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Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia

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Abstract. Very few coral reefs are located close enough to metropolitan cities to study the influence of large urban populations on reef communities. Here, we compare the impact of a large-scale disturbance gradient with local-scale disturbance on coral richness, cover, and composition in the Jakarta Bay and Pulau Seribu reef complex off Jakarta, Indonesia. We found no effect of local land-use type of coral reef islands on richness, composition or cover, nor did taxon richness differ among zones at the large-scale. There was, however, a pronounced difference in composition and coral cover among zones. Cover was very low and composition differed markedly in the near-shore zone 1 (Jakarta Bay) where human-induced disturbance is most intense. Cover was highest in the outlying reefs of zone 3. The highly perturbed zone 1 reefs were, furthermore, distinguished by the virtual absence of otherwise abundant coral taxa such as *Acropora hyacinthus* and *Porites rus* and the prevalence of taxa such as *Oulastrea crispata* and *Favia maxima*. Almost 60% of the spatial variation in composition was related to variation in shelf depth and island size. The importance of shelf depth was related to the prevalence of a strong environmental gradient in reef depth, pollution, and mechanical reef disturbance and salinity from Jakarta Bay to the outlying reefs. Although there was a significant univariate relationship between spatial variation in composition and distance, this did not enter into the multivariate model, except when presence-absence data was used, indicating that environmental processes are the primary structuring forces in determining local coral assemblage composition across the Pulau Seribu complex.

Introduction

The realisation that coral reefs provide critical goods and services to tropical and subtropical maritime nations has stimulated the establishment of marine reserves (Hughes et al. 2003). It is often unclear, however, to what extent reserve establishment has been able to mitigate adverse human or natural perturbations that affect reefs around the globe (Bruner et al. 2001). The reserves themselves are also coming under increasing pressure as resources are depleted outside of reserve boundaries (Sala et al. 2002). In addition to this, conservation planning has generally not been systematic and new reserves have often been located in places that do not contribute to the representation of

biodiversity (Margules and Pressey 2000). Reserves alone are thus not sufficient for nature conservation and strategies are required for managing whole landscapes including areas allocated to production (Margules and Pressey 2000). Bellwood and Hughes (2001), therefore, note the need to develop management strategies to protect coral reefs over large regional scales. Focus should then shift from individual taxa to habitat and community characteristics.

In order to preserve coral reef diversity by designing and placing conservation refugia, it is essential to understand how assemblages change in space and time (Plotkin and Muller-Landau 2002; Hughes et al. 2003; Pandolfi et al. 2003). The coral reefs of Indonesia, for example, are among the most diverse in the world (Best et al. 1989; Hoeksema 1992; Hoeksema and Putra 2002; Wallace et al. 2002). We are only just beginning to learn more about spatial variation in diversity within and among reef systems and the mechanisms that maintain this diversity (Karlson and Cornell 1998, 1999, 2002; Cornell and Karlson 2000; Bellwood and Hughes 2001; Hughes et al. 2002). The lack of a thorough understanding of this spatial variation in diversity represents an important hiatus in our understanding of coral reef ecosystems, especially in light of recent findings that suggest that many coral reefs may disappear or will be severely degraded within the next few decades (Sheppard 2003). More research is thus needed to monitor and assess reef ecosystems both within and outside of established reserves. Formal scientific research programs are essential to understanding and improving the management and protection of ecological integrity. An especially important goal is the examination of greater park ecosystems (Zorn et al. 2001).

In the present study, we assess coral richness and community composition in the Jakarta Bay and Pulau Seribu reef complex. This area was chosen as a prime area to initiate a pilot project of the Coastal Zone and Small Islands endeavours coordinated by UNESCO (United Nations Education, Scientific and Cultural Organisation) in cooperation with the LIPI (Indonesian Institute of Sciences) research centre for oceanography (Kuijper 2003). Its goal is to support inland and small island communities towards appropriate integrated coastal management by reducing the impact of a coastal mega-city on the island ecosystems of Jakarta Bay and Seribu Islands. Through the collection of time series baseline data, this component was implemented to study the dynamic changes of coral assemblages in 1985. Coral reefs in the vicinity of Jakarta are suitable for this purpose because they have been monitored since the late 1920s and more recently have become increasingly affected by various activities such as river discharge, urban development, tourism, destructive fisheries and coral mining (Moll and Suharsono 1986; Harger 1986a, b, 1998; Sukarno 1987). Pulau Seribu was Indonesia's first established marine national park, founded in 1982 (Djohani 1994). It is located to the northwest of Jakarta, Indonesia and consists of 105 islands or cay-crowned reefs that are administered by the Jakarta city government. Most cays have designated land-uses that can be divided into three main categories; these include: (1) conservation, (2) residential, and (3) tourism. In addition to this, there are some uninhabited

