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Variation in the composition of corals, fishes, sponges, echinoderms, ascidians, molluscs, foraminifera and macroalgae across a pronounced in-to-offshore environmental gradient in the Jakarta Bay–Thousand Islands coral reef complex

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ABSTRACT

Substrate cover, water quality parameters and assemblages of corals, fishes, sponges, echinoderms, ascidians, molluscs, benthic foraminifera and macroalgae were sampled across a pronounced environmental gradient in the Jakarta Bay–Thousand Islands reef complex. Inshore sites mainly consisted of sand, rubble and turf algae with elevated temperature, dissolved oxygen, pH and chlorophyll concentrations and depauperate assemblages of all taxa. Live coral cover was very low inshore and mainly consisted of sparse massive coral heads and a few encrusting species. Faunal assemblages were more speciose and compositionally distinct mid- and offshore compared to inshore. There were, however, small-scale differences among taxa. Certain midshore sites, for example, housed assemblages resembling those typical of the inshore environment but this differed depending on the taxon. Substrate, water quality and spatial variables together explained from 31% (molluscs) to 72% (foraminifera) of the variation in composition. In general, satellite-derived parameters outperformed locally measured parameters.

1. Introduction

A central aim in ecology is to explain the spatial and temporal variation in biodiversity (Mora et al., 2003). Understanding the causes of this variation is an important issue in ecosystems such as coral reefs, particularly those that have been severely affected by over-harvesting, pollution, disease and coral bleaching (Roberts et al., 2002; Walther et al., 2002; Mora et al., 2003; Bellwood et al., 2004). Evidence over the last 40 years has revealed a widespread loss of coral cover in tropical coastal waters of the Indo-West Pacific and the western Atlantic. In some areas, entire coral reefs have been overgrown and killed by fast-growing species of macroalgae, leading to 'coral–algal shifts' (Raffaelli et al., 1998; Bellwood et al., 2004; Schaffelke et al., 2005). This kind of reef degradation has been attributed to a decline in herbivory as top-down mechanism and an increasing supply of nutrients as bottom-up mechanism (Burkepile et al., 2013; Bruno et al., 2014). In addition to this, corals may also undergo mortality as a result of mass bleaching events, which impacts some species more than others (Carpenter et al., 2008) and therefore may also have a selective effect on coral communities.

The community composition of coral reef taxa is structured by often pronounced in-to-offshore gradients in parameters including depth, salinity, nutrient concentrations and sedimentation (Cleary et al., 2005, 2008, 2014; Fox and Bellwood, 2007). Coral reef communities have also been structured by infrequent past events (e.g., hurricanes) and chronic stress related to human activities such as fishing and the release of heavy metals and other contaminants. Many of these pressures also have a pronounced spatial component (Goatley and Bellwood, 2013). Taxa also interact and can have important effects on the community composition of other taxa (Bellwood et al., 2004; Berumen and Pratchett, 2006; Hughes et al., 2010). Herbivory is considered to be a

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significant selective factor structuring macroalgal assemblages (Littler and Littler, 1984) and can increase species diversity by removing dominant spatial competitors (Menge and Farrell, 1989), by clearing substrate for new individuals (Menge and Lubchenco, 1981), and by maintaining the equilibrium between competing species (Gleeson and Wilson, 1986). Herbivory can also reduce diversity by selectively removing preferred food items (Lubchenco and Gaines, 1981) and altering rates of succession (McClanahan, 1997). Major grazers include fishes, molluscs and sea urchins (Hay, 1981a, 1981b, 1981c).

The crown-of-thorns starfish, *Acanthaster planci*, a ferocious coral predator, has also caused widespread damage to Indo-Pacific coral reefs (Baird et al., 2013; Pratchett et al., 2014; Plass-Johnson et al., 2015). Other taxa such as sponges, ascidians and benthic algae in contrast may not prey on corals, but compete with corals for habitat space (Jackson and Buss, 1975; Lirman, 2014), which may be more problematic for some corals than others (van der Ent et al., 2015). In addition to studying communities of coral, it is important to understand how the various coral reef communities vary spatially and in relation to environmental conditions in order to assess management strategies and the exploitation of natural products (Tuomisto et al., 2003).

The main objective of the present study was to assess the composition of several abundant coral reef taxa across a pronounced in-to-offshore gradient in the Jakarta Bay–Thousand Islands reef complex. To achieve this objective, we sampled data on reef-dwelling corals, fishes, sponges, echinoderms, ascidians, molluscs, large benthic foraminifera (LBF) and macroalgae. We also measured substrate variables including live coral and algal cover, dead coral, rubble and sand cover and local water quality variables including water transparency, pH and dissolved oxygen content. The water quality variables were supplemented with satellite-derived parameters including chlorophyll-a concentration, remote sensing reflectance at 645 nm (Rrs_645), sea surface temperature (SST) and coloured dissolved organic matter index (CDOM). The satellite-derived parameters were chosen as proxies of potential threats to coral reefs, namely eutrophication (chlorophyll-a concentrations), bleaching (sea surface temperature), sedimentation (remote sensing reflectance at 645 nm) and runoff (colored dissolved organic matter index) (Miller and Mckee, 2004; Chen et al., 2007). In addition to assessing compositional change across the in-to-offshore gradient, we also assessed to what extent spatial, substrate and water quality variables are able to explain variation in the composition of coral reef taxa.

2. Material and methods

2.1. Study site

The Jakarta Bay–Thousand Islands reef complex (hereafter referred to as JBTI) consists of cay-crowned platform reefs that extend from Jakarta Bay to more than 80 km to the north in the Java Sea (Fig. 1). Several rivers transport sewage and storm water over a 2000 km^2 catchment area to the central sector of the bay (Williams et al., 2000; Rinawati et al., 2012), defined by two flanking delta systems, both of which have a large sediment input in a catchment area of 6000 km^2 (Rees et al., 1999; Williams et al., 2000). The river discharge in JBTI also contains pollutants, such as industrial waste and household litter (Willoughby, 1986; Uneputty and Evans, 1997; Willoughby et al., 1997), heavy metals (Hosono et al., 2011), and nutrients (Baum et al., 2015). Annual precipitation averages 1700 mm yr^{-1} with a ‘wet’ season during the northwest monsoon (November–March) and a ‘dry’ season during the southeast monsoon (May–September) (Rees et al., 1999).

2.2. Data collection

Sampling took place from September 7th to 23rd 2005, predominantly at the northwestern side of the surveyed reefs with the exception of a single reef (Tikus) where the southern and northwestern sides were sampled. This entailed estimating the cover of coral colonies and other benthic cover categories (algae, dead coral, coral rubble and sand) using the line intercept transect survey method (English et al., 1997). In each site, three 30-m transects were laid out at two depths (3 and 5 m) for a total of six transects per site. A total of 43 sites were sampled that included a core set of 28 sites (Table 1). For certain taxa, some core sites were not sampled due to logistical constraints and additional sites were sampled. Along each transect, we measured the intercept distance of individual live coral colonies and other substrate cover categories.

Consistent with previous studies of the area (DeVantier et al., 1998; Cleary et al., 2006, 2008), all sample sites fell within specific zones along an in-to-offshore gradient. These included an inshore zone (zone 1) to the south of −5.97° latitude, a midshore zone (zone 2) between −5.77° and −5.97° latitude, and an offshore zone (zone 3) to the north of −5.77° latitude (Fig. 1). The offshore zone is largely contained within the Pulau Seribu National Marine Park, the first marine park established in Indonesia (Farhan and Lim, 2012).

2.3. Corals

Scleractinian coral species were visually identified during line-intercept transect surveys (English et al., 1997). Photos of unrecognized specimens were taken for closer examination and identification using Veron (2000). The line-intercept transect data was analysed in order to calculate the percent cover of each coral species and life form surveyed (see below). In each site, we surveyed six transects (30 m long) at each of the two studied depths (3 and 5 m). In total, 28 sites were surveyed for corals.

2.4. Fishes

Fishes were visually assessed along six transects (30 m long) at each of the two studied depths (3 and 5 m). Individuals observed within 5 m on either side of the transect were identified to species, if possible, and recorded. Individuals that left the transect area and re-entered were not counted again (Hoey and Bellwood, 2008; Dickens et al., 2011). In total, 28 sites were surveyed for fishes.

2.5. Sponges

Thirty patch reefs were visually surveyed during a one-hour dive from deep to shallow water (3–25 m) using a presence/absence classification. Smaller (cryptic, boring, and thinly encrusting <4 cm) specimens were excluded from this study. Species were visually identified in the field, and fragments of all species were collected for closer examination. Voucher specimens were preserved in 70% ethanol and deposited in the sponge collection at Naturalis Biodiversity Center, Leiden, the Netherlands.

2.6. Echinoderms

In close proximity of the transects, a visual census was made of asteroids and echinoids (starfish and sea urchins; referred to as echinoderms in the present study for simplicity) using a presence/absence classification. No attempt was made to locate cryptic species. In total, 31 sites were surveyed for echinoderms.

2.7. Ascidians

In the neighbourhood of the transects, a visual census was made of ascidians using a presence/absence classification. In total, 25 sites were surveyed for ascidians. It was not possible to identify all ascidians to species level, as many species have not been described and also because immature specimens of some species lacked diagnostic characters. Following a similar study off Halmahera, Moluccas, Indonesia,

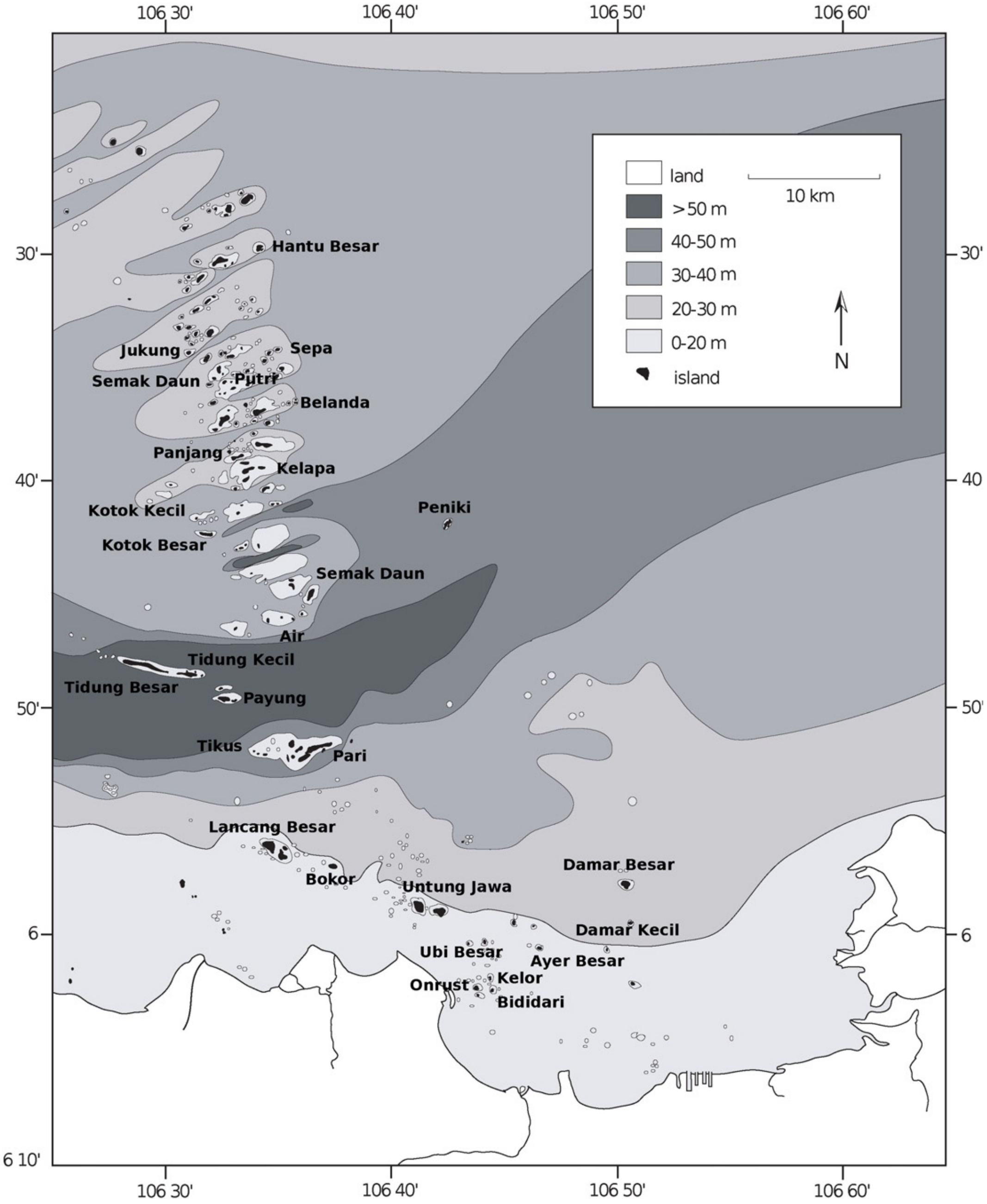

Fig. 1. Map of the study area (Jakarta Bay and Thousand islands, Indonesia). The names of selected islands adjacent to our sampling sites are shown.

specimens that could not be identified were assigned to morphotypes (Gittenberger et al., 2014). Whenever possible, specimens were photographed underwater revealing diagnostic characters. Sampled specimens were photographed in the laboratory, preserved in either 96% ethanol and/or formalin 4% as reference material and deposited in the ascidian collection at Naturalis Biodiversity Center, Leiden, the Netherlands.

