77	1.33	0.17	33.17
118.34	211.00	15.23	1.17	0.17	10.17	25.90	32.00	4.33	14.50
118.39	58.00	14.35	0.00	0.67	52.33	19.00	0.33	0.00	23.50
118.39	140.00	10.81	1.67	2.67	47.00	10.33	10.00	3.67	20.00
118.40	101.00	14.63	0.00	0.00	63.33	6.67	0.00	2.33	20.33
118.40	187.00	16.47	3.17	1.00	23.17	15.33	2.67	5.33	36.00
118.51	117.00	18.63	1.80	0.00	16.47	16.17	0.00	4.23	54.27
118.51	444.00	19.62	11.53	0.00	4.50	14.60	0.00	17.90	34.40
118.51	953.00	2.83	0.00	0.00	8.67	71.67	0.33	1.67	15.83
118.51	794.00	5.87	2.67	0.33	12.00	35.67	3.00	1.00	42.67
118.59	159.00	14.45	0.00	1.00	36.00	33.67	0.00	2.17	21.00
118.59	199.00	17.00	2.17	0.67	13.00	31.33	0.67	8.50	31.83
118.64	194.00	14.26	14.33	0.00	7.67	14.33	3.00	5.00	42.00
118.64	260.00	16.34	14.17	0.67	8.33	9.00	0.67	6.67	32.83
118.59	114.00	13.03	1.67	2.00	38.00	26.67	0.00	0.33	29.67
118.59	259.00	16.60	4.33	1.67	6.00	32.00	0.67	3.33	27.67
118.63	35.00	14.00	1.33	4.67	13.67	13.00	0.00	3.67	55.67
118.63	170.00	16.04	3.67	28.67	14.33	21.67	0.00	1.67	13.67
118.65	65.00	6.11	1.00	5.00	22.00	48.00	2.00	0.00	7.67
118.65	160.00	13.45	5.00	8.33	19.33	23.67	4.00	5.00	19.17

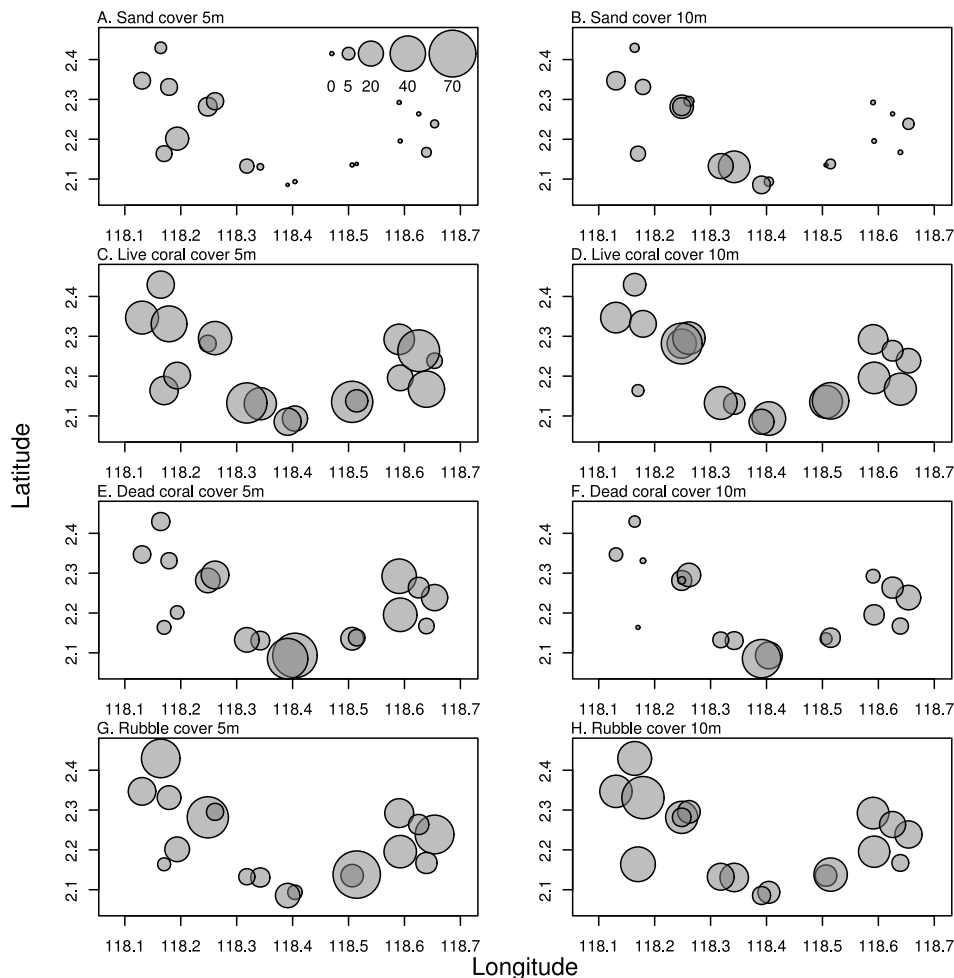


Figure 2. Cover of sand, live coral cover, dead coral and rubble across the Derawan Islands. (A) Sand at 5 m (range = 0 to 17.0%), (B) sand at 10 m (0 to 32.0%), (C) live scleractinian coral at 5 m (7.7 to 55.7%), (D) live scleractinian coral at 10 m (4.5 to 54.4%), (E) dead coral at 5 m (5.7 to 63.3%), (F) dead coral at 10 m (0 to 19.3%), (G) rubble at 5 m (5.3 to 71.7%) and (H) rubble at 10 m (9 to 57%)