islands and some islands that are so severely degraded by humans (e.g., Ayer Kecil, Ubi Kecil, and Nyamuk Kecil) that they have virtually eroded away (Onkosongo 1986, Ongkosongo and Sukarno 1986; Stoddart and Brown 1986). The nature reserves (conservation land-use) include the islands of Kelor, Rambut, Bokor, and Belanda. Locals, who engage in fishing, sand mining or catering to tourists, inhabit other islands. In general, the islands are small (<10 ha) and low-lying (<3 m a.s.l.). The bathymetry, geomorphology, hydrochemical and geochemical setting of Pulau Seribu have been described in some detail, making it one of the better-known reefs systems in Indonesia (Umbgrove 1928, 1929, 1939; Verwey 1931; Rees et al. 1999; Williams et al. 2000).

Here we present data from the first UNESCO survey (1985) where coral assemblages were assessed at 28 patch reefs throughout the Pulau Seribu reef complex (including Jakarta Bay). Reef assemblages are described at three taxonomic levels of detail (species, genus, and family level) and we, furthermore, relate assemblage turnover to spatial and environmental variables in order to assess the relative contribution of both to structuring coral assemblages. Previous studies have shown that environmental parameters such as salinity, sea surface temperature and currents are important in structuring coral assemblages (Veron 1995; Chen 1999). In addition, we make use of environmental data collected during the project, including data on household density, litter abundance, salinity and temperature (Willoughby 1986). Litter, for example, may originate from domestic, industrial or agricultural sources and can be used as an indication of environmental degradation; it is not only an eyesore on beaches but may also collect in sublittoral sinks and smother benthic communities (Uneputti and Evans 1997).

The aims of this study are to:

1. Compare live coral cover, diversity, and community composition at three taxonomic levels among large-scale and local-scale disturbance zones.
2. Relate total live coral cover and community composition at three taxonomic levels to spatial and environmental conditions.

Materials and methods

Research site

All research took place in the Pulau Seribu marine national park and adjacent reefs in Jakarta Bay that extends from Jakarta bay on the northwestern coast of Java, Indonesia to more than 80 km to the Northwest. Jakarta is one of the largest urban environments in the world with more than 10 million people living in a 460-km² area. Several rivers transport sewage and storm-water over a 2000 km² catchment area to the central sector of the bay, which is, furthermore, defined by two flanking delta systems with a large sediment input (Rees et al. 1999). Annual precipitation averages 1700 mm/yr with a 'wet'

season during the northwest monsoon (November–March) and a ‘dry’ season during the southeast monsoon (May–September) (Rees et al. 1999). In the present study, we assess the Pulau Seribu reef system by studying 28 reefs associated with islands in three zones and three different designated land-use types, namely conservation, residential, and tourism. The zones are based on geomorphology, oceanography, and distance from Jakarta (Tomascik et al. 1994; DeVantier et al. 1998) and include: (1) reefs within Jakarta bay, (2) mid region reefs (15–50 km offshore from Jakarta), and (3) outer-region reefs (> 50 km offshore from Jakarta). The three land-use types include: (1) conservation, (2) residential, and (3) tourism (DeVantier et al. 1998). The zones represent a gradient from severe large-scale disturbance in zone 1 to relatively minor disturbance in zone 3. The land-use types likewise reflect variation in local disturbance from islands with a residential and tourism designation to uninhabited islands with a conservation designation. The zone, geographic position, and land-use classification for all islands are presented in Table 1. Note that some islands did not have a designated land-use type. This included uninhabited islands such as Lancang Besar, islands such as Panjang that had no residential designation but were used for coconut harvesting and additionally had a small airport, and finally islands such as Nyamuk Besar and Ubi Besar that had eroded below sea level.