2.8. Molluscs

Sediment samples were collected along each transect. For the purposes of this study, and due to the available taxonomic expertise, we focused on species belonging to the bivalve families Cardiidae and Pectinidae and the gastropod families Conidae, Cypraeidae and Nassariidae. For simplicity, we refer to these as molluscs although they do not represent total molluscan diversity. In total, 37 sites were surveyed for molluscs.

2.9. Large benthic foraminifera

Large benthic foraminifera (hereafter referred to as LBF) were collected every 3 m of depth along a depth transect starting at the reef base to the reef crest using methods described in Renema (2008). However, in this study, only samples collected between 1 and 10 m depth were included. On the reef slope a sample of the reef substratum was collected down to a depth in the sediment/rubble where no LBF were observed anymore. Afterwards the samples were washed to remove the LBF from the larger and heavier parts of coral rubble, dried, and further processed in the laboratory. LBF larger than 500 μm were subjected to further study. Following previous studies (Renema, 2008), LBF in all

Table 1
Number of observed species of corals (Cor.sp), fishes (Fis.sp), sponges (Spo.sp), echinoderms (Ech.sp), ascidians (Asc.sp), molluscs (Mol.sp), LBF (LBF.sp) and algae (Alg.sp) and number of observed individuals for corals (Cor.ab), fishes (Fis.ab) and LBF (LBF.ab). The minimum, maximum, mean and standard deviation (std) are given for all sites (total) and for zones 1, 2 and 3 separately.

Code	Location	Zone	Long	Lat	Cor.sp	Cor.ab	Fis.sp	Fis.ab	Spo.sp	Ech.sp	Asc.sp	Mol.sp	LBF.ab	LBF.sp	Alg.sp
AyB	Ayer Besar Island	1	106.775	−6.001	33	90	–	–	8	2	7	7	6	4	8
Bid	Bidadari Island	1	106.741	−6.026	2	4	16	46	18	8	1	7	520	9	3
DaK	Damar Kecil Island	1	106.841	−5.983	3	6	34	376	6	2	3	8	–	–	12
Kel	Kelor Island	1	106.740	−6.022	2	5	7	16	12	2	3	8	12	3	4
NyB	Nyamuk Island	1	106.851	−6.024	9	46	35	783	–	4	–	–	–	–	–
Onr	Ounrust Island	1	106.726	−6.034	0	0	5	7	14	5	–	–	–	–	7
UbB	Ubi Island	1	106.737	−5.993	9	19	45	277	8	3	2	2	–	0	–
UnJ	Untung Jawa Island	1	106.702	−5.971	47	122	73	860	16	2	6	1	1210	9	18
Bok	Bokor Island	2	106.623	−5.939	27	59	57	1189	24	5	7	14	762	7	18
Bur	Burung Island N-side	2	106.601	−5.859	–	–	–	–	–	2	–	–	–	–	–
DaB	Damar Besar Island	2	106.838	−5.953	58	204	70	1456	12	3	8	2	456	7	11
Dap	Dapur Island	2	106.721	−5.941	40	212	101	3051	15	3	5	14	1120	13	7
JoE	Karang Jong reef E-side	2	106.643	−5.851	–	–	–	–	–	–	5	22	–	–	–
JoN	Karang Jong reef NW-side	2	106.641	−5.851	–	–	–	–	–	–	5	2	–	–	–
Kon	Kongsi Island	2	106.593	−5.853	–	–	–	–	–	–	–	3	–	–	–
KoS	Kongsi Island S-side	2	106.607	−5.869	–	–	–	–	–	–	–	7	–	–	–
LaB	Lancang Besar Island	2	106.588	−5.923	40	119	77	1431	23	8	10	3	777	10	26
PaB	Payung Besar Island E-side	2	106.558	−5.820	–	–	–	–	–	–	––	10	–	–	–
PaE	Pari Island E-side	2	106.637	−5.853	–	–	–	–	–	–	9	13	1469	14	–
PaK	Payung kecil Isl	2	106.543	−5.808	56	306	82	2031	29	5	–	16	–	–	30
PaO	Pari Island S-side offshore	2	106.635	−5.875	–	–	–	–	–	–	–	19	–	–	–
PaS	Pari Island S-side	2	106.607	−5.869	–	–	–	–	–	4	–	–	–	–	–
PaW	Pari Island W-side South of jetty	2	106.607	−5.858	–	–	–	–	–	–	–	7	–	–	–
PeE	Peniki Island E-side	2	106.717	−5.689	–	–	–	–	35	–	–	20	–	–	–
PeW	Peniki Island NW-side	2	106.709	−5.691	–	–	–	–	35	–	–	21	–	–	–
TdK	Tidung Kc Island	2	106.517	−5.793	55	411	118	4141	39	7	6	16	451	15	36
Tid	Tidung Besar Isl	2	106.475	−5.788	121	518	114	1781	37	7	17	20	970	12	35
TkE	Tikus Island NE-side	2	106.584	−5.850	–	–	–	–	–	–	–	12	–	–	–
TkS	Tikus Selatan Island	2	106.576	−5.859	41	124	86	2026	27	6	8	12	321	13	15
TkU	Tikus Utara Island	2	106.574	−5.852	95	364	118	4329	32	1	–	17	665	15	27
TkW	Tikus Island W-side	2	106.569	−5.855	–	–	–	–	28	8	12	15	–	–	–
Air	Air Island	3	106.741	−5.756	74	272	100	2301	33	9	6	17	508	17	37
Bel	Belanda Island	3	106.602	−5.602	84	386	127	3047	34	6	7	11	534	11	27
HaB	Hantu Besar Island	3	106.537	−5.525	96	350	147	3361	41	8	10	–	656	13	11
HaK	Hantu Kecil Island	3	106.526	−5.535	70	242	136	2995	–	6	–	–	412	15	16
Juk	Jukung Island	3	106.523	−5.567	41	113	119	3933	38	–	9	14	–	–	14
KoB	Kotok Besar Island	3	106.537	−5.693	54	264	103	3856	31	3	–	17	574	14	33
KoK	Kotok Kecil Island	3	106.534	−5.687	67	410	114	3847	37	9	12	20	211	11	29
Kpa	Kelapa Island	3	106.555	−5.653	110	305	86	3631	31	3	–	13	674	13	25
Pan	Panjang Island	3	106.556	−5.639	69	374	114	3320	42	7	15	9	269	15	29
Put	Putri Island	3	106.567	−5.588	71	344	111	9524	37	9	8	1	538	14	22
SeB	Sepa Island	3	106.575	−5.572	77	303	97	5117	25	5	–	11	421	14	23
SeD	Semak Daun Island	3	106.571	−5.726	91	349	122	3732	37	4	6	6	1488	16	37
	Total sites sampled				28	28	28	28	30	31	25	37	24	24	27
	Min total				2	4	5	7	6	1	1	1	6	3	3
	Max total				121	518	147	9524	42	9	17	22	1488	17	37
	Mean total				55.1	225.8	86.2	2588.0	26.8	5.0	7.5	11.3	626.0	11.8	20.7
	std total				32.9	149.2	39.5	2029.6	11.0	2.5	3.8	6.3	392.8	3.7	10.7
	Min zone 1 (inshore)				2	4	5	7	6	2	1	1	6	3	3
	Max zone 1 (inshore)				47	122	73	860	18	8	7	8	1210	9	18
	Mean zone 1 (inshore)				15.0	41.7	30.7	337.9	11.7	3.5	3.7	5.5	437.0	6.3	8.7
	Std zone 1 (inshore)				17.8	47.2	24.0	359.2	4.5	2.1	2.3	3.1	568.9	3.2	5.6
	Min zone 2 (midshore)				27	59	57	1189	12	1	5	2	321	7	7
	Max zone 2 (midshore)				121	518	118	4329	39	8	17	22	1469	15	36
	Mean zone 2 (midshore)				59.2	257.4	91.4	2381.7	28.0	4.9	8.4	12.6	776.8	11.8	22.8
	Std zone 2 (midshore)				30.1	152.7	22.3	1179.4	8.4	2.4	3.6	6.5	364.7	3.1	10.5
	Min zone 3 (offshore)				41	113	86	2301	25	3	6	1	211	11	11
	Max zone 3 (offshore)				110	410	147	9524	42	9	15	20	1488	17	37
	Mean zone 3 (offshore)				75.3	309.3	114.7	4055.3	35.1	6.3	9.1	11.9	571.4	13.9	25.3
	Std zone 3 (offshore)				18.5	80.5	17.1	1850.3	4.9	2.3	3.1	5.6	336.7	1.9	8.5

samples were identified to species level using a stereomicroscope but only samples containing more than 200 individuals have been included in this study. In total, 24 sites were surveyed for LBF.

2.10. Macroalgae

One snorkeler and one SCUBA diver made a presence–absence visual census of red, brown, and green macroalgae (Rhodophyta, Phaeophyceae and Chlorophyta) during 1 h on the reef slope, on the reef crest, and on the reef flat (lagoon) at 27 sites. Encrusting algae and many (but not all) turf algae were excluded. Algae were identified to species level or if unreliable to genus level. Reference vouchers are kept at the herbarium (L) of the Naturalis Biodiversity Center, Leiden, the Netherlands.

2.11. Habitat structure

In the present study, habitat variables consisted of 12 distinct substrate forms. Since the high habitat heterogeneity of reef systems is essentially created by the complex and diverse colonial structures of scleractinian corals, seven of the 12 substrate forms used to characterise the habitat heterogeneity of the JBTI reef system were based on live coral cover. Coral-related variables were not used to predict variation in coral composition, nor were algal variables used to predict variation in algal composition. The 12 distinct forms of substrate assessed included the cover of *Acropora* corals, branching corals, encrusting corals, foliose corals, massive corals, submassive corals, free-living mushroom corals, turf algae, macroalgae, dead coral, rubble and sand.

2.12. Water quality

We used an aqua Troll water quality instrument (In situ Inc., Fort Collins, CO, USA) to measure water temperature (Tmp), pH, dissolved oxygen (DO; Clark DO μg s l^{-1}) and salinity (Sal: parts per thousand (ppt) or ‰). Water transparency was also measured once in each site during each sampling event using a Secchi disk. In addition to the above, we also used satellite imagery to measure four water quality variables namely, coloured dissolved organic matter index (CDOM), near-surface chlorophyll-a concentration (Chla), sea surface temperature (SST) and remote sensing reflectance at 645 nm (Rrs_645) following previously described methods (Polónia et al., 2015). CDOM was used as a tracer of riverine inputs and Rrs_645 as a proxy for total suspended sediments derived from land-based erosion (Miller and Mckee, 2004; Chen et al., 2007). CDOM is largely composed of humic and fulvic substances resulting either from decaying plant material brought by land run-off in areas with high vegetation productivity or originating from mangroves and seagrasses (Carder et al., 1999; Martin, 2004; Richardson and LeDrew, 2006). Since the accuracy of satellite data (compared to in situ data) tends to be higher with long-term averaging (Patt et al., 2003), time series of monthly mean data were generated. Long-term mean values were generated for the previously mentioned satellite-derived parameters for the years 2002–2005.