Results

Live scleractinian coral cover ranged from 7.7 to 55.7% at 5 m and 5.7 to 63.3% at 10 m depth (Fig. 2, Table 1). Average live coral cover across sites and depths was 28.9%. The percentage cover of rubble was highest inshore and offshore and markedly less midshore, and across all sites ranged from 5.3 to 71.7% (at KaS; see Fig. 1 for site abbreviations) with a mean of 25.4%. Dead coral cover appeared to have quite a different pattern to rubble. Dead coral cover was higher midshore than inshore or offshore and was also somewhat higher at 5 than 10 m depth (Fig. 2). Overall, dead coral cover ranged from 0 to 63.3% with a mean of 16.1%. We sampled 7810 individual sponges and identified a total of 168 sponge species belonging to 62 genera

and 37 families (see the complete species list in Table S1 in the electronic supplement at www.int-res.com/articles/suppl/m396p169_app.pfd). The median number of individuals recorded per transect was 119.5 (range = 35 to 953 individuals) at 5 m depth and 202 (range = 132 to 794 individuals) at 10 m depth (Fig. 3). Mean sponge cover varied from 4.40% (range = 0 to 16%) at 5 m depth to 5.37% (range = 1 to 17.9%) at 10 m depth. Rarefied species richness varied from 14.17 species (range = 2.83 to 19.48 species) at 5 m depth to 15.73 species (range = 5.87 to 21.05 species) at 10 m depth (Fig. 3). Only 8 species were common (as defined by Kaandorp 1986), i.e. co-occurred in >23 different transects of the total of 36 transects (66% level of transects), namely *Carteriospongia foliascens*, *Cinachyrella* spp., *Clathria reinwardti*, *Hyrtios erectus*, *Ircinia ramosa*, *Lamellodysidea herbacea*, *Niphates* sp. 'blue' and *Petrosia nigricans*. The 10 most abundant species sampled during the present study were *Amphimedon paraviridis* (234), *Clathria reinwardti* (237), *Carteriospongia foliascens* (250), *Hyrtios erectus* (254), *Haliclona* aff. *amboinensis* (280), *Petrosia nigricans* (298), *Niphates* sp. 'blue' (304), *I. ramosa* (327), *L. herbacea* (603) and *Stelletta clavosa* (1540). The distribution of 4 of these species is shown in Fig. 4. *Haliclona* aff. *amboinensis* had a pronounced preference for inshore sites whereas *A. paraviridis* was more patchily distributed, although it attained high local abundance. The sponge *P. nigricans* was found in most sites in moderate densities. *Stelletta clavosa*, the most abundant species overall, was curiously enough only recorded in 3 transects. In one transect (DeE 5 m) only 4 individuals were recorded, whereas 645 to 891 individuals were recorded in the other 2 transects (KaW 5 m and KaW 10 m).

Species composition, based on the first 2 axes of a PCA, showed a largely inshore–offshore gradient in composition along the first (8.69% of total variation explained) and second axes (7.59% of total variation explained) (Fig. 5). The most distinct sponge assemblages were found at sites RaR 10 m (score on PC1 = 11.63) and KaS 10 m (score on PC1 = 13.28; PC2 = -15.44). Both sites had a number of species that were not recorded in any other transect (5 for RaR 10 m and 6 for KaS 10 m). One species, *Axinyssa* sp. '118', was represented by 9 individuals at KaS 10 m. In total, 38 species were only recorded at a single transect, indicating that actual diversity was higher than recorded. In addition, a total of 26 singletons and 11 duplicates were recorded at the study area. Estimates using the Chao1 and Chao2 richness estimators both yielded an expected lower bound richness of 198 species compared to the 168 species we observed. There was a significant relationship between space and community composition. Using a forward selection procedure, 5 PCNM variables were selected out of a total of 11. Significant PCNM variables are shown in Fig. S1 in the supplement. The same technique yielded 4 significant environmental variables and 4 significant habitat structure variables. Significant environmental variables included the distance from the river ($F = 3.259$, $p < 0.001$, R^2 adj = 0.061), water transparency/visibility ($F = 1.925$, $p = 0.002$, R^2 adj = 0.025), temperature ($F = 1.855$, $p = 0.002$, R^2 adj = 0.023) and pH ($F = 1.447$, $p = 0.028$, R^2 adj = 0.012). The variation in visibility is shown in Fig. S1 in the supplement, revealing an increase in visibility away from the river. Significant habitat structure variables included cover of sand ($F = 2.135$, $p < 0.001$, R^2 adj = 0.031), encrusting coral ($F = 1.643$, $p = 0.007$, R^2 adj = 0.018), turf algae ($F = 1.549$, $p = 0.011$, R^2 adj = 0.016) and rubble ($F = 1.372$, $p = 0.050$, R^2 adj = 0.011).