Reefs of zone 1 are located within the Jakarta bay area (Figure 1) and are dominated by sand, rubble, and algae. The water quality is very poor, with high plankton concentrations, and accumulated rubbish (Ongkosongo 1986). Hungspreugs (1988) and Ongkosongo (1986) reported severe contamination in the sediments and water of Jakarta bay including heavy metals (Hg, Cd, and Pb), pesticides (DDT and dieldrin) and petroleum. There is also a marked lack of primary sewer treatment (Ongkosongo 1986). In addition to water-borne pollution, these reefs have been seriously affected by dredging operations (DeVantier et al. 1998). Despite the dilapidated state of most of the reefs in zone 1 they once contained thriving coral communities (Umbgrove 1939). Although Umbgrove (1928) already mentioned some localised disturbances to various reefs, most of the damage to reefs of zone 1 and throughout the Pulau Seribu reef system can be attributed to a series of perturbations from the 1940s onwards; the environmental conditions have continued to deteriorate at an accelerating rate since the 1980s. Small-scale (manual) extraction of coral and sand for building combined with dredging, for example, was still localised in the 1970s, intensified and spread during the 1980s and, although officially banned, is now an important resource for various small communities along the coast. Mangrove destruction has generally been the result of land reclamation and fishpond establishment leading to increased sedimentation and general environmental degradation.

The reefs of zone 2 are outside the major influence of Jakarta bay but have been subject to widespread phenomena related to ENSO events (Brown and Suharsono 1990) and localised disturbance related to fishing (Erdmann 1998). During the dry season, the predominantly south-easterly winds cause polluted

Table 1. Summary data for each island sampled during the 1985 coral survey.

Island	Code	Zone	Activity	Transects	Shelf depth (m)	Col.	Coral Cover	% Cover	Species richness	Latitude S	Longitude E
Ayer Besar	AyB	1	Tourism	2	20	97	1017	16.95	7.76	6 00.04	106 46.80
Ayer kecil	AyK	1	Other	2	19	64	512	8.53	7.66	5 59.10	106 45.50
Bidadari	Bid	1	Tourism	2	10	16	184	3.07	7.50	6 01.91	106 44.78
Kelor	Kel	1	Conservation	2	12	21	277	4.62	7.21	6 01.51	106 44.62
Nyamuk besar	NyB	1	Other	2	18	20	225	3.75	7.95	6 01.80	106 51.00
Nyamuk kecil	NyK	1	Other	2	18	28	310	5.17	6.77	6 00.30	106 49.85
Onrust	Onr	1	Tourism	2	9	51	373	6.22	5.89	6 01.93	106 44.00
Ubi besar	UbB	1	Other	2	15	10	53	0.88	8.00	5 59.91	106 44.42
Bokor	Bok	2	Conservation	4 (2)	24	136	2198	36.63	7.24	5 56.61	106 37.64
Damar besar	DaB	2	Residential	2	29	95	1938	32.30	8.73	5 57.27	106 50.44
Damar kecil	DaK	2	Residential	2	19	108	1082	18.03	8.53	5 59.02	106 50.72
Dapur	Dap	2	Other	2	28	122	2102	35.03	6.62	5 55.73	106 43.93
Lancang Besar	Lan	2	Other	2	21	182	3379	56.32	6.72	5 55.59	106 35.50
Rambut	Ram	2	Conservation	2	14	112	1895	31.58	8.47	5 58.30	106 41.20
Tidung	Tid	2	Residential	2	33	207	3718	61.97	8.81	5 48.04	106 31.54
Tikus	Tik	2	Residential	2	32	235	4007	66.78	8.74	5 51.94	106 34.94
Untung Jawa	UnJ	2	Residential	2	15	61	1040	17.33	8.24	5 58.40	106 41.00
Air	Air	3	Residential	2	33	132	2904	48.40	8.75	5 45.65	106 35.69
Belanda	Bel	3	Conservation	2	31	216	7778	129.63	7.93	5 36.23	106 36.15
Hantu Besar	HaB	3	Tourism	2	29	100	2593	43.22	6.91	5 31.74	106 32.31
Hantu kecil	HaK	3	Tourism	2	29	139	3604	60.07	7.88	5 32.18	106 31.79
Jukung	Juk	3	Residential	2	27	192	7442	124.03	7.10	5 34.01	106 31.64
Kelapa	Kpa	3	Residential	2	35	182	3074	51.23	8.60	5 39.30	106 33.55
Kotok Besar	KoB	3	Tourism	3 (2)	31	47	4119	68.65	8.42	5 41.92	106 32.38
Kotok Kecil	KoK	3	Residential	1	31	128	985	32.83	8.47	5 41.37	106 31.98
Panjang	Pan	3	Other	2	30	177	3890	64.83	6.47	5 38.59	106 33.58
Putri	Put	3	Tourism	2	31	234	5610	93.50	8.20	5 35.39	106 34.03
Sepak	Sep	3	Tourism	2	29	126	3176	52.93	8.25	5 34.45	106 34.79