2.13. Analyses

Taxon (species-by-site), water quality, habitat and spatial (latitude and longitude of each sample site) matrices (see Appendices 1–14 in the online version at http://dx.doi.org/10.1016/j.marpolbul.2016.04.042.) were imported into R (R Core Team, 2013). Species abundance matrices were $\log_e(x+1)$ transformed (in order to normalise the distribution of the data) and a distance matrix was constructed using the Bray–Curtis index for species matrices or the Euclidean index for water quality and substrate form matrices with the vegdist() function in the VEGAN package (Oksanen et al., 2009) in R. The Bray–Curtis index is one of the most frequently applied (dis)similarity indices used in ecology (Legendre and Gallagher, 2001). Variation in species composition, water quality and substrate composition among zones was assessed with Principal Coordinates Analysis (PCO) using the cmdscale() function in R with Bray–Curtis (species composition) or Euclidean (water quality and substrate composition) distance matrices as input. Variation among zones was tested for significance using the adonis() function in VEGAN. In the adonis analysis, the Bray–Curtis or Euclidean distance matrices of species composition, water quality or substrate composition were the response variables with the zone as independent variable. The number of permutations was set at 999; all other arguments used default values, which were set in the function. We also used the adonis() function to test for significant differences among zones for selected individual water quality variables (transparency, Tmp, pH, Sal and DO). Weighted averages scores were computed for species, water quality or substrate variables on the first two PCO axes using the wascores() function in the vegan package. We tested for significant differences in substrate cover (*Acropora* coral, branching coral, encrusting coral, foliose coral, massive coral, submassive coral, mushroom coral, macroalgae, turf algae, dead coral, rubble and sand) among zones with an analysis of deviance using the glm() function in R. As data were proportional, we first applied a GLM with the family argument set to binomial. However, the ratio of residual deviance to residual d.f. in the models substantially exceeded one so we set family to 'quasibinomial'. In the 'quasibinomial' family, the dispersion parameter is not fixed at one so that it can model over-dispersion. Using the GLM model, we tested for significant variation among habitats using the anova() function in R with the F test, which is most appropriate when dispersion is estimated by moments as is the case with quasibinomial fits.

Redundancy analysis (RDA) and variance partitioning (Borcard and Legendre, 2002) were used to assess to what extent spatial, habitat and water quality variables were able to predict variation in taxon composition. Spatial variation in the study area was modelled using principal coordinates of neighbour matrices (PCNM). PCNM is a 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 and Legendre, 2002). For a detailed description of PCNM see Borcard and Legendre (2002). Significant PCNM eigenvectors were selected using the pcnm() function in the Vegan package in R (Oksanen et al., 2009) with 999 permutations. Quantitative taxon data matrices (corals, fishes and LBF) were $\log_e(x+1)$ transformed and further 'transformed' using the decostand() function in Vegan. Qualitative (presence/absence) data matrices were only transformed using the decostand() function in Vegan. With the decostand transformation, the species data were adjusted so that subsequent ordination analyses preserved the chosen distance among sample sites. In the present case, the Hellinger distance was used, as recommended by Legendre and Gallagher (2001). For each taxon/group, we then set up two models using redundancy analysis with the Hellinger-transformed matrix as response variable and spatial, substrate and water quality variables as explanatory variables respectively. RDA arranges the data points in a multidimensional space where the axes represent gradients in species abundances, constrained by the explanatory variables (spatial, substrate and water quality variables) (Makarenkov and Legendre, 2002; Cleary et al., 2005). Here, the amount of variation in composition explained by the explanatory variables is the sum of all constrained eigenvalues divided by the total variation in the species data (Cleary et al., 2005). We used the ordistep() function in vegan to select significant spatial, substrate and water quality predictors of variation in composition using backward selection, maximum permutations set to 1000 and a selection criterion of $P = 0.10$. Variance partitioning (with the varpart function in vegan; Borcard and Legendre, 2002; Cleary et al., 2004) was then used to partition the variance explained (1) purely by habitat variables, (2) purely by water quality variables, (3) purely by spatial variables and (4) by combinations of habitat, water quality and spatial variables. The significance of the RDA ordination axes was tested with the anova() function in Vegan with the 'by' argument set to 'axis'. This function tests the joint effect of constraints in RDA using an ANOVA like permutation test. All figures were made using R.

3. Results

There were highly significant differences in substrate cover among zones (Fig. 2). *Acropora*, branching, foliose, submassive and dead coral cover was higher in mid- and offshore sites than inshore sites whereas sand cover was higher inshore than mid- and offshore. There was no significant difference in the cover of encrusting and massive corals, macro- and turf algae or rubble among zones. There were also significant differences in selected locally measured environmental parameters among zones with salinity and water transparency higher mid- and offshore than inshore and temperature, pH and dissolved oxygen concentration higher inshore than mid- and offshore (Fig. 3).

Substrate composition differed significantly among zones ($F_{2,26} = 11.85$, $P < 0.001$, $R^2 = 0.477$). The ordination based on substrate form showed clear separation between inshore and mid- and offshore sites. The substrate composition of the midshore site Bok, however, resembled that of inshore sites whereas that of the midshore site Dap resembled that of offshore sites. Inshore sites were characterised by high sand

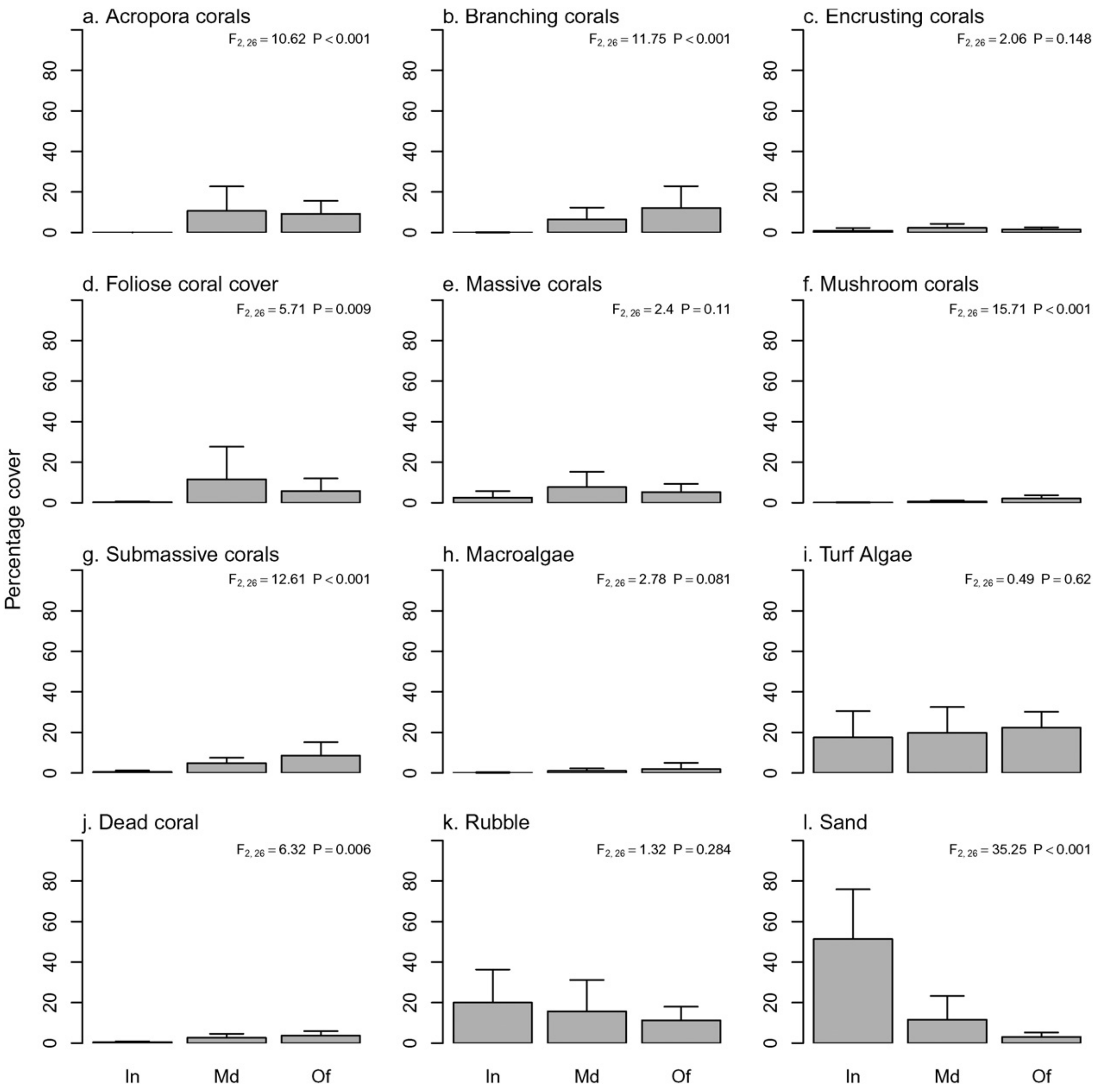

Fig. 2. Mean percentage cover (error bars represent a single standard deviation) of selected substrate forms in inshore (In), midshore (Md) and offshore (Of) zones. Results of the GLM analysis are shown in the top-right corner of each sub-figure.

cover whereas the more distant offshore sites (and Dap) were characterised by high *Acropora*, branching and foliose coral cover (Fig. 4a). The other midshore sites closest to shore (LaB and DaB) had values close to zero on the first PCO axis indicating substrate structure intermediate between inshore and the more distant mid-shore and offshore sites (Fig. 4b). As was the case with substrate form, water quality also differed significantly among zones ($F_{2,27} = 13.63$, $P < 0.001$, $R^2 = 0.522$). Inshore sites (and the midshore site Bok) were associated with high Chla values whereas mid- and offshore sites were associated with higher CDOM values and greater water transparency (Fig. 4c, d).

The number of species encountered per site varied widely across zones and taxa (Table 1 and Fig. 5). The number of coral species varied from 0 (Onr, inshore) to 121 (Tidung, midshore), fish species from 5 (Onr, inshore) to 147 (HaB, offshore), sponge species from 6 (DaK, inshore) to 42 (Pan, offshore), echinoderm species from 1 (TkU, midshore) to 9 (Air, KoK and Put, all offshore), ascidian species from 1 (Bid, inshore) to 17 (Tid, midshore), mollusc species from 1 (UnJ and Put, inshore and offshore) to 22 (JoE, midshore), LBF species from 3 (Kel, inshore) to 17 (Air, offshore) and macroalga species from 0 (UbB, inshore) to 37 (Air and SeD, both offshore). The mean number (and standard deviation) of coral species encountered per site varied from 13.1 (±17.3) inshore to 59.2 (±30.07) midshore and 78.5 (±15.7) offshore. The mean number of fish species per site varied from 30.7 (±24.0) inshore to 91.4 (±22.3) midshore and 114.3 (±17.9) offshore. All taxa, with the exception of molluscs, showed a similar pattern of increasing number of species encountered (species density) per site from inshore to mid- and offshore.