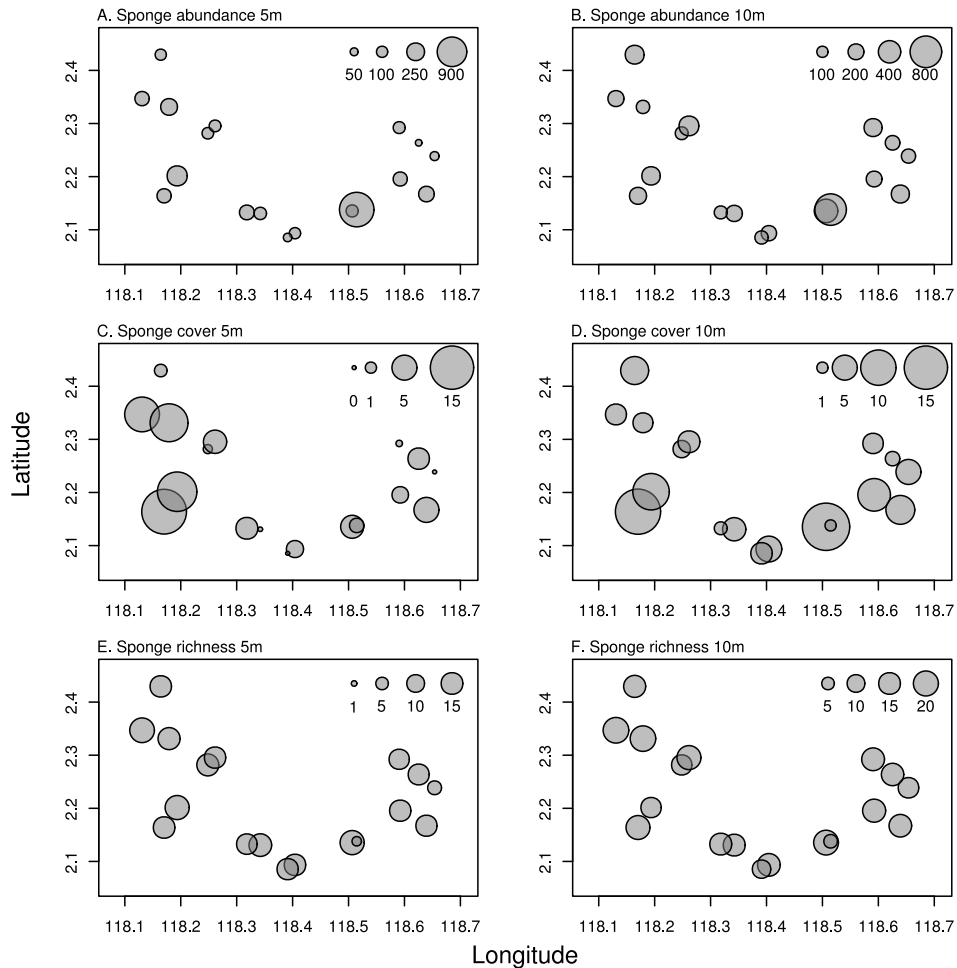


Figure 3. Abundance, cover and species richness of sponges in the Derawan Islands. (A) Sponge abundance at 5 m (range = 35 to 953 individuals per transect) and (B) 10 m across sampling sites (132 to 794 individuals per transect). (C) Sponge cover as percentage of total cover at 5 m (range = 0 to 16% per transect) and (D) 10 m across sampling sites (1 to 17.9% per transect). (E) Sponge rarefied ($n = 35$ individuals) species richness at 5 m (range = 2.83 to 19.48 species per transect) and (F) 10 m across sampling sites (5.87 to 21.05 species per transect)

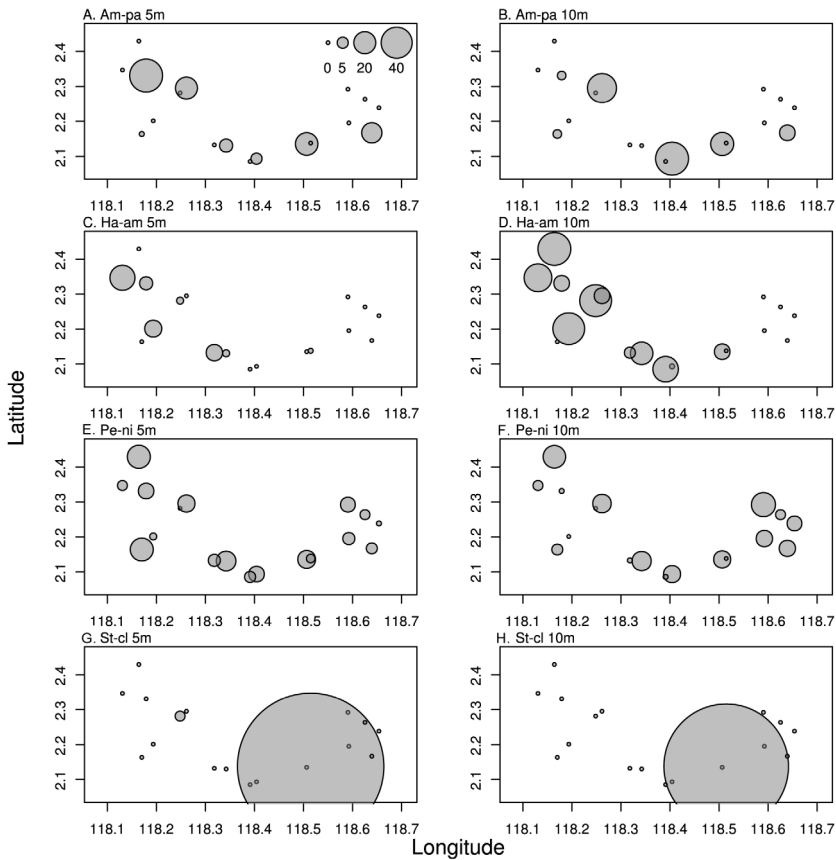


Figure 4. Variation in the abundance of selected species across the Derawan Islands. (A) *Amphimedon paraviridis* (Am-pa) at 5 m (range = 0 to 45 individuals per transect) and (B) 10 m across sampling sites (range: 0 to 26 individuals per transect). (C) *Haliclona* aff. *amboinensis* (Ha-am) at 5 m (0 to 26 individuals per transect) and (D) 10 m across sampling sites (0 to 45 individuals per transect). (E) *Petrosia nigricans* (Pe-Ni) at 5 m (0 to 22 individuals per transect) and (F) 10 m across sampling sites (0 to 24 individuals per transect). (G) *Stelletta clavosa* (St-cl) at 5 m (0 to 891 individuals per transect) and (H) 10 m across sampling sites (0 to 645 individuals per transect).