Note that at each site a shallow and deeper transect were sampled except in Kotak Kecil. In Kotak Besar and Bokor a total of three and four transects were sampled, respectively, but only two of these were used in the present analyses. Under land-use, 'other' generally refers to uninhabited islands. Col. refers to the number of coral colonies sampled. Coral cover (cm) refers to the length of transect occupied by live coral colonies. % cover refers to the percentage of the transect with live coral cover; note that this could exceed 100% due to overlapping coral colonies. Species richness indicates the mean number of species obtained using rarefaction based on ten individuals.

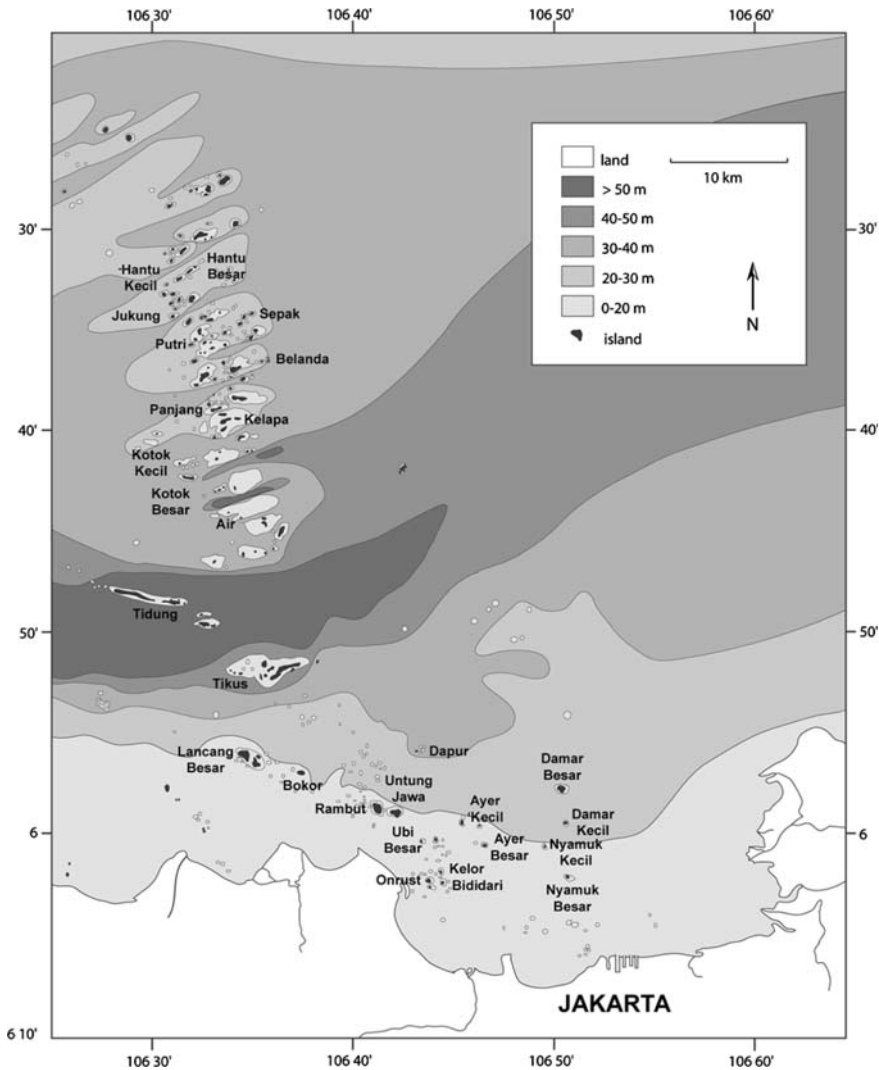


Figure 1. Map of the Jakarta Bay and Pulau Seribu reef complex. The reefs sampled during this study are indicated.

surface waters from Jakarta and proximate rivers to flow over these reefs, but during the wet season the monsoon winds change direction and blow mainly from the north-west, thereby limiting the spread of pollutants.