The composition of all taxa differed significantly among zones (Figs. 6 and 7) and was primarily structured along the pronounced in-to-offshore gradient in JBTI with the most pronounced differences between inshore versus mid- and offshore sites (Figs. 8 and 9). The midshore sites closest to shore (LaB, Bok, Dap and DaB), however, appear to represent a transition zone. Coral and fish assemblages in Bok, for example, were more similar to inshore sites, whereas assemblages in Dap were more similar to offshore sites and assemblages in LaB and DaB were intermediate. For sponges and echinoderms, in contrast, assemblages in LaB and Bok were more similar to offshore sites whereas

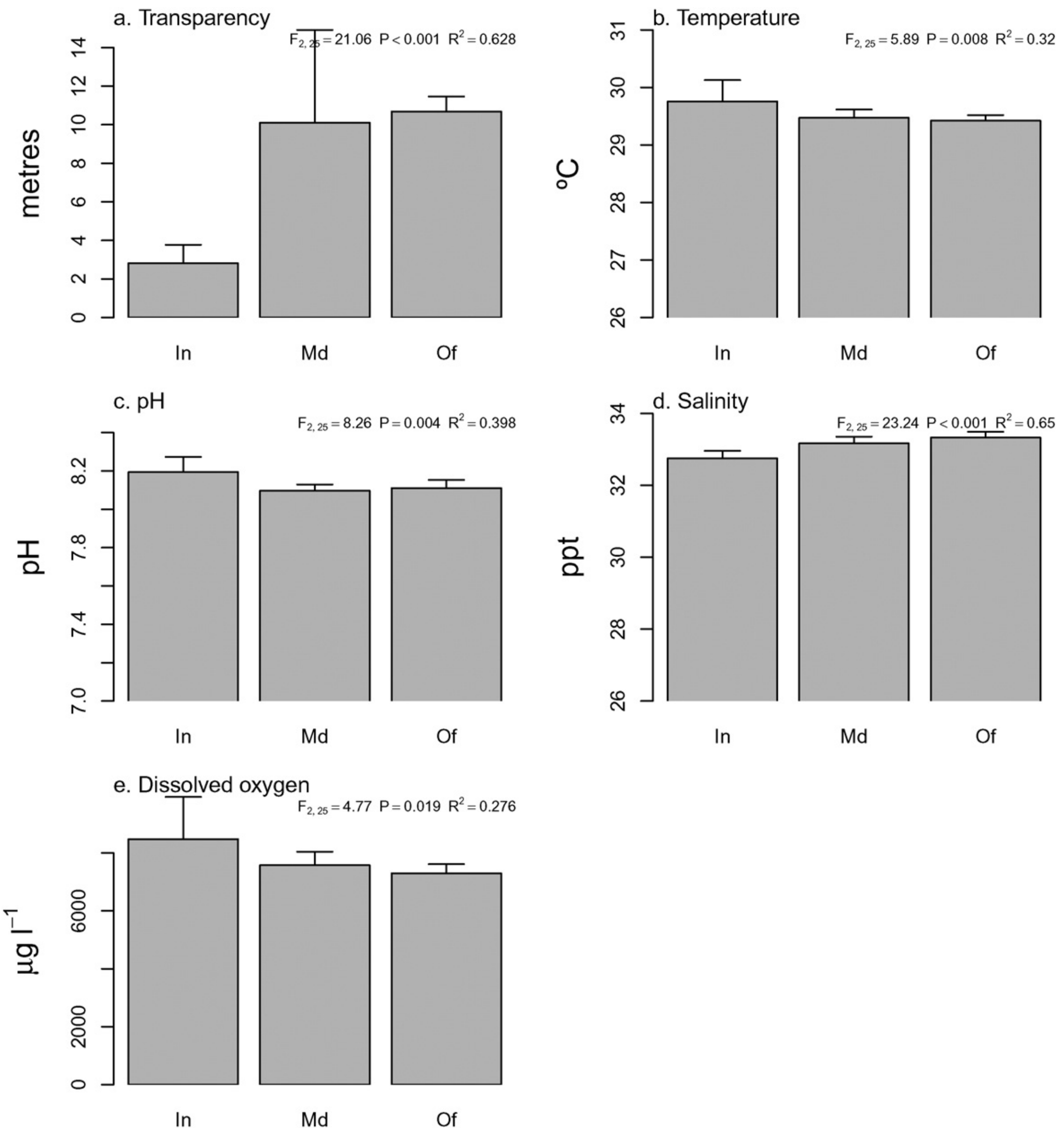

Fig. 3. Mean (error bars represent a single standard deviation) a) water transparency, b) temperature, c) pH, d) salinity and e) dissolved oxygen in inshore (In), midshore (Md) and offshore (Of) zones. Results of the adonis analysis are shown in the top-right corner of each sub-figure.

assemblages in Dap and DaB were more similar to inshore sites (Fig. 8). For ascidians assemblages in all four of these midshore sites were more similar to inshore sites (Fig. 9). In contrast to the other taxa, assemblages of echinoderms and molluscs in certain offshore sites (e.g., PaS and SeD) were more similar to inshore than offshore sites. The midshore site Dap represents an interesting site with very high coral cover and the highest foliose coral cover overall at 48.4%. At this site assemblages of corals, fishes, molluscs and LBF were similar to offshore sites whereas assemblages of sponges, echinoderms, ascidians and algae were similar to inshore sites. This suggests that although taxa may globally respond to environmental conditions in a similar fashion, there may still be smaller-scale differences in response.

Coral species mainly found inshore included the coral species *Oulastrea crispata* (Ou-cr) and *Polyphyllia talpina* (Po-ta) (Fig. 6). *Porites lobata* (Po-lo), *P. lutea* (Po-lu) and *Galaxea fascicularis* (Ga-fa), in contrast, were found across a wide range of sites. Most species, however, were associated with mid- and offshore reefs, e.g., *Seriatopora hystrix* (Se-hy), *Montipora foliosa* (Mo-fo), *Porites rus* (Po-ru) and *Acropora millepora* (Ac-mp). Fish species observed inshore included *Canthigaster compresus* (Ca-co), *C. valentini* (Ca-va), *Scolopsis monogramma* (Sp-mo), *Diploprion bifasciatus* (Di-bi) and *Monacanthus* sp. (Mo-sp). Most fish species, including all of the most abundant (>1000 individuals) species, were, however, mainly found in mid- and offshore sites, e.g., *Pomacentrus amboinensis* (Po-am), *Pomacentrus alexanderae* (Po-al), *Cirrhilabrus cyanopleura* (Ci-cy), *Amblyglyphidodon leucogaster* (Am-le), *Amblyglyphidodon leucogaster* (Am-le), *Caesio teres* (Ca-te), *C. cyanopleura* (Ci-cy) and *Chromis ternatensis* (Cr-te). Sponge species associated with inshore sites included *Chondrilla* sp. (Cn-sp), *Haliclona* cf. *cymaeformis* and *Spongia ceylonensis* (Sp-ce). The species *Callyspongia joubini* (Ca-jo) and *Ptilocaulis* sp. (Pt-sp) were mainly found inshore and midshore whereas the species *Amphimedon* cf. *paraviridis* (Am-pa), *Spheciospongia inconstans* (Sp-in), *Xestospongia testudinaria* (Xe-te), *Petrosia nigricans* (Pe-ni), *Aaptos suberitioides* (Aa-su), *Clathria reinwardtii* (Cl-re), *Cinachyrella australiensis* (Ci-au) and *Dysidea arenaria* (Dy-ar) were found across a wide range of sites from inshore to offshore suggesting tolerance to a wide range of ecological conditions. Other sponge species were restricted to mid- and offshore sites including *Hyrtios erectus* (Hy-er), *Stylissa carteri* (St-ca), *Callyspongia aerizusa* (Ca-ae), *Dysidea frondosa* (Dy-fr), *Axinyssa* cf.

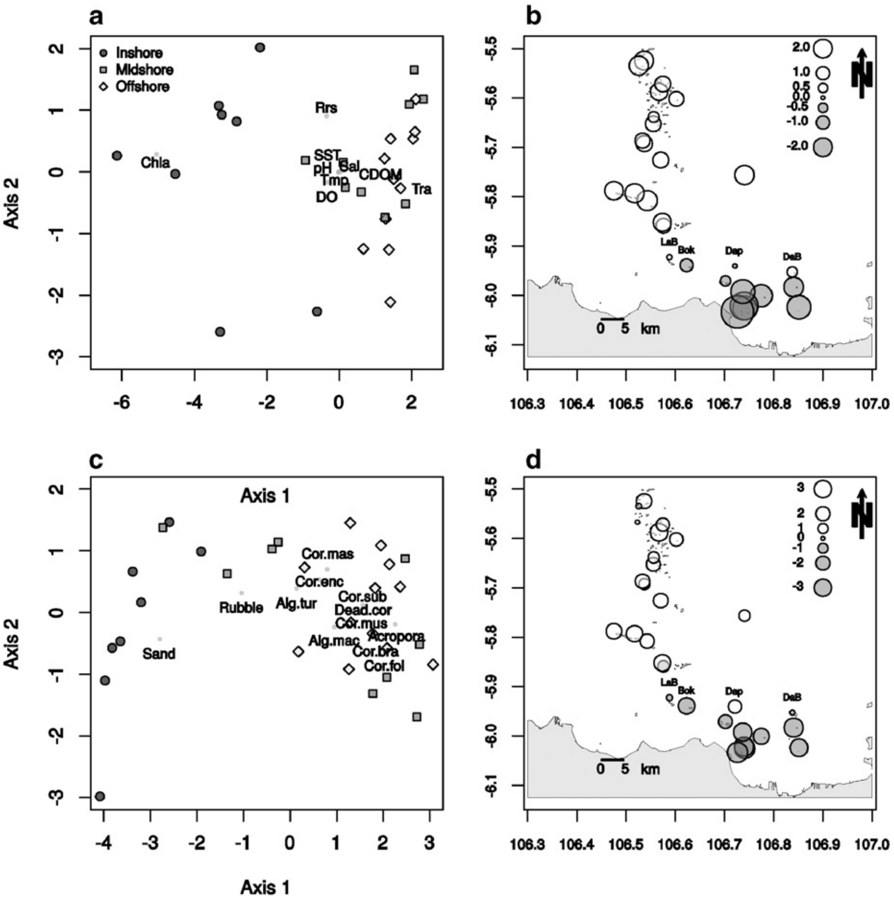

Fig. 4. Ordination showing the first two axes of the PCO analysis for a) substrate variables and c) water quality variables. Symbols represent sites from inshore, midshore and offshore zones. Variation in site scores of the first PCO axis on a map of the study area for b) substrate variables and d) water quality variables. Open symbols indicate positive values along the first PCO axis and shaded symbols negative values. The size of the symbol is proportional to the score. Codes for the midshore sites closest to shore are given: LaB, Bok, Dap and DaB. Codes for a) transparency (Tra), salinity (Sal), temperature (Tmp), dissolved oxygen (DO), sea surface temperature (SST) and Rrs (remote sensing reflectance and 645 nm). Codes for b) branching coral (Cor.bra), encrusting coral (Cor.enc), foliose coral (Cor.fol), massive coral (Cor.mas), mushroom coral (Cor.mus), submassive coral (Cor.sub), dead coral (Dead.cor), macroalgae (Alg.mac) and turf algae (Alg.tur).

aculeata (Ax-ac) and *Clathria cervicornis* (Cl-ce). Echinoderm species found in inshore sites included the sand dollar *Laganum depressum* (La-de) and the sea urchins *Brissus agassizii* (Br-ag), *Echinothrix calamaris* (Et-ca) and *Diadema setosum* (Di-se) whereas the starfish species *Linckia laevigata* (Li-la), *A. planci* (Ac-pl), and *Culcita novaeguinea* (Cu-no) were mainly found in offshore sites.

The ascidian species *Aplidium* sp. (Ap-sp) and *Botrylloides* sp. (Bo-sp) were only found in inshore and the midshore sites closest to the coast (Fig. 7). The species *Pseudodistoma fragile* (Ps-fr), *Didemnum molle* (Di-mo), *D. rubeum* (Di-ru), *Archidistoma richerie* (Ar-ri) and *Leptoclinides reticulates* (Le-re) were, in contrast, found in mid- and offshore sites. The mollusc species *Nassarius pauper* (Na-pa) and *Acrosterigma flava* (Ac-fl) were mainly restricted to inshore and midshore sites with high sand cover. Other mollusc species found in inshore sites included *Conus geographus* (Co-ge), *Conus glans* (Co-gl) and *Fulvia papyracea* (Fu-pa). Mollusc species found in mid- and offshore sites included *Laevichlamys cuneata* (La-cu), *Nassarius silvardi* (Na-si), *Semipallium fulvicostatum* (Se-fu), *Acrosterigma rubicundum* (Ac-ru), *Excellichlamys histrionica* (Ex-hi), *Afrocardium richardi* (Af-ri) and *Decatopecten radula* (De-ra). The LBF species *Calcarina* sp. (Ca-s2) was found in inshore sites whereas most other species were strongly associated with or restricted to mid- and offshore sites, e.g., *Amphistegina lobifera* (Am-lo), *Amphistegina lessonii* (Am-le), *Sorites orbiculus* (So-or). Most macroalga species were associated with mid- and offshore sites, for example, *Actinotrichia fragilis* (Ac-fr), *Caulerpa cupressoides* (Ca-cu), *Bornetella nitida* (Bo-ni) and *Valonia ventricosa* (Ve-ve). Species mainly found inshore and in perturbed midshore sites (e.g., Bok) included *Rhipidosiphon javensis* (Rh-ja), *Lobophora papenfussii* (Lo-pa) and *Bryopsis pennata* (Br-pe).