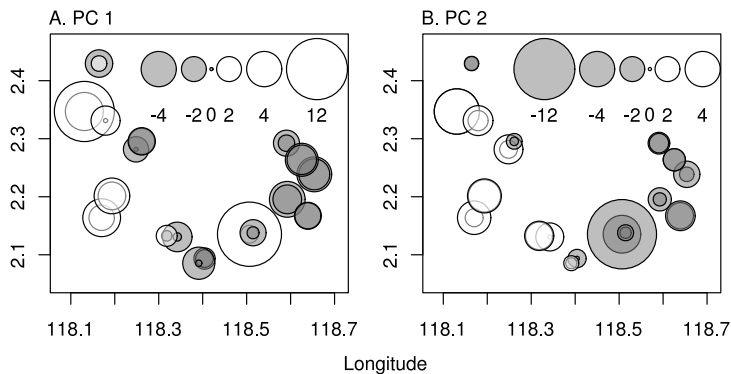


Figure 5. Variation in site scores of (A) PC1 (range: -4.12 to 13.26) and (B) PC2 (-15.44 to 6.60). Open symbols indicate positive values and shaded symbols negative values. The size of the symbol is proportional to the score

The spatial variation in community composition in relation to environmental variables is shown in Fig. 6. There was a highly significant relationship between the set of spatial, environmental and habitat structure variables and community composition ($F = 1.916$, $p < 0.001$, $R^2 = 0.531$, $R^2 \text{ adj} = 0.254$). Space, environment and habitat structure together thus explained more than 25% of the variation in composition. Space, environment and habitat structure alone explained 9, 10 and 5% of total variation in composition, respectively. The major axis of variation was determined by sites with high sand cover versus sites that were distant from the river and had good water transparency/visibility. More or less perpendicular to this axis, there was a gradient from sites with a high cover of encrusting corals to sites with high turf algae cover. Species with high values along axis 1 (high sand cover) included *Haliclona* aff. *amboinensis*, *Echinodictyum mesenterinum*, *Paratetilla* aff. *bacca* and *Stylissa carteri*, whereas species with low values along axis 1 (good water visibility) included *Placospongia melobesioides* and *Petrosia corticata*. Species with low values along axis 2 included *Niphates* sp. 'blue', *Haliclona* (*Soestella*) 'brown' and *Amphimedon paraviridis*, whereas species with high values along axis 2, thus associated with areas of relatively high rubble and turf algae cover, included *Hyrtios erectus*, *Lamellodysidea herbacea* and *Agelas* aff. *nemoechinata*.

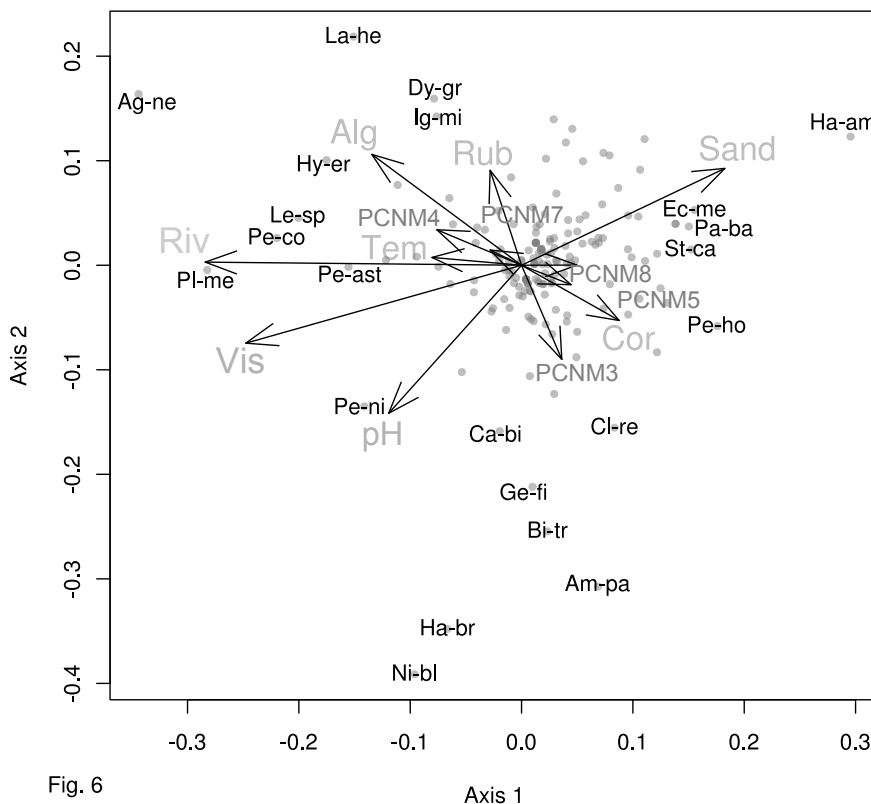


Fig. 6

Figure 6. Ordination of sponges based on redundancy analysis. Arrows represent significant spatial, habitat and environmental variables, and their direction and length indicates their contribution to variation along those axes. Significant variables include principal coordinates of neighbor matrices (PCNM) 3, 4, 5, 7 and 8, the cover of sand, encrusting corals (Cor), turf algae (Alg) and rubble (Rub), temperature (Tem), pH, water transparency/visibility (Vis) and the distance from the Berau River (Riv). Species are indicated by dots; selected species are indicated by codes: Ag-ne: *Agelas* aff. *nemoechinata*; Am-pa: *Amphimedon paraviridis*; Bi-tr: *Biemna triraphis*; Ca-bi: *Callyspongia biru*; Cl-re: *Clathria reinwardti*; Dy-gr: *Dysidea granulosa*; Ec-me: *Echinodictyum mesenterinum*; Ge-fi: *Gelliodes fibulata*; Ha-am: *Haliclona* aff. *amboinensis*; Ha-br: *Haliclona* (*Soestella*) sp.; Hy-er: *Hyrtios erectus*; Ig-mi: *Igernella mirabilis*; La-he: *Lamellodysidea herbacea*; Le-sp: *Lendenfeldia* sp.; Ni-bl: *Niphates* sp.; Pa-ba: *Paratetilla* aff. *bacca*; Pe-ast: *Petrosia* aff. *strongylata*; Pe-co: *Petrosia corticata*; Pe-ho: *Petrosia hoeksema*; Pe-ni: *Petrosia nigricans*; Pl-me: *Placospongia melobesioides*; St-ca: *Stelletta clavosa*