The reefs of zone 3 are furthest from Jakarta and therefore distant from the source of most waterborne pollutants, although there is some oil exploration and extraction going on to the northwest. Other disturbances in zone 3 include blast- and poison-fishing, widespread ENSO-related phenomena, local population pressure and periodic outbreaks of coral predators such as

Acanthaster planci (De Vantier et al. 1998; Vail and Thamrongnawasawat 1998). There is, however, no large-scale dredging activity as is the case in zone 1.

Sampling

All sampling took place between May 6–16th, 1985. Twenty-eight patch reefs (Figure 1) were sampled at two depth ranges (i.e., 1–3 m range and 3–5 m range). In each site a shallow and a deep line-transect (30 m) were established, except in Kotak Kecil island in which only one transect was established (Moll and Suharsono 1986). The sampling methodology used was the line-intercept transect method (English et al. 1994). Individual coral colonies were identified to species and their cover measured using a fibreglass measuring tape. In addition to assessing coral colonies located on the line transect, the area surrounding the line transect was also surveyed for coral species presence, which was used in a presence–absence analysis. A list of all species encountered is presented by Moll and Suharsono (1986). Besides the coral guide by Umbgrove (1939), the series *Scleractinia* of Eastern Australia was used for coral identification during the survey (Veron and Pichon 1976, 1979, 1982; Veron et al. 1977; Veron and Wallace 1984). In the present paper, the nomenclature of the species (see Table 2) is updated according to the most recent taxonomic revisions (Hoeksema 1989; Wallace 1999).

Analyses

Richness and cover

For all subsequent analyses we pooled the shallow and deep transects so that assessments are made on an island basis. Estimates of the number of families, genera, and species were obtained using rarefaction based on a sample size of 10 (minimum number of colonies per island) using PRIMER v5 (Clarke and Gorley 2001). Since the data did not deviate significantly from normality we used one-way ANOVAs within Statistica 6.1 (Statsoft, Tulsa, USA) to test for significant differences in the number of families, genera, species, and coral cover among zones (1–3) and among land-use types (conservation, residential, and tourism).

Community composition and indicator taxa

Variation in coral community composition among zones (1, 2, and 3) and among land-use types (conservation, residential, and tourism) was tested for significance using ANOSIM (nonparametric analysis of similarities; Clarke and Gorley 2001) based on a Bray–Curtis similarity matrix (Bray and Curtis 1957) within the package PRIMER v5 (Clarke and Gorley 2001). The results of the ANOSIM analyses are presented in addition to multidimensional

Table 2. List of significant indicator taxa ($p < 0.05$).

Level	Indicator taxon	IV	Zone
Family	Dendrophylliidae	37.50	1
	Acroporidae	92.69	2/3
	Pocilloporidae	81.82	2/3
	Merulinidae	80.15	2/3
	Oculinidae	77.57	2/3
	Fungiidae	72.23	2/3
	Agaricidae	67.74	2/3
	Poritidae	65.71	2/3
	Mussidae	58.63	2/3
Genus	<i>Oulastrea</i>	46.26	1
	<i>Turbinaria</i>	37.50	1
	<i>Montipora</i>	59.08	2
	<i>Galaxea</i>	57.39	2
	<i>Coeloseris</i>	47.47	2
	<i>Euphyllia</i>	33.33	2
	<i>Seriatopora</i>	64.06	3
	<i>Acropora</i>	56.41	3
	<i>Echinopora</i>	54.67	3
	<i>Ctenactis</i>	51.48	3
	<i>Porites</i>	47.84	3
	<i>Oulastrea crispata</i>	46.26	1
	<i>Favia maxima</i>	43.55	1
Species	<i>Turbinaria peltata</i>	37.50	1
	<i>Montipora hispida</i>	80.73	2
	<i>Acropora divaricata</i>	75.64	2
	<i>Acropora cytherea</i>	68.49	2
	<i>Montipora stellata</i>	62.75	2
	<i>Fungia repanda</i>	59.02	2
	<i>Acropora granulosa</i>	55.35	2
	<i>Montipora digitata</i>	54.51	2
	<i>Coeloseris mayeri</i>	47.47	2
	<i>Acropora yongei</i>	38.19	2
	<i>Cyphastrea microphthalma</i>	33.33	2
	<i>Galaxea astreata</i>	33.33	2
	<i>Acropora tenuis</i>	75.21	3
	<i>Acropora brueggemanni</i>	71.61	3
	<i>Acropora muricata</i>	71.47	3
	<i>Acropora aspera</i>	66.08	3
	<i>Acropora nasuta</i>	65.16	3
	<i>Seriatopora hystrix</i>	63.51	3
	<i>Acropora longicyathus</i>	60.67	3
	<i>Porites lutea</i>	58.38	3
	<i>Echinopora lamellosa</i>	52.44	3
	<i>Acropora humilis</i>	49.08	3
	<i>Favia stelligera</i>	45.91	3
	<i>Hydnophora rigida</i>	45.60	3
	<i>Lobophyllia corymbosa</i>	45.45	3
	<i>Goniastrea retiformis</i>	42.71	3
	<i>Acropora cerealis</i>	40.02	3