Significant predictors of variation in composition included satellite-derived CDOM concentrations (all taxa except ascidians and LBF), water transparency (corals, fishes, sponges, molluscs and algae), salinity (ascidians), branching coral cover (echinoderms), free-living mushroom coral cover (echinoderms and algae) and foliose coral cover (ascidians) (Table 2). Significant predictors of variation in composition associated with inshore sites included satellite-derived chlorophyll-a (corals, fishes, ascidians, LBF and algae), dissolved oxygen (fishes and forams), temperature (corals, fishes, ascidians and LBF), SST (fishes, sponges, echinoderms, LBF and algae), sand (all taxa) and rubble (corals, fishes and molluscs). Ordinations based on redundancy analysis that show the relationship between species and environmental variables can be seen in the Supplementary material (Supplementary Figs. 1 and 2 in the online version at http://dx.doi.org/10.1016/j.marpolbul.2016.04.042.).

The amount of variation in species composition only explained by substrate variables, thus after factoring out variation explained by water quality and spatial variables (the pure substrate component) varied from 6% (fishes) to 16% (ascidians). The amount of variation explained by the pure water quality component (thus after factoring out the variation explained by substrate and spatial variables) varied from 8% (echinoderms and molluscs) to 23% (LBF). The pure spatial component explained from 5% (echinoderms) to 17% (LBF) of variation in taxon composition (Supplementary material: Supplementary Figs. 3 and 4 in the online version at http://dx.doi.org/10.1016/j.marpolbul.

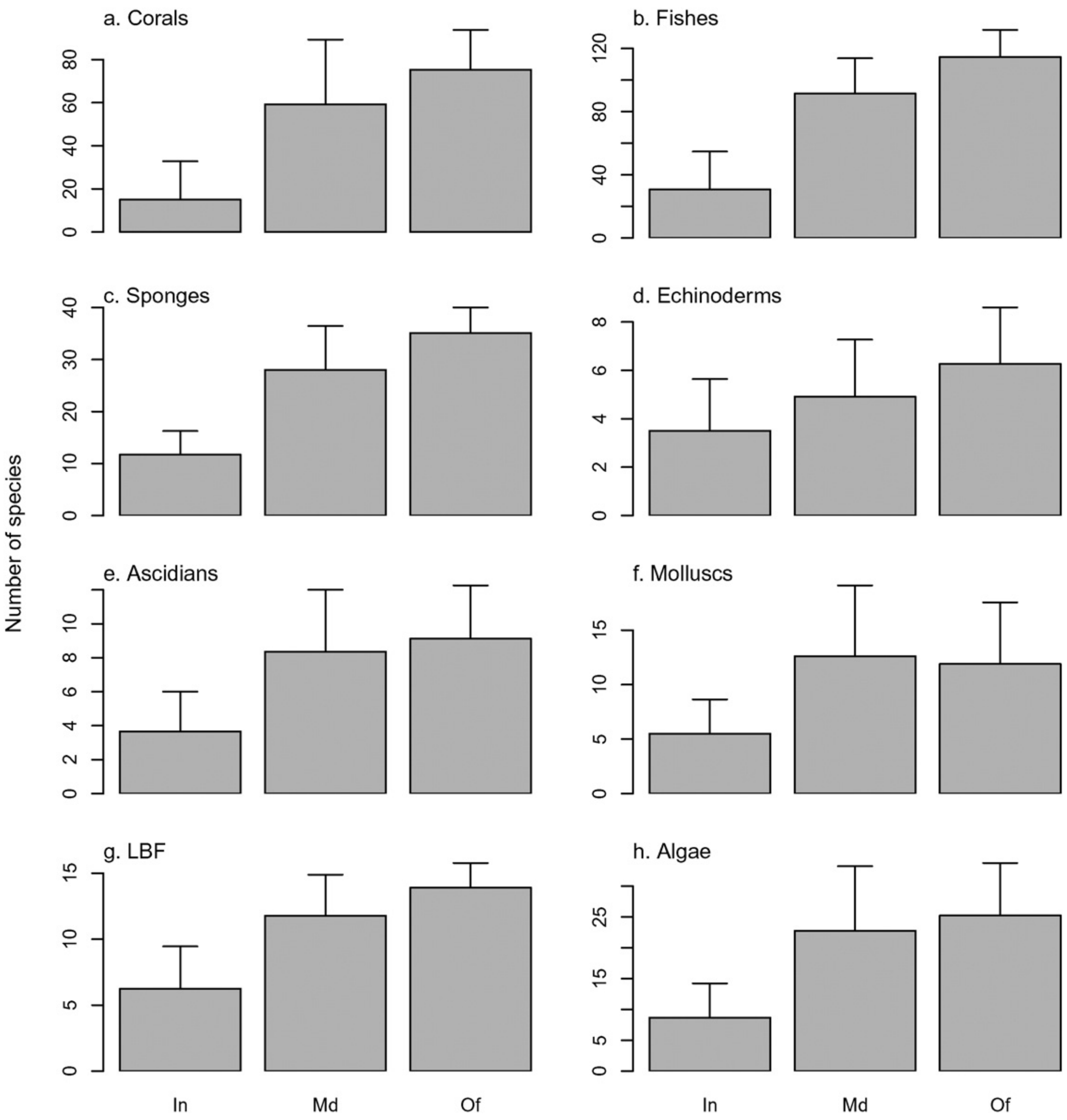

Fig. 5. Mean species density (error bars represent a single standard deviation) of focal taxa in inshore (In), midshore (Md) and offshore (Of) zones.

2016.04.042.). The combined effects of all three of these parameters explained from 3% (molluscs) to 17% (corals) of the variation in composition. The combined effects of habitat and water quality, habitat and space and water quality and space explained from 0% (corals, sponges and molluscs) to 7% (sponges). The percentage of unexplained variation varied from 28% (LBF) to 69% (molluscs). Substrate variables explained more of the compositional variation of echinoderms (14%) and molluscs (9%) whereas water quality variables explained more of the variation of corals (16%), fishes (21%), sponges (11%), ascidians (19%), LBF (23%) and algae (18%).

4. Discussion

A number of previous studies have reported on the strong in-to-offshore gradient in JBTI (Moll and Suharsono, 1986; DeVantier et al., 1998; Cleary et al., 2008, 2014; de Voogd and Cleary, 2008; Renema, 2008; Maduppa et al., 2013). In the present study, inshore sites were characterised by poor water transparency and higher mean temperature, pH, dissolved oxygen concentrations, satellite-derived chlorophyll-a concentrations and lower mean salinity. The substrate inshore mainly consisted of sand, rubble and turf algae with very low live coral cover. The inshore waters are subject to riverine runoff lowering salinity and introducing a heavy nutrient load. The coast adjacent to Jakarta has long been subjected to occasional severe algal blooms (Rees et al., 1999). The introduction of nutrients may lead to some initial acidification. Phytoplankton, however, quickly utilise the available nutrients and the byproducts of their photosynthesis increase seawater pH. Likewise, algal blooms can cause super saturation of oxygen and consequently high dissolved oxygen levels. This can cause substantial physiological stress for resident fauna (Ross et al., 2001). Die-off, however, following a bloom can deplete oxygen leading to hypoxic conditions detrimental to the resident fauna. Eutrophied waters may also experience a daily cycle of high oxygen concentrations during the day due to photosynthesising phytoplankton and macroalgae and occasional severe oxygen depletion at night when both of these groups respire. This seasonal and daily variation in oxygen concentration and other variables such as salinity make eutrophied inshore waters an inhospitable environment for numerous taxa.

The number of species encountered inshore was a fraction of that encountered mid- and offshore. This indicates that many of these taxa are sensitive to the poor water quality (high chl-a concentrations and poor water transparency) and degraded habitat (high sand and low coral cover) of inshore reefs. Although all taxa appeared to be adversely affected, these conditions seemed to be particularly detrimental to