Discussion

In general, coastal coral reefs are being increasingly exposed to elevated nutrient and sediment loads. Terrestrial runoff is therefore a growing concern for many coral reefs across the globe and can, if unabated, lead to serious degradation (Fabricius 2005). Although the coral reefs of the Derawan Islands have always been subjected to fluctuating sedimentation rates originating from the Berau River, particle influx may have gradually increased in recent years due to intensified terrestrial runoff into the river following large-scale deforestation as a result of logging and forest fires (Siebert et al. 2001, Cleary 2003, Cleary & Mooers 2004). The combination of terrestrial-based pollution and other sources of disturbance such as blast fishing appear to have adversely affected the coral reefs of the Derawan Islands. Average live coral cover across sites and depths was only 28.9%, hardly what one would consider pristine. The combined mean cover of rubble and dead coral (41.6%) was in fact well above the mean of live coral cover. Only 4 of the 36 transects, furthermore, had more than 50% live coral cover and would thus fall into the 'good' category of Gomez & Yap (1988), whereas 15 of the 36 transects had less than 25% live coral cover and would be classified as 'poor'. Various and possibly different scenarios may be responsible for the high cover of rubble. On the more offshore islands, the rubble is almost certainly the result of illegal blast fishing, a nefarious practice that has shifted to more remote sites following increased policing of the more accessible reefs (Erdmann 1998). Inshore, in contrast, the rubble may be the remnant vestiges of coral reefs that died in the more distant past; the exact sources of disturbance that led to this demise remain unknown. The large cover of dead coral midshore and in more shallow reefs suggests a different mechanism. Among other things, this may be the result of severe coral bleaching (Brown & Suharsono 1990), a crown-of-thorns starfish outbreak (DeVantier & Done 2007), pollution such as chronic oil spills, or a combination of these factors. In NW Java, Cleary et al. (2008) also observed high dead coral cover offshore. They also noted that offshore live coral cover had dropped dramatically between surveys conducted there in 1985 and 1995. As is probably the case in the Berau region, they attributed this loss to a number of documented sources of environmental stress including a marked increase in the number of crown-of-thorns starfish observed during that time period. In the present study, the highest number of sponge species (between 45 and 57) was found at the offshore sites of Kakaban (KaS) and some inshore reefs (BeL, BeS, RaR) at both depth intervals. These results are in concordance with the high sponge cover at those locations. The inshore sites of BeL, BeS and RaR are under the direct influence of the Berau River, and were typified by low visibility (less than 6 m); these reefs were also covered by a fine layer of sand, mud and silt. Large coral colonies were scarce in these sites with only small patches of encrusting and massive corals present; the dense fields of branching and tabular corals characteristic of many offshore sites were virtually absent. The marked absence of branching and tabular corals such as *Montipora* spp. and *Acropora* spp. from inshore sites is in line with findings that these species are less resilient to environmental stress than other corals such as the massive *Porites* (Edinger & Risk 2000).

Environmental conditions in the Derawan Islands appeared to have a positive effect on filter-feeding heterotrophic benthic taxa, in contrast to corals. Not only did we observe the highest number of sponge species, including numerous records of unique species, at the inshore reefs, the sponge individuals also tended to be larger at these sites. In particular, the species *Echinodictyum mesenterinum*, *Ianthella basta*, *Iotrochota purpurea* and *Xestospongia testudinaria* attained larger sizes close to the river. This pattern was in marked contrast to other studies of the inshore sponge fauna in NW Java and SW Sulawesi (de Voogd et al. 2006, de Voogd & Cleary 2008). In both of these areas, the inshore sponge fauna was markedly depauperate compared to the offshore fauna, indicating that urban-related disturbances have had an overwhelming impact on all

taxa of inshore reefs adjacent to the large cities of Jakarta and Makassar. The inshore reefs of the Derawan Islands had very low live coral cover, but the lack of a major conurbation and thus severe environmental stress has enabled other taxa to flourish and to a large extent occupy space that presumably was previously occupied by coral. In inshore sites close to Jakarta, for example, the majority of the substrate consisted of sand and turf algae (Cleary et al. 2008). The lowest number of sponge species was found at several sites at the eastern side of the offshore Maratua atoll. The eastern side of Maratua borders the Makassar Strait, and has a narrow reef crest with a well developed spur-and-groove zone in contrast to the wide reef on the western side (up to 300 m) (Tomascik et al. 1997). The eastern reef crest abruptly drops to several hundred meters and has a maximum visibility of more than 45 m. The reefs of the southeastern sides of Maratua have, however, been heavily damaged by blast fishing, and long patches of unstable coral rubble probably prevent recolonization of benthic taxa (Fox & Caldwell 2006). Some sites had very high rubble cover including MaE (almost 50% rubble) due to blast fishing, but this did not appear to have a pronounced effect on sponge composition. However, the sponges that we observed in these rubble fields were, in general, small and had the tendency to glue loose pieces of rubble together. These species may therefore play a hitherto undescribed, but important, role in consolidating the coral rubble and thus facilitating reef regeneration.