Table 2. Continued.

Level	Indicator taxon	IV	Zone
	<i>Acropora robusta</i>	36.36	3
	<i>Ctenactis crassa</i>	36.36	3
	<i>Favia danae</i>	36.36	3
	<i>Porites cylindrica</i>	32.40	3

IV = indicator value. Zone: significant indicator of given zone.

**t*-Test based on computations of the weighted distance between randomised values and the observed values.

scaling (MDS) ordinations based on the same similarity matrix. Analyses were performed separately at three different taxonomic levels (species, genus, and family) and for the presence-absence data separately. Multidimensional scaling has various advantages over other multivariate techniques for use in ecological studies; the results have been found to be robust under a wide range of conditions. MDS, furthermore, does not have stringent model assumptions, such as correspondence analysis, which assumes a unimodal response, and any similarity measure can be used for ordination (Beck et al. 2002).

Following the ANOSIM analyses, we identified coral indicator taxa using the Indicator Value (IndVal) method (Dufrêne and Legendre 1997). This method assesses, for each taxon, whether it is a significant indicator of a particular habitat (zone) based on the criteria of specificity to and its frequency within that habitat. The IndVal measure represents the degree to which a given taxon is unique to a particular habitat and frequent within that habitat (van Rensburg et al. 1999). The higher the IndVal score, the more representative a taxon is for a given habitat. Species with high IndVal scores are thus good indicator taxa because they are habitat specific and have a high probability of being sampled during monitoring. Rare taxa cannot have a high IndVal measure because they will be absent from the majority of sites within a given habitat even though they may be restricted to that habitat.

The taxon abundance matrix was used as the input for the programme IndVal 2.0 (Dufrêne 1998). The sites were arranged in a hierarchical typology, which tested between sites in zone 1 with sites in zones 2 and 3 and among sites in all three zones. Significance was based on a randomisation procedure (with 999 iterations) of sites. The randomisation test randomly reallocated sites among site groups (zones) to test for significance in the IndVal measure for each taxon separately. Only taxa that were significant (at an $\alpha < 0.05$) for tests of both the IndVal Index and a *t*-test, which computed the weighted distance between randomised values and the observed value, are here considered significant.

Community similarity

To examine whether community similarity was dependent upon environmental variables and geographic distance between sampling sites, we used non-parametric forward matrix regression within the program *Permute!* 3.4.9 (Casgrain 2001). First, we constructed a Bray–Curtis (Bray and Curtis 1957) community similarity matrix using $\log_{10}(x + 1)$ transformed abundance data for families, genera, and species separately, and a Sørensen (Sørensen 1948) community similarity matrix using the species-level presence–absence data. We then tested whether these community similarity matrices were dependent upon a series of variables based on Euclidean (distance) or normalised Euclidean (environmental) matrices. These variables were: (1) a spatial matrix of geographic distance between sites; (2) an environmental matrix of $\log_{10}(x + 1)$ transformed island size; (3) an environmental matrix of $\log_{10}(x + 1)$ transformed number of households; (4) an environmental matrix of $\log_{10}(x + 1)$ transformed rubbish abundance; (5) an environmental matrix of $\log_{10}(x + 1)$ transformed visibility; (6) an environmental matrix of $\log_{10}(x + 1)$ transformed shelf depth; (7) an environmental matrix of $\log_{10}(x + 1)$ transformed temperature; (8) an environmental matrix of $\log_{10}(x + 1)$ transformed salinity. In addition to the above analyses, we also tested to what extent variation in $\log_{10}(x + 1)$ transformed live coral cover was dependent upon the above-mentioned set of distance and environmental variables. The options for 999 permutations, forward selection and a Bonferroni-corrected p -to-enter value of 0.10 were selected.