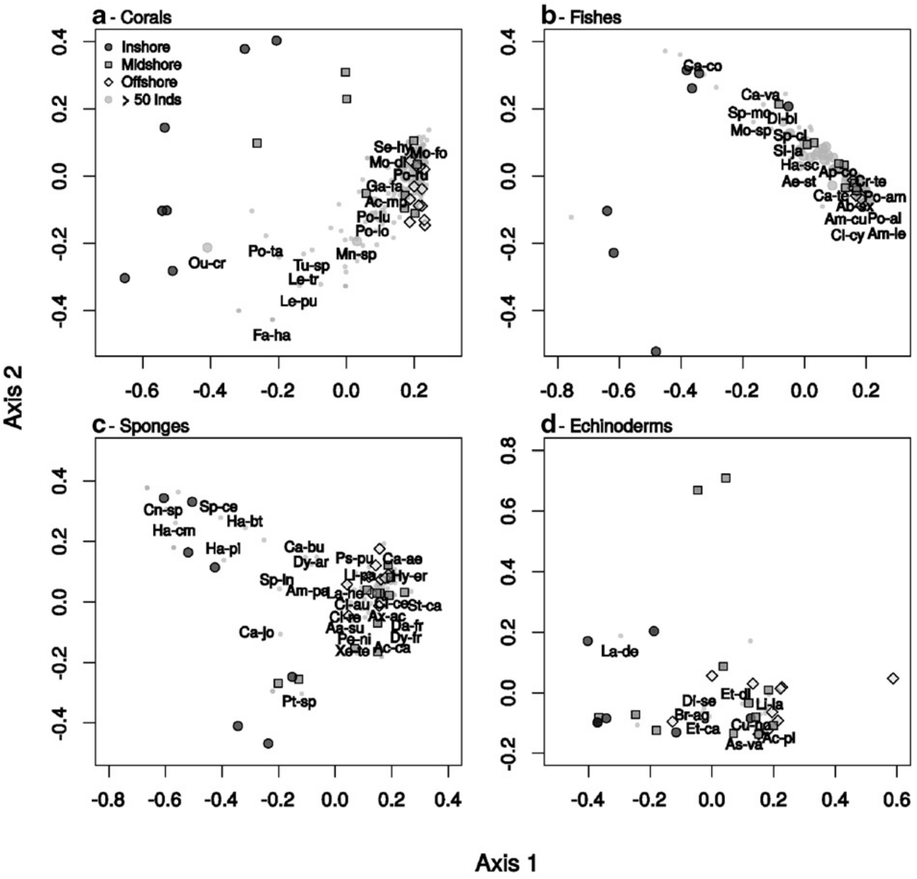

Fig. 6. Ordination showing the first two axes of the PCO analysis for a) corals, b) fishes, c) sponges and d) echinoderms. Symbols represent samples from the inshore, midshore and offshore zones. For corals and fishes, large grey symbols represent species ≥50 individuals. Codes for a) *Acropora millepora* (Ac-mp), *Favia halicora* (Fa-ha), *Galaxea fascicularis* (Ga-fa), *Leptastrea purpurea* (Le-pu), *L. transversa* (Le-tr), *Montastrea* sp. (Mn-sp), *Montipora digitata* (Mo-di), *M. foliosa* (Mo-fo), *Oulastrea crispata* (Ou-cr), *Porites lobata* (Po-lo), *P. lutea* (Po-lu), *P. rus* (Po-ru), *Polyphyllia talpina* (Po-ta), *Seriatopora hystrix* (Se-hy) and *Turbinaria* sp. (Tu-sp). Codes for b) *Abudefduf sexfasciatus* (Ab-sx), *Aeoliscus strigosus* (Ae-st), *Amblyglyphidodon curacao* (Am-cu), *A. leucogaster* (Am-le), *Apogon compressus* (Ap-co), *Canthigaster compresus* (Ca-co), *C. valentini* (Ca-va), *Caesio teres* (Ca-te), *Cirrhilabrus cyanopleura* (Ci-cy), *Chromis ternatensis* (Cr-te), *Diploprion bifasciatus* (Di-bi), *Halichoeres scapularis* (Ha-sc), *Monacanthus* sp. (Mo-sp), *Pomacentrus alexanderae* (Po-al), *P. amboinensis* (Po-am), *Siganus javus* (Si-ja), *Scolopsis ciliatus* (Sp-ci) and *S. monogramma* (Sp-mo). Codes for c) *Aaptos suberitioides* (Aa-su), *Acanthella cavernosa* (Ac-ca), *Amphimedon* cf. *paraviridis* (Am-pa), *Axinyssa* cf. *aculeata* (Ax-ac), *Callyspongia aerizusa* (Ca-ae), *Callyspongia* sp 'bug' (Ca-bu), *Callyspongia joubini* (Ca-jo), *Cinachyrella australiensis* (Ci-au), *Clathria cervicornis* (Cl-ce), *C. reinwardtii* (Cl-re), *Chondrilla* sp. (Cn-sp), *Dasychalina fragilis* (Da-fr), *Dysidea arenaria* (Dy-ar), *D. frondosa* (Dy-fr), *Haliclona* sp. 'black-tubes' (Ha-bt), *Haliclona* cf. *cymaeformis* (Ha-cm), *Haliclona* 'pink' (Ha-pi), *Hyrtios erectus* (Hy-er), *Lamellodysidea herbacae* (La-he), *Liosina paradoxa* (Li-pa), *Petrosia nigricans* (Pe-ni), *Pseudoceratina purpurea* (Ps-pu), *Ptilocaulis* sp. (Pt-sp), *Spongia ceylonensis* (Sp-ce), *Spheciospongia inconstans* (Sp-in), *Stylissa carteri* (St-ca) and *Xestospongia testudinaria* (Xe-te). Codes for d) *Acanthaster planci* (Ac-pl), *Asthenosoma varium* (As-va), *Brissus agassizii* (Br-ag), *Culcita novaeguinea* (Cu-no), *Diadema setosum* (Di-se), *Echinothrix calamaris* (Et-ca), *E. diadema* (Et-di), *Laganum depressum* (La-de), *Linckia laevigata* (Li-la). Results of the adonis analysis comparing composition among zones: corals: $F_{2,27} = 6.40$, $P < 0.001$, $R^2 = 0.339$; fishes: $F_{2,25} = 7.70$, $P < 0.001$, $R^2 = 0.381$; sponges: $F_{2,27} = 5.98$, $P < 0.001$, $R^2 = 0.307$; and echinoderms: $F_{230,} = 3.72$, $P < 0.001$, $R^2 = 0.210$).

photosymbiont-hosting organisms such as corals and LBF (although not all of the LBF included in the present study are symbiont-bearing) and taxa that depend on intact coral reefs for food and cover. Corals were completely absent from one inshore site and sparse in most other inshore sites. Chronic exposure to land-based perturbations have also led to the severe degradation of the habitat matrix whereby the complex three dimensional structure of a healthy coral reef has been replaced by a much more simple habitat dominated by sand, turf algae and coral rubble with a few remaining massive coral heads. Importantly, the inshore reefs of Jakarta Bay formerly housed diverse and thriving coral reefs. Umbgrove (1939) noted that reef faunas such as those surrounding the inshore island of Nyamuk Besar consisted of acroporid corals such as *Montipora digitata*, *M. foliosa* and *Acropora aspera*. Furthermore, corals of JBTI have suffered from severe coral bleaching in 1983, which affected some species more than others (Brown and Suharsono, 1990; Hoeksema, 1991). Coral mortality has also been reported as a result of predation by *A. planci* (e.g., Baird et al., 2013) and by overgrowth of an aggressive sponge species (de Voogd et al., 2013). Since coral species vary in their susceptibility to these factors, this will affect some coral species more than others, adding to the variation in coral degradation.

Water quality variables were more important predictors of variation in composition for corals, fishes, sponges, ascidians, LBF and algae whereas substrate variables were more important predictors for echinoderms and molluscs. In line with this, the biotic composition of selected taxa (ascidians, macroalgae, and corals) on the west side of Halmahera (Moluccas, Indonesia) appeared also to depend on water quality parameters, such as salinity and turbidity (Gittenberger et al., 2014). This contrasts somewhat with Polónia et al. (2015) who studied assemblages of corals, sponges, LBF and sediment archaea and bacteria in the Spermonde Archipelago. In the Spermonde, habitat variables were more important explanatory factors than water quality variables with the exception of sediment bacteria. The present work, however, confirms previous work in JBTI (Cleary et al., 2006) where proxies of water quality variables (e.g., distance to shore) were the primary explanatory factors of coral composition. This discrepancy may be related to the much poorer water quality of inshore reefs in JBTI compared to the Spermonde archipelago. The present study, in which water quality variables were more important predictors of the composition of ascidians than habitat variables, is in line with Gittenberger et al. (2014) where various ascidian species were found to be very good indicators for bioregions, varying

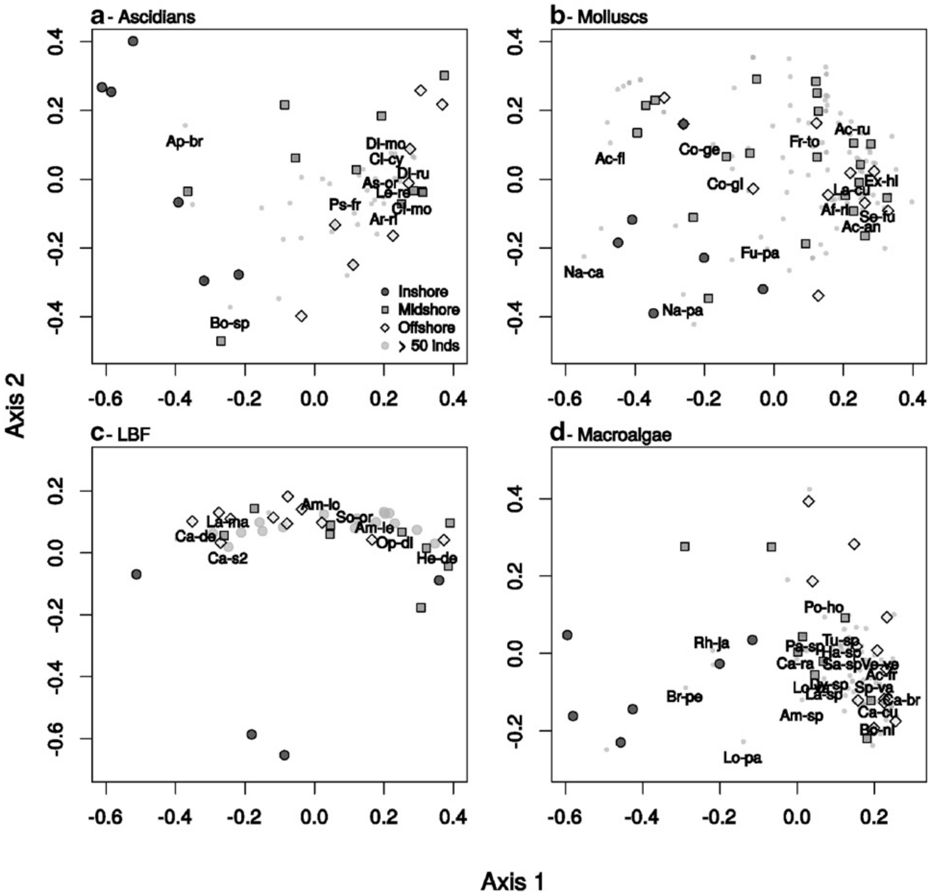

Fig. 7. Ordination showing the first two axes of the PCO analysis for a) ascidians, b) molluscs, c) forams and d) algae. Symbols represent samples from inshore, midshore and offshore zones. For forams, large grey symbols represent species ≥50 individuals. Codes for a) *Aplidium breviventer* (Ap-br), *Archidistoma richerie* (Ar-ri), *Ascidia ornata* (As-or), *Botrylloides* sp. (Bo-sp), *Clavelina cyclus* (Cl-cy), *C. moluccensis* (Cl-mo), *Didemnum molle* (Di-mo), *D. rubeum* (Di-ru), *Leptoclinides reticulates* (Le-re), *Pseudodistoma fragile* (Ps-fr). Codes for b) *Acrosterigma angulata* (Ac-an), *A. flava* (Ac-fl), *A. rubicundum* (Ac-ru), *Afrocardium richardi* (Af-ri), *Conus geographus* (Co-ge), *C. glans* (Co-gl), *Excellichlamys histrionica* (Ex-hi), *Frigidocardium torresi* (Fr-to), *Fulvia papyracea* (Fu-pa), *Laevichlamys cuneata* (La-cu), *Nassarius canaliculatus* (Na-ca), *N. pauper* (Na-pa), *Semipallium fulvicostatum* (Se-fu). Codes for c) *Amphistegina lessonii* (Am-le), *Amphistegina lobifera* (Am-lo), *Calcarina defrancei* (Ca-de), *C.* sp2 (Ca-s2), *Heterostegina depressa* (He-de), *Laevipeneroplis malayensis* (La-ma), *Operculina discoidalis* (Op-di), *Sorites orbiculus* (So-or). Codes for d) *Actinotrichia fragilis* (Ac-fr), *Amphiroa* spp. (Am-sp), *Bornetella nitida* (Bo-ni), *Bryopsis pennata* (Br-pe), *Caulerpa brachypus* (Ca-br), *C. cupressoides* (Ca-cu), *C. racemosa* species complex (Ca-ra), *Dictyota* spp. (Dy-sp), *Halimeda* spp. (Ha-sp), *Laurencia* spp. (La-sp), *Lobophora papenfussii* (Lo-pa), *L. variegata* (Lo-va), *Padina* spp. (Pa-sp), *Portieria hornemannii* (Po-ho), *Rhipidosiphon javensis* (Rh-ja), *Sargassum* spp. (Sa-sp), *Spongocladia (Cladophoropsis) vaucheriaeformis* (Sp-va), *Turbinaria* spp. (Tu-sp), *Ventricaria (Valonia) ventricosa* (Ve-ve). Results of the adonis analysis comparing composition among zones: ascidians: $F_{2,22} = 3.56$, $P < 0.001$, $R^2 = 0.244$; molluscs: $F_{2,34} = 1.75$, $P = 0.006$, $R^2 = 0.094$; LBF: $F_{2,21} = 4.07$, $P < 0.001$, $R^2 = 0.279$; and algae: $F_{2,27} = 5.82$, $P < 0.001$, $R^2 = 0.327$).

in their distance offshore, while no correlations were found between ascidian communities and habitats.

The results of the 2005 survey showed that the inshore reefs of Jakarta Bay were clearly the poorest with regard to coral species numbers (Table 1); this was also observed during similar surveys in 1985, 1995 and 2011 (Cleary et al., 2006, 2008, 2014). This low species density is most probably related to the river discharge along the shore line of Jakarta Bay, causing an influx of sediment, nutrients and other pollutants (Verstappen, 1988; Farhan and Lim, 2012; Johan et al., 2015). It is important to note, however, that a study of historical museum collections has indicated that coral species richness in Jakarta Bay was much higher in the 1920s (van der Meij et al., 2009). A similar decline in species richness was observed for molluscs between the 1930s and 2005 (van der Meij et al., 2010). The zebra coral, *O. crispata*, is an exception by being the most common scleractinian coral species in most of the inshore reefs, whereas it was absent in mid- and offshore reefs, as also observed in 1985 (Cleary et al., 2006). This coral species is known to occur predominantly in shallow, turbid environments where other corals are rare (Yamashiro, 2000; Chen et al., 2011). In the Spermonde archipelago, coral species density was also relative low inshore; this has been attributed to the close proximity of inshore reefs to river outlets and the shallower depth of the surrounding sea floor (Cleary et al., 2005; Becking et al., 2006; Hoeksema, 2012a, 2012b; Polónia et al., 2015).