A total of 38 (22%) unique species (only found in a single transect) and a high number of singletons (26 species) were observed indicating that actual diversity is higher than recorded. Many of these unique species and singletons are new records for Indonesia or have not yet been described. Van Soest (1989) showed that different geographic regions within the Indo-West Pacific all have some endemic species but are, in the complement of their common species, very similar. Indeed, many of 59 mentioned common species observed by van Soest (1989) at various localities were found in the Berau region. Within a sponge community, some species can be self-seeding and are important for maintaining the local sponge population, whereas others may act as a source for downstream regions. For example, *Amphimedon paraviridis* showed a more patchy distribution across the Derawan Islands and was sometimes locally abundant. This species was also very common in the Spermonde Archipelago, whereas it has only been sporadically observed from other regions within Indonesia. *Haliclona* aff. *amboinensis* had a pronounced preference for the more inshore sites, whereas *Petrosia nigricans* was found in most sites in moderate densities. The species *Stelletta clavosa* accounted for a high proportion of the total sponge abundance; however, this was largely due to very high abundances on 2 transects, at 5 and 10 m depth, near the island of Kakaban (KaS), where more than 500 individuals were recorded at both depth intervals. The southeastern side of Kakaban consists of a steep carbonate wall, where to the east the coral reef is interrupted by valleys of fine coral rubble overgrown with macroalgae (Renema 2006a,b). The fine coral rubble is highly unstable, and the small globular *S. clavosa* seems good at attaching to this substrate and as such is able to dominate the local sponge assemblage. Quantitative studies on sponges in the Indo-Pacific region remain rare. However, in the Dampier Archipelago, Fromont et al. (2006) observed pronounced spatial heterogeneity in species composition. Composition varied with environmental factors such as substrate type, aspect, substrate configuration and depth. Likewise, in the central Torres Strait, Duckworth & Wolff (2007) found strong variation in the composition of dictyoceratid sponges across small spatial scales. They concluded that these patterns were largely species-specific and were explained by localised disturbance events, differences in food availability and patterns of water transport affecting larval dispersal.

Space, abiotic environmental conditions and habitat all contributed to structuring sponge assemblages across the Derawan Islands. Both spatial and abiotic environmental variables, however, explained more variation than local habitat structure. The most important habitat structure variables were sand cover and encrusting

coral cover. There appeared to be a clear effect of the river on the cover of sand, with sites closer to the river having a higher sand cover. The cover of encrusting corals and turf algae was, in contrast, patchier, while the cover of coral rubble was higher at the most inshore and offshore sites. Generally, sand dominated sites are associated with a low density and diversity of constituent species (Nakamura & Sano 2005, Carballo 2006). Sand cover in the Derawan Islands, however, did not exceed 17% at 5 m depth and 32% at 10 m depth, compared to a high of >90% for inshore reefs in Jakarta Bay (Cleary et al. 2008). The most important abiotic environmental variables were distance from the Berau River and water visibility. Depth proved to be a poor predictor of variation in composition, in contrast to expectations: in previous studies, the diversity of coral reef sponges increased with depth (Adjeroud 1997, Hooper & Kennedy 2002, de Voogd et al. 2006, Fromont et al. 2006). Lesser (2006) suggested that food supply and, therefore, bottom-up processes significantly influenced the distribution and abundance of sponges with increasing depth in coral reefs located in Florida, Belize and the Bahamas. In the present study, rarefied species richness did not vary much between the 2 depth intervals. Remarkably, at a depth of 5 m, sponge cover was higher at the sites closer to the river than further away from the river. Our results may be explained by the pronounced onshore–offshore gradient in water visibility; much less light, for example, reached inshore reefs at 5 m than reached offshore reefs at 10 m. In marine environments, there are often pronounced depth-related gradients in a number of environmental parameters, including current velocity and temperature, but one of the most biologically important parameters is the amount of photic energy, which generally decreases with depth.

Although our set of spatial, environmental and habitat structure variables were able to explain a significant amount of spatial variation in sponge composition, a large amount of variation remained unexplained. In addition to previously mentioned factors that may be operating at different spatial scales, there are a number of unmeasured sources of variation. Biotic processes such as predation and competitive interaction play an important role in the population dynamics and size structure of sponges on coral reefs (Duffy & Paul 1992, Aerts & van Soest 1997). In addition to biotic processes, large-scale oceanographic processes or local physical differences that change with depth, such as flow velocities, might also structure sponge assemblages (Wilkinson & Evans 1989, Lesser 2006). In conclusion, we found a highly significant relationship between the variation in sponge species composition and a set of spatial, environmental and habitat structure variables in the research area. Sponge diversity and abundance is notably high when compared to other surveyed coral reefs within the Indonesian Archipelago (van Soest 1989, Bell & Smith 2004, de Voogd et al. 2006, Cleary & de Voogd 2007).

Although disturbances, including riverine transport of sediments and nutrients inshore and blast fishing offshore, have adversely affected coral cover and composition, these disturbances do not appear to have had a seriously adverse effect on sponge diversity and composition. The distinct difference in the impact of disturbance on corals and other benthic taxa differs from that found in areas close to major conurbations and merits further study.

Acknowledgements

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Supplementary material

Sponge community composition in the Derawan Islands, NE Kalimantan, Indonesia

Systematic list of sponge species observed at the sampled locations in the the Derawan Islands.

Demospongiae

Homosclerophorida

Plakinidae

Corticium niger Pulitzer-Finali, 1996

Plakortis lita (de Laubenfels, 1954)

Plakortis nigra Lévi, 1953

Spirophorida

Tetillidae

Cinachyrella australiensis (Carter, 1886)

Cinachyrella sp.

Paratetilla merguensis (Carter, 1883)

Astrophorida

Ancorinidae

Dercitus (Halinastra) berau van Soest, Beglinger, de Voogd, 2010

Jaspis splendens (de Laubenfels, 1954)

Melophlus sarassinorum Thiele, 1899

Penares sollasi Thiele, 1900

Rhabdastrella globostellata (Carter, 1883)

Stelletta clavosa Ridley, 1884

Stelletta sp.