Results

Richness and cover

We recorded a total of 13 families, 44 genera, and 158 species over 3504 individuals. There were no significant differences in the number of families ($F_{2, 25} = 0.150$, $p = 0.861$; Figure 2a), genera ($F_{2, 25} = 2.436$, $p = 0.108$; Figure 2b), or species ($F_{2, 25} = 1.750$, $p = 0.194$; Figure 2c) among zones, but cover (Figure 2d) was significantly higher ($F_{2, 25} = 17.975$, $p < 0.001$) in zone 3 than in zones 1 ($p < 0.001$) and 2 ($p = 0.021$) and significantly higher in zone 2 than in 1 ($p = 0.018$). There were no significant differences in the number of families ($F_{2, 17} = 0.450$, $p = 0.645$), genera ($F_{2, 17} = 0.226$, $p = 0.800$) or species ($F_{2, 17} = 1.750$, $p = 2.941$) among land-use types, nor was there a significant difference in cover among land-use types ($F_{2, 17} = 0.386$, $p = 0.685$).

Community composition and indicator taxa

At the family level (Figure 3a), composition differed significantly between zones 1 and 2 ($R_{\text{ANOSIM}} = 0.586$, $p = 0.002$) and between 1 and 3

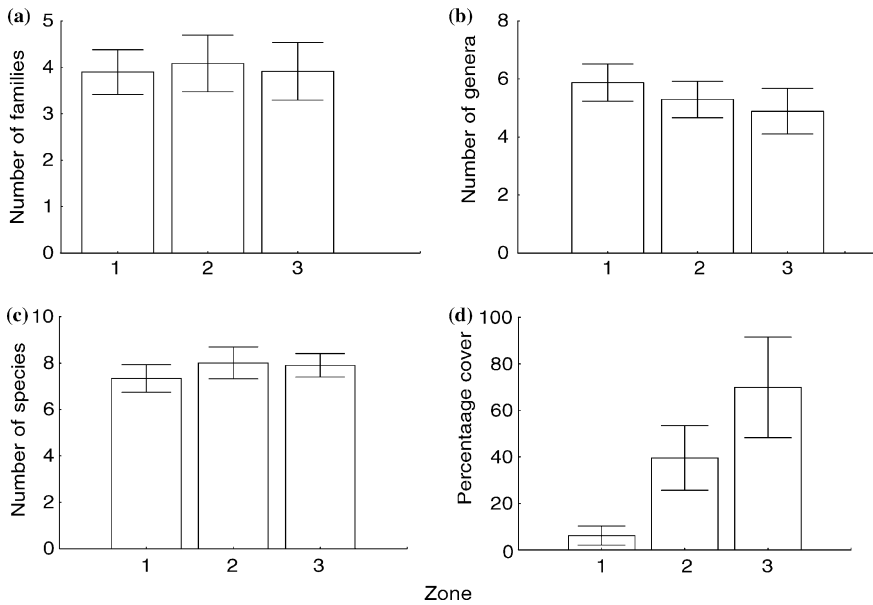


Figure 2. Mean ($\pm 95\%$ confidence intervals) (a) number of families, (b) number of genera, (c) number of species and (d) percentage of live coral cover per zone.

($R_{\text{ANOSIM}} = 0.617$, $p < 0.001$), but there was no significant difference between zones 2 and 3 ($R_{\text{ANOSIM}} = -0.047$, $p = 0.785$). At the generic level (Figure 3b), composition differed significantly between zones 1 and 2 ($R_{\text{ANOSIM}} = 0.590$, $p < 0.001$), 1 and 3 ($R_{\text{ANOSIM}} = 0.715$, $p < 0.001$) and 2 and 3 ($R_{\text{ANOSIM}} = 0.213$, $p = 0.003$). Species composition (Figure 3c) also differed significantly between zones 1 and 2 ($R_{\text{ANOSIM}} = 0.546$, $p < 0.001$), 1 and 3 ($R_{\text{ANOSIM}} = 0.780$, $p < 0.001$) and between zones 2 and 3 ($R_{\text{ANOSIM}} = 0.546$, $p < 0.001$). Using the presence-absence data (Figure 3d), composition differed significantly between zone 1 and zones 2 ($R_{\text{ANOSIM}} = 0.499$, $p < 0.001$) and 3 ($R_{\text{ANOSIM}} = 0.832$, $p < 0.001$) and between zones 2 and 3 ($R_{\text{ANOSIM}} = 0.521$, $p < 0.001$). There was no significant difference in composition at family (Global $R_{\text{ANOSIM}} = -0.010$, $p = 0.498$), genus (Global $R_{\text{ANOSIM}} = 0.012$, $p = 0.404$) or species-level (Global $R_{\text{ANOSIM}} = 0.068$, $p = 0.177$) among land-use types, nor was there a significant difference using presence-absence data (Global $R_{\text{ANOSIM}} = 0.090$, $p = 0.177$).