The pure water quality component was a more important predictor of variation in fish (21% versus 6%) and LBF (23% versus 9%) composition than the pure substrate component. This contrasts somewhat with previous studies of coral reef fishes. Substrate structure, for example, as opposed to just the amount of live coral cover has previously been shown to strongly affect the composition of fish assemblages (Lewis, 1997; Syms and Jones, 2000; Emslie et al., 2008; Baum et al., 2015). Likewise, in Bocas del Toro, Panama, fish with a given set of traits were associated with specific habitats. For example, highly mobile species and oceanic planktivores were more abundant in exposed reef environments while demersal zooplankton feeders, territorial herbivores and sedentary species were found in sheltered environments such as massive and foliaceous coral zones. Omnivores were more abundant in areas of sand and rubble (Dominici-Arosemena and Wolff, 2005). In the Ryukyu Islands Japan, however, fish assemblages varied with reef zone, water depth and offshore distance but not with coral abundance or density (Lecchini et al., 2003).

Symbiont bearing larger foraminifera are among the most important calcifiers in healthy reef systems (Scoffin and Tudhope, 1985; Renema, 2006). They are sensitive to environmental parameters and widely used as indicators of water quality (Hallock et al., 2003; Uthicke and Nobes, 2008). Poor water quality results in fewer obligate symbiont-bearing taxa relative to non-symbiont-bearing taxa (Hallock et al.,

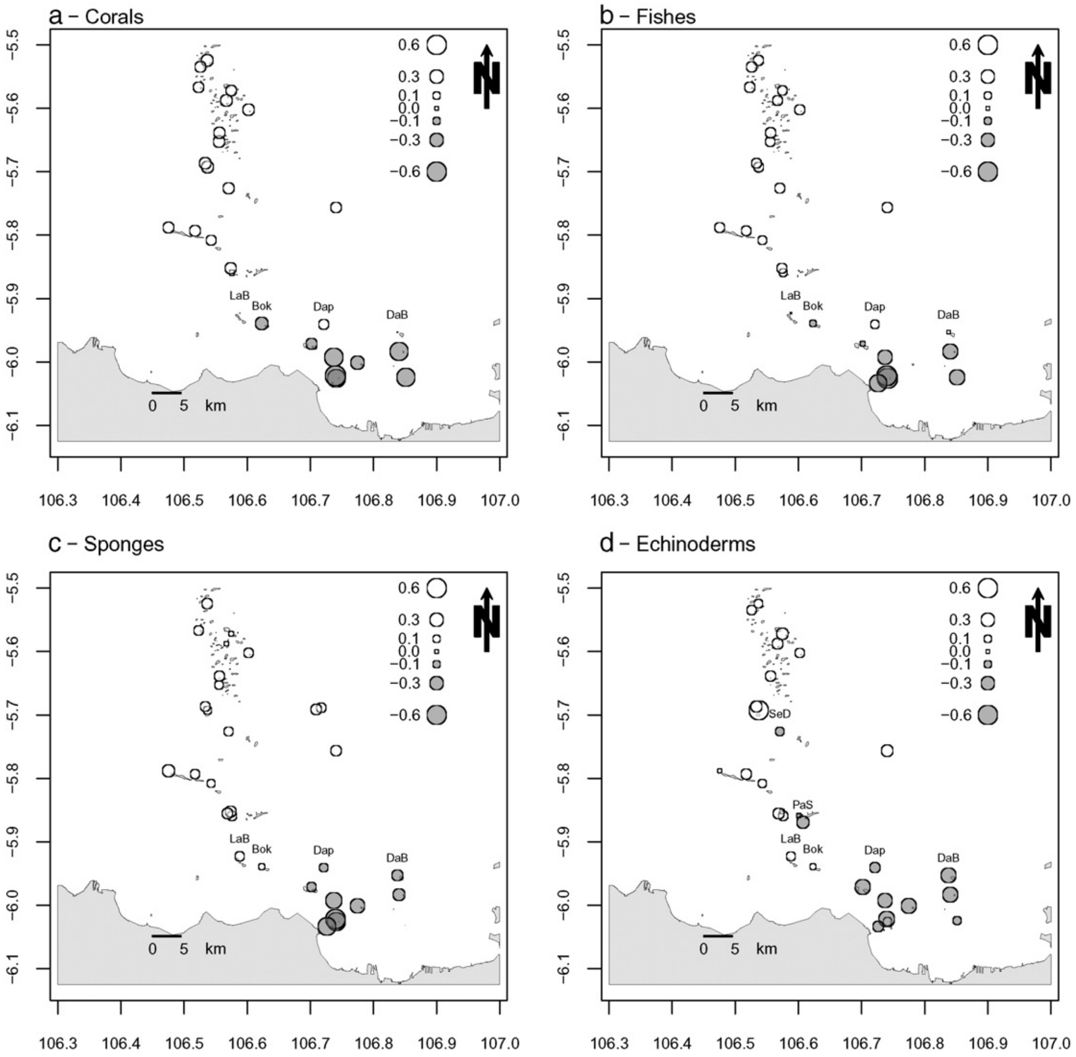

Fig. 8. Variation in site scores of the first PCO axis on a map of the study area for a) corals, b) fishes, c) sponges and d) echinoderms. Open symbols indicate positive values along the first axis and shaded symbols negative values. The size of the symbol is proportional to the score. Codes for the midshore sites closest to shore are given: LaB, Bok, Dap and DaB. For echinoderms additional extra codes are shown for the mid- and offshores sites: PaS and SeD.

2003), as observed in the inshore reefs. Depth is an important component determining the assemblage composition of LBF within reef systems, and most variation in assemblage composition is observed in either shallow (reef flat) assemblages (Renema, 2010) or deeper on the reef slope (Hohenegger, 1994). In Caribbean reef systems, members of the genus *Amphistegina* are an important component of LBF assemblages. Variation in the proportion of symbiont-bearing LBF in the total benthic LBF assemblage is for a large part determined by the abundance of *Amphistegina* species. In the Indo-West-Pacific, however, there are more LBF species and they occupy a greater variety of habitats (Hohenegger, 1994; Renema, 2008, 2010). Within LBF, certain taxa, particularly members of the genus *Calcarina* tolerate both poor water quality and benthic habitats dominated by algae as opposed to corals (Renema, 2010). Within this group, some species are particularly sensitive to substrate type, including the presence of corals and the absence of sand and others to water quality (Renema, 2010). Compared to other reef systems in the region, reefs in JBTI are dominated by *Calcarina* species that tolerate poor water quality. Furthermore, taxa that tolerate algal rather than rubble substrates dominated as well. In this study, we confirm that water quality appears to be an important driver of LBF assemblage composition.

Very few macroalgae were recorded in the highly perturbed inshore reefs of Jakarta Bay. Eutrophication tends to shift the dominant primary producers in coastal marine environments from slow growing seagrasses to frondose macroalgae to turf algae to faster growing phytoplankton (Duarte, 1995). Although macroalgae may temporarily benefit from high nutrient levels, increasing nutrification eventually leads to them being out-competed by turf algae and phytoplankton. The latter prevent sufficient light reaching the benthic seaweeds eventually leading to their demise. Moreover, most macroalgae need a hard substrate to attach to and the dominant substrate inshore mainly consisted of sand, silt and shifting rubble (Rachello-Dolmen and Cleary, 2007). Furthermore, the relatively high density of grazing sea urchins inshore may have a profound effect on the macroalgae. Additionally, the inshore islands lack lagoons and the shallower reefs provide less variation in habitat than the reefs around the deeper channel in the center of the study area, i.e., the northern part of zone 2 and the southern part of zone 3. The greatest number of macroalgal species were found around this channel. Interestingly, known indicator taxa of eutrophication, such as *Ulva* and *Chaetomorpha* (Barile, 2004; Teichberg et al., 2010) were only found in zone 3, but always entangled in *Sargassum* plants and at inhabited islands with perhaps locally elevated nutrient levels. The species *B. pennata*, which can be classified as a turf alga was, in contrast, restricted to inshore islands and may be considered a eutrophication indicator species. Other taxa that were common in inshore islands consisted of taxa belonging to species-rich genera that were also found mid- and offshore, e.g., *Dictyota*, *Lobophora* and *Padina*.

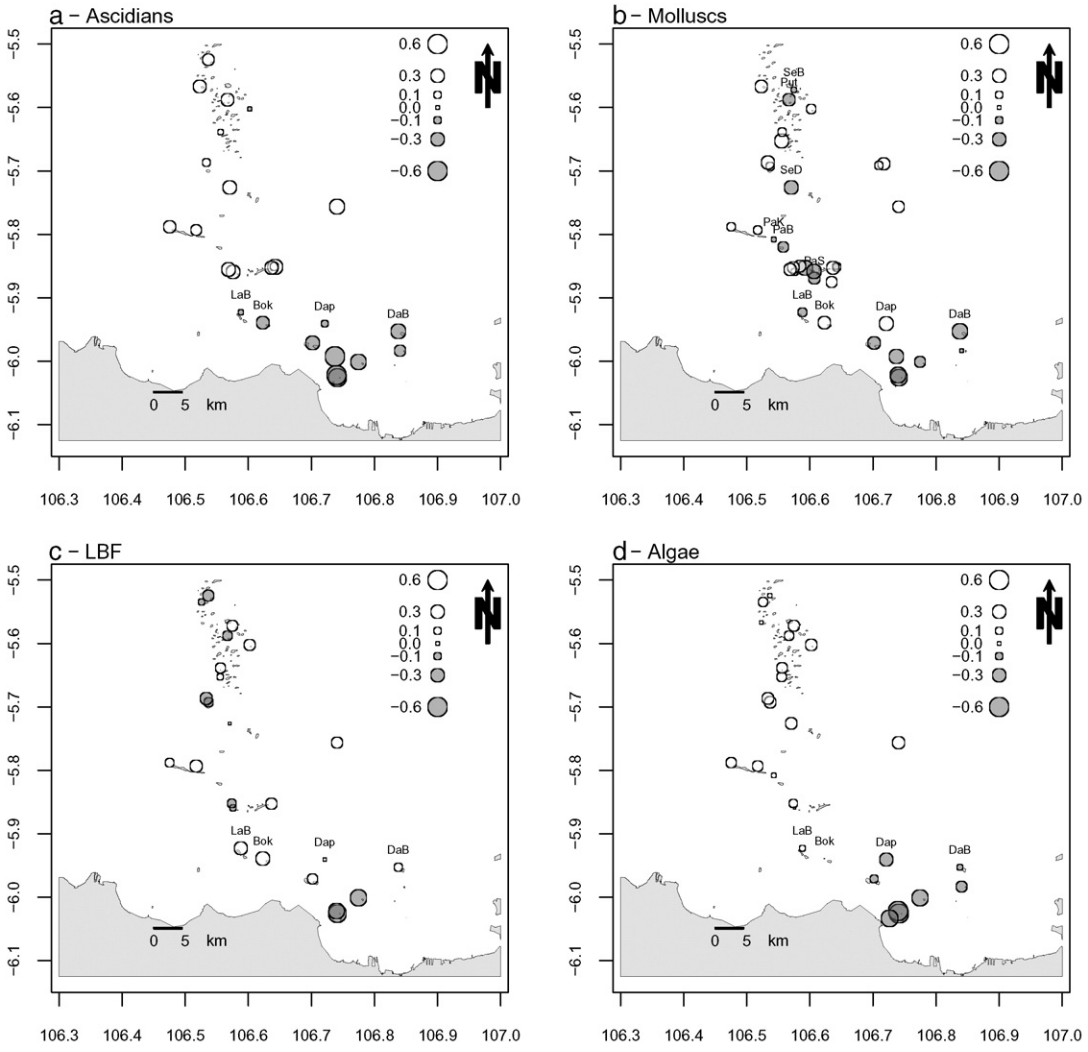

Fig. 9. Variation in site scores of the first PCO axis on a map of the study area for a) ascidians, b) molluscs, c) LBF and d) algae. Open symbols indicate positive values along the first axis and shaded symbols negative values. The size of the symbol is proportional to the score. Codes for the midshore sites closest to shore are given: LaB, Bok, Dap and DaB. For molluscs additional extra codes are shown for other mid- and offshores sites: PaS, PaB, PaK, SeD, Put and SeB.