Geodiidae

Erylus aff. *lendenfeldi* Sollas, 1888

Hadromerida

Clionidae

Sphaciospongia vagabunda (Ridley, 1884)

Placospongiidae

Placospongia melobesioides Gray, 1867

Placospongia aff. *carinata* (Bowerbank, 1858)

Suberitidae

Aptos suberitioides Brønsted, 1934

Suberites aff. *diversicolor* Becking & Lim, 2009

Tethyidae

Tethya cf. *seychellensis* (Wright, 1881)

‘Lithistid’ Demospongiae

Theonellidae

Theonella swinhoei Gray, 1868

Theonella mirabilis (de Laubenfels, 1954)

Scleritodermidae

Aciculites aff. *ciliate* (Wilson, 1925)

Poecilosclerida

Microcionina

Microcionidae

Clathria (Clathria) basilana Lévi, 1961
Clathria (Isociella) eccentrica (Burton, 1934)
Clathria (Thalysias) cervicornis (Thiele, 1903)
Clathria (Thalysias) reinwardti Vosmaer, 1880
Clathria (Thalysias) vulpina (Lamarck, 1813)
Clathria (Wilsonella) mixta Hentschel, 1912
Echinochalina (Protophlitaspongia) mucronata (Topsent, 1897)

Raspailiidae

Echinodictyum mesenterinum (Lamarck, 1814)
Endectyon (Endectyon) fruticosum aruense Hentschel, 1912
Thrinacophora cervicornis Ridley & Dendy, 1886

Rhabderemiidae

Rhabderemia forcipula (Lévi & Lévi, 1989)
Rhabderemia aff. *indica* Dendy, 1905

Myxillina

Chondropsidae
Chondropsis sp.

Coelosphaeridae

Lissodendoryx (Acanthodoryx) fibrosa (Lévi, 1961)

Crambeidae

Monanchora dianchora de Laubenfels, 1935

Iotrochotidae

Iotrochota baculifera Ridley, 1884
Iotrochota purpurea (Bowerbank, 1875)

Mycalina

Desmacellidae

Biemna aff. *humilis* Thiele, 1903
Biemna trirhaphis (Topsent, 1897)
Biemna / *Stelletta* sp.

Esperiopsidae

Ulosa aff. *ada* (de Laubenfels, 1954)

Mycalidae

Mycale (Naviculina) flagellifera Vacelet & Vasseur, 1971
Mycale (Arenochalina) aff. euplectelloides (Row, 1911)
Mycale (Mycale) vansoesti Calcinai, Cerrano, Totti, Romagnoli & Bavestrello, 2006

Podospongiidae

Diacarnus megaspinorhabdosa Kelly-Borges & Vacelet, 1995

Isodictyidae

Coelocarteria agglomerans Azzini, Calcinai & Pansini, 2007

Halichondrida

Axinellidae

Ptilocaulis aff. *fusiformis* Lévi, 1967

Dictyonellidae

Acanthella cavernosa Dendy, 1922
Acanthella aff. *cavernosa* Dendy, 1922
Dictyonella sp.
Liosina paradoxa Thiele, 1899

- Stylissa carteri* Dendy, 1889
Stylissa sp.
- Halichondriidae
Axinyssa aff. *aplysinoidea* Dendy, 1922
Axinyssa spp.
Halichondria cartilaginea Esper, 1794
Halichondria (*Halichondria*) sp.
- Heteroxyidae
Didiscus sp.
Higginsia mixta Hentschel, 1912
Myrmekioderma granulata (Esper, 1794)
- Agelasida**
- Agelasidae
Agelas ceylonica Dendy, 1905
Agelas aff. *nemoechinata* Hoshino, 1985
Agelas nakamurai Hoshino, 1985
- Haplosclerida**
- Haplosclerina**
- Callyspongiidae
Callyspongia (*Cladochalina*) *aerizusa* Desqueyroux-Faundez, 1984
Callyspongia (*Cladochalina*) aff. *confoederata* Ridley, 1884
Callyspongia (*Cladochalina*) *joubini* (Topsent, 1897)
Callyspongia (*Cladochalina*) *samarensis* (Wilson, 1925)
Callyspongia (*Cladochalina*) aff. *subarmigera* (Ridley, 1884)
Callyspongia (*Toxohalina*) aff. *ramosa* (Gray, 1843)
Callyspongia (*Euplacella*) *biru* de Voogd, 2004
Callyspongia spp.
- Chalinidae
Chalinula confusa (Dendy, 1922)
Chalinula hooperi (Bakus & Nishiyama 2000)
Cladocroce acuelata Pulitzer-Finali, 1982
Cladocroce sp.
Haliclona (*Gellius*) aff. *amboinensis* Lévi, 1959
Haliclona (*Gellius*) *cymaeformis* (Esper, 1794)
Haliclona (*Gellius*) sp.
Haliclona (*Halichoclona*) *vanderlandi* de Weerd & van Soest, 2001
Haliclona (*Reniera*) *fascigera* Hentschel, 1912
Haliclona (*Reniera*) *poseidon* (de Laubenfels, 1954)
Haliclona (*Soestella*) sp.
Haliclona spp.
- Niphatidae van Soest, 1980
Amphimedon paraviridis Fromont, 1988
Cribochalina sp.
Dasyschalina fragilis Ridley & Dendy, 1886
Gelliodes fibulata (Carter, 1881)
Gelliodes aff. *hamata* (Thiele, 1903)
Gelliodes spp.

Niphates olemda (de Laubenfels, 1954)

Niphates spp.

Pachychalina sp. Schmidt, 1868

Petrosina

Phloeodictyidae

Aka sp.

Oceanapia sagittaria Sollas, 1902

Petrosiidae

Acanthostrongylophora ingens (Thiele, 1899)

Neopetrosia exigua (Kirkpatrick, 1900)

Neopetrosia aff. *carbonaria* (Lamarck, 1814)

Neopetrosia spp.

Petrosia (*Petrosia*) *alfiani* de Voogd & van Soest, 2002

Petrosia (*Petrosia*) *hoeksemai* de Voogd & van Soest, 2002

Petrosia (*Petrosia*) aff. *microxea* (Vacelet, Vasseur & Lévi, 1976)

Petrosia (*Petrosia*) *nigricans* Lindgren, 1897

Petrosia (*Strongylophora*) *corticata* (Wilson, 1925)

Petrosia (*Strongylophora*) aff. *strongylata* Thiele, 1903

Xestospongia aff. *mammillata* Pullitzer-Finali, 1982

Xestospongia vansoesti Bakus & Nishiyama, 2000

Xestospongia testudinaria (Lamarck, 1813)

Xestospongia spp.

Dictyoceratida

Irciniidae Gray, 1867

Ircinia ramosa Keller, 1889

Ircinia spp.

Thorectidae Bergquist, 1978

Thorectinae

Cacospongia mycofijiensis (Kakou, Crews & Bakus, 1987)

Dactylospongia elegans (Thiele, 1899)

Fascaplysinopsis reticulata (Hentschel, 1912)

Hyrtios erectus Keller, 1889

Hyrtios reticulatus Thiele, 1899

Hyrtios sp.

Luffariella variabilis (Polejaeff, 1884)

Semitaspongia sp.

Phyllospongiinae

Carteriospongia foliascens (Pallas, 1766)

Lendenfeldia sp.

Phyllospongia papyracea (Esper, 1806)

Phyllospongia aff. *lamellose* (Esper, 1794)

Strepsichordaia aliena Wilson, 1925

Spongiidae

Hippospongia sp.

Leiosella ramosa Bergquist, 1995

Spongia (*Spongia*) *ceylonensis* Dendy, 1905

Dysideidae

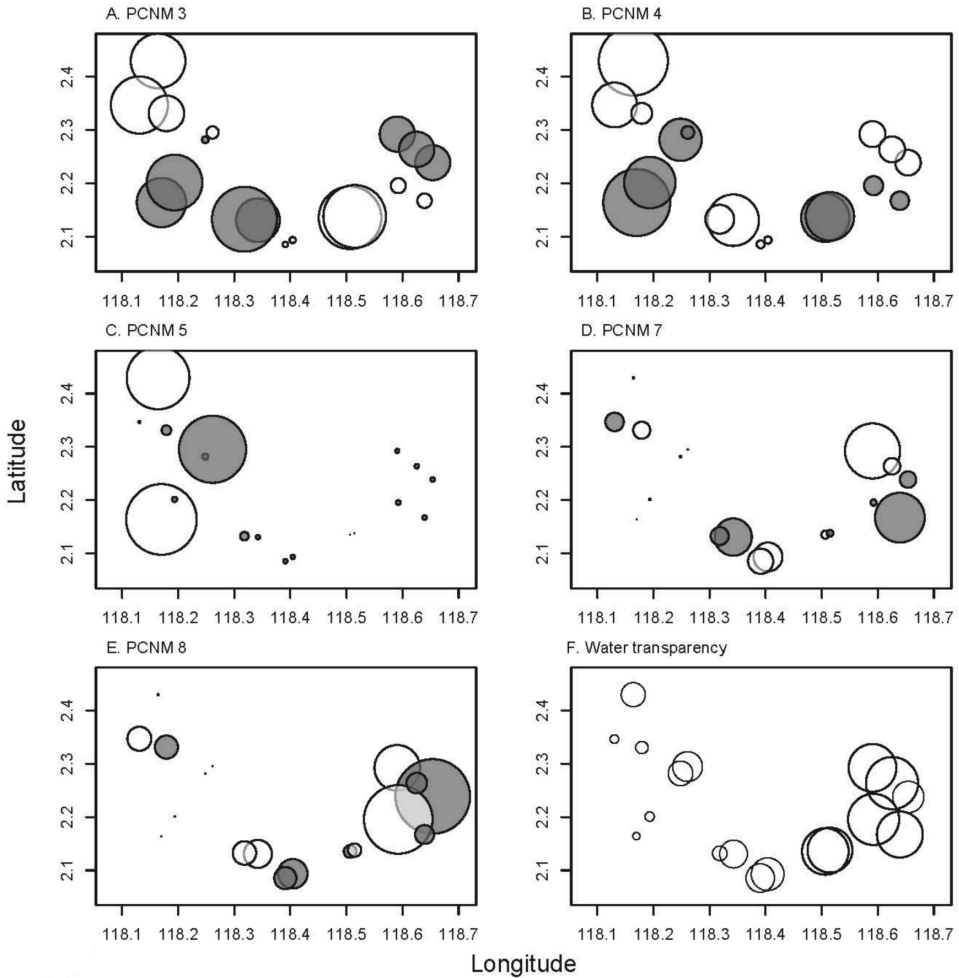


Fig. S1 Scores for (A) PCNM 3 (range in scores: $-0.23 - 0.22$, $F = 1.587$, $P = 0.022$, $R^2_{adj} = 0.017$), (B) PCNM 4 (range in scores: $-0.24 - 0.25$, $F = 1.753$, $P = 0.005$, $R^2_{adj} = 0.021$), (C) PCNM 5 (range in scores: $-0.24 - 0.25$, $F = 1.617$, $P = 0.012$, $R^2_{adj} = 0.017$), (D) PCNM 7 (range in scores: $-0.04 - 0.05$, $F = 1.480$, $P = 0.038$, $R^2_{adj} = 0.014$), (E) PCNM 8 (range in scores: $-0.03 - 0.03$, $F = 1.537$, $P = 0.013$, $R^2_{adj} = 0.016$) and (F) water transparency/visibility (range in visibility: $6.5 - 46.5$ m). For (A) to (E), clear symbols indicate positive values and shaded symbols negative values. The size of the symbol is proportional to the score. The size of the symbol is proportional to the score. Large clear symbols, therefore, have similar PCNM scores and very different scores from large shaded symbols. Note that the significant PCNM's represent intermediate scale variation.