In contrast to the other taxa, habitat variables were the most important predictors of echinoderms (14% versus 8%) and molluscs (9% versus 8%). Both of these groups, however, only consisted of a subset of all taxa and are not truly representative of the full taxon diversity. Nevertheless, in French Polynesia, Adjeroud (1997) found that encrusting coralline algal and macroalgal cover, depth and turbidity were significant predictors of mollusc composition. In our study water transparency, CDOM, sand and rubble cover were significant predictors of variation in mollusc composition. Adjeroud (1997) also found that conductivity, organic carbon, exposure and carbonates were significant predictors of echinoderm composition. In our study, significant predictors were CDOM, free-living mushroom and branching coral cover, sand cover and SST. In Moorea, sea urchins and damselfishes interacted to determine coral regeneration with much higher density and diversity of post-disturbance corals in damselfish territories. Sea urchins in Moorea (*D. setosum*, *Echinometra mathaei* and *E. calamaris*) in contrast caused widespread destruction of dead standing coral skeletons (Done et al., 1991). Although we only collected presence/absence data on echinoderm assemblages, during sampling we did notice very high densities of sea urchin species, particularly *D. setosum*, in inshore reefs. It is likely that these urchins have contributed to the highly simplified habitat structure prevalent in inshore reefs due to their bioeroding activity. In addition to the above, echinoderms and molluscs both deviated from the general pattern of clear compositional differences between inshore and mid- to offshore sites. Reef sites close to the islands of Pari (PaS) and Semak Daun (SeD), for example, both contained assemblages of echinoderms and molluscs resembling those of inshore reefs. Both of these islands also have areas of aquaculture in the surrounding water (pers. obs. DFR Cleary). It is possible that both of these groups respond to the local perturbation related to the aquaculture activities.

The purely spatial component was an important explanatory component (>10%) for corals, fishes, sponges and LBF. It should, however, be noted that despite the importance of this component, the explained variation may be related to unmeasured spatially structured environmental parameters. Sponges are an important component of coral reefs. Sponges compete with corals and other benthic taxa for available substrate and are therefore important components of reef dynamics (VanVeghel et al., 1996; Aerts and van Soest, 1997; de Voogd et al., 2004). The number of species encountered was highest offshore, whereas considerably fewer species were recorded inshore, particularly within the inner bay. The inshore sites tended to be very shallow, and seldom exceeded 10 m in depth. It has been shown that the diversity of coral reef-associated sponges increases with increasing depth (Fromont et al., 2006; de Voogd et al., 2006). However, although coral cover was also adversely affected by disturbance including riverine transport of sediments and nutrients inshore in the Berau region (East Borneo), these specific environmental conditions seemed to have a positive effect on sponges, as they were more abundant, larger and diverse

Table 2

Results of stepwise model building for constrained ordination for corals, fishes, sponges, echinoderms, ascidians, molluscs, LBF and algae. Type: substrate: substrate predictors; water quality: water quality predictors; spatial: spatial predictors; variable: explanatory variable; AIC: Akaike information criterion; Perm: number of permutations.

Taxon	Type	Variable	AIC	F	Perm	P
Corals	Substrate	Turf algae cover	−17.00	1.54	99	0.030
		Rubble cover	−16.91	1.63	99	0.010
		Sand cover	−12.39	6.12	99	0.010
	Water quality	CDOM	−16.82	1.42	199	0.045
		Temperature	−16.54	1.65	99	0.010
		Dissolved oxygen	−16.53	1.66	99	0.010
		Chlorophyll-a	−16.47	1.71	99	0.010
		Transparency	−16.39	1.77	99	0.010
	Spatial	PCNM2	−16.16	1.34	299	0.057
		PCNM5	−15.99	1.49	99	0.030
		PCNM10	−15.60	1.83	99	0.010
		PCNM1	−10.57	6.72	99	0.010
Fishes	Substrate	Rubble cover	−27.97	2.15	99	0.020
		Sand cover	−22.89	7.57	99	0.010
	Water quality	CDOM	−28.4	1.4	999	0.090
		Temperature	−28.27	1.5	199	0.050
		Dissolved oxygen	−28.13	1.61	99	0.030
		SST	−27.45	2.17	99	0.020
		Transparency	−27.86	1.83	99	0.010
		Chlorophyll-a	−27.44	2.17	99	0.010
	Spatial	PCNM5	−26.23	1.47	399	0.050
		PCNM10	−25.93	1.73	199	0.045
		PCNM14	−25.94	1.72	99	0.010
		PCNM1	−21.13	6.35	99	0.010
Sponges	Substrate	Encrusting coral cover	−14.49	1.38	599	0.066
		Sand cover	−11.73	4.11	99	0.010
	Water quality	Transparency	−14.98	1.96	99	0.010
		CDOM	−14.77	2.15	99	0.010
		SST	−14.66	2.25	99	0.010
		PCNM9	−14.13	1.59	199	0.035
	Spatial	PCNM3	−14.1	1.62	99	0.03
		PCNM2	−13.6	2.06	99	0.01
		PCNM1	−11.13	4.36	99	0.01
Echinoderms	Substrate	Branching coral cover	−19.54	1.81	199	0.060
		Sand cover	−19.44	1.88	99	0.045
		Mushroom coral cover	−18.90	2.37	99	0.020
		Acropora	−18.85	2.42	99	0.020
	Water quality	SST	−19.07	1.76	199	0.030
		CDOM	−18.12	2.68	99	0.010
	Spatial	PCNM1	−17.26	4.61	99	0.010
Ascidians	Substrate	Foliose coral cover	−5.04	1.53	299	0.030
		Macroalgae cover	−5.03	1.54	99	0.030
		Sand cover	−3.17	3.24	99	0.010
	Water quality	Salinity	−5.912	1.57	199	0.030
		Temperature	−5.802	1.67	199	0.030
		Chlorophyll-a	−5.395	2.03	99	0.010
	Spatial	PCNM3	−5.425	1.35	999	0.083
		PCNM1	−3.139	3.57	99	0.010
Molluscs	Substrate	Rubble cover	−2.81	1.56	99	0.030
		Sand cover	−2.55	1.81	99	0.010
	Water quality	Transparency	−2.95	1.55	99	0.010
		CDOM	−2.542	1.94	99	0.010
	Spatial	PCNM3	−2.373	1.43	99	0.03
		PCNM1	−2.364	1.44	99	0.03
LBF	Substrate	Sand cover	−24.95	3.52	99	0.020
		Encrusting coral cover	−23.84	4.68	99	0.020
	Water quality	Dissolved oxygen	−23.84	2.12	599	0.062
		Rrs_645	−23.32	2.56	199	0.05
		Chlorophyll-a	−21.43	4.23	99	0.03
		Temperature	−22.72	3.07	99	0.02
		SST	−22.03	3.69	99	0.02
	Spatial	PCNM2	−23.85	1.81	99	0.100
		PCNM9	−23.77	1.88	99	0.097
		PCNM5	−23.80	1.85	99	0.087
		PCNM11	−22.90	2.61	19	0.050
		PCNM1	−22.58	2.88	19	0.030
Algae	Substrate	Mushroom coral cover	−16.63	1.74	99	0.020
		Sand cover	−15.19	3.14	99	0.010
	Water quality	CDOM	−16.73	1.37	199	0.050
		Transparency	−16.51	1.56	99	0.030
		SST	−16.49	1.58	99	0.030
		Chlorophyll-a	−16.3	1.74	99	0.020
	Spatial	PCNM2	−16.85	1.47	199	0.035
		PCNM1	−13.7	4.62	99	0.01

inshore (de Voogd et al., 2009). As mentioned previously, the environment of the inshore zone was characterised by high turbidity and very low live coral cover with the dominant substrate composed of silt, sand and rubble. The inshore reefs are probably degraded to such an extent that most sponge species cannot cope. There were, however, some sponge species found in inshore sites including *Amphimedon* cf. *paraviridis*, *C. joubini*, *S. inconstans*, *Chalinula hooperi*, *D. arenaria* and *S. ceylonensis*. *Spheciospongia inconstans* is a massive cake forming sponge, the early growth stages of which can excavate coral limestone. The species may appear as thick encrustations and can also grow very well on soft bottom substrate. Also the Indo-Pacific bath sponge *S. ceylonensis* has a preference for soft bottom substrate, particularly in shallow water environments. Other sponge species often associated with perturbed environments such as the moon sponge *Cinachyrella australiensis* and *Paratatetilla bacca* were absent from the inshore sites. Sponge species associated with offshore sites included *H. erectus*, *Ircinia ramosa*, *S. carteri* and *C. cervicornis*. These sponges are common throughout the Indonesian archipelago and usually occur across a wide range of environmental conditions (de Voogd et al., 2006, 2009).

In general, satellite-derived water quality variables outperformed locally measured water quality variables in line with a previous study of a set of coral reef taxa in the Spermonde archipelago (Polónia et al., 2015). Chlorophyll-a and CDOM concentrations in particular proved important predictors. Chlorophyll-a concentration and/or transparency were the most significant explanatory water quality variables of variation in the composition of corals, fishes, ascidians and algae whereas CDOM was the most significant explanatory water quality variable of variation in the composition of echinoderms and molluscs (Table 2). SST was the most significant explanatory water quality variable of variation in the composition of sponges and LBF. Chlorophyll-a concentrations were much higher in the waters surrounding inshore reefs than waters surrounding mid- and offshore reefs (Appendices 4 and 5 in the online version at http://dx.doi.org/10.1016/j.marpolbul.2016.04.042.). Chlorophyll-a is an important eutrophication indicator (Boyer et al., 2009) and the elevated levels found inshore highlight the dilapidated state of the Jakarta Bay environment.

The importance of CDOM as a predictor of variation in composition is inline with previous studies that have pointed to dissolved organic matter as an important factor in structuring coastal communities (Ayoub et al., 2009; Baña et al., 2014). High chlorophyll-a concentrations also appear to enhance dissolved organic matter fluxes, which provide an important source of food for LBF and corals (Renema and Troelstra, 2001; Eberwein and Mackensen, 2006; Houlbreque and Ferrier-Pagès, 2009). Our study, however, contrasts with previous studies (e.g., Polónia et al., 2015) where chlorophyll-a and CDOM concentrations were higher inshore than offshore. In contrast, the highest CDOM concentrations in our study were measured offshore as can be seen in the association of CDOM with offshore sites (Supplementary Figs. 1 and 2 in the online version at http://dx.doi.org/10.1016/j.marpolbul.2016.04.042.). However, this anomaly is probably related to the particular environment of Jakarta Bay and the inshore reefs. High CDOM concentrations are normally found in inshore coastal areas with intact shorelines, i.e., relatively undisturbed coastlines with still intact coastal mangroves, forests and seagrass beds (Ayoub et al., 2009, 2012). Destruction of coastal forests and wetlands has, however, led to a reduction in natural sources of CDOM to coastal waters. The coastal environment of Jakarta Bay is highly modified, consisting mainly of built-up and agricultural land. Most of the original forests and mangroves have been destroyed, which can be seen as the cause of the low CDOM values inshore. A close examination of remote sensing images of CDOM plumes offshore appeared to show that they originated from the still intact coastline of Borneo (pers. obs. ARM Polónia). Importantly, CDOM has been shown to protect marine organisms from ultraviolet (UV) radiation and shorter wavelengths of PAR (Shank et al., 2010; Ayoub et al., 2012). The coastal forests of Borneo may thus be protecting JBTI coral reefs from the adverse effects of excessive UV radiation, a phenomenon which has also been linked to coral bleaching (Gleason and Wellington, 1993).

5. Conclusion

Water quality, substrate and spatial variables were significant predictors of the variation in composition of a wide range of coral reef taxa. There were, however, differences in the relative importance of these variables with water quality variables more important predictors of the compositional variation of corals, fishes, sponges, LBF, ascidians and algae whereas substrate variables were more important predictors of echinoderm and mollusc composition. Remotely sensed water quality variables also tended to be more important predictors of variation in composition than locally measured variables. This highlights the importance of these variables as predictors of both water quality and the composition of coral reef taxa.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marpolbul.2016.04.042.

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