At the family level, we found eight significant indicator taxa for zones 2 and 3 combined and only one weak indicator taxon (Dendrophylliidae) for zone 1 (Table 2). At the generic level, we found two significant indicator taxa for zone 1, four for zone 2 and five for zone 3. At the species level, we found three significant indicator taxa for zone 1, 11 for zone 2 and 19 for zone 3. In addition to indicator species for each zone separately, there were also

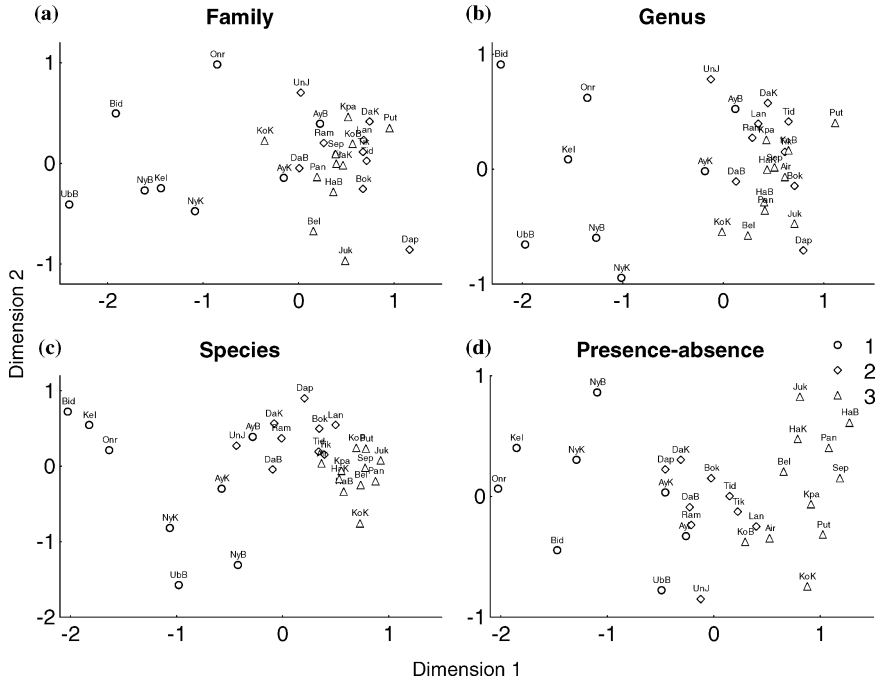


Figure 3. Multidimensional scaling ordinations based on (a) family level data, (b) genus-level data, (c) species-level data and (d) presence-absence data. Islands from different zones are indicated by symbols (circles: zone 1; diamonds: zone 2; triangles: zone 3). Point labels identify islands following the codes used in Table 1.

significant indicator species (e.g., *Acropora hyacinthus*, $IV = 76.56$ and *Porites rus*, $IV = 86.59$) that differentiated zones 2 and 3 combined from zone 1. Indicator values were, furthermore, substantially higher for species from zones 2 (e.g., *Montipora hispida*, 80.73; *Acropora divaricata*, 75.64) and 3 (e.g., *Acropora tenuis*, 75.21; *Acropora brueggemanni*, 71.61) than for species from zone 1 (e.g., *Oulastrea crispata*, 46.26; *Favia maxima*, 43.55).

Community similarity

We found a negative relationship between community similarity and distance between sampling sites for families ($b = -0.115$, $p = 0.064$, $R^2 = 0.013$; Figure 4a), genera ($b = -0.181$, $p = 0.012$, $R^2 = 0.033$; Figure 4b), species ($b = -0.322$, $p < 0.001$, $R^2 = 0.104$; Figure 4c) and presence-absence data ($b = -0.536$, $p < 0.001$, $R^2 = 0.287$; Figure 4d). Distance, however, only entered significantly into the multivariate model when we used presence-absence data (Table 3). In all other analyses the only significant predictors of similarity were shelf depth and island size (Figure 5) but the amount of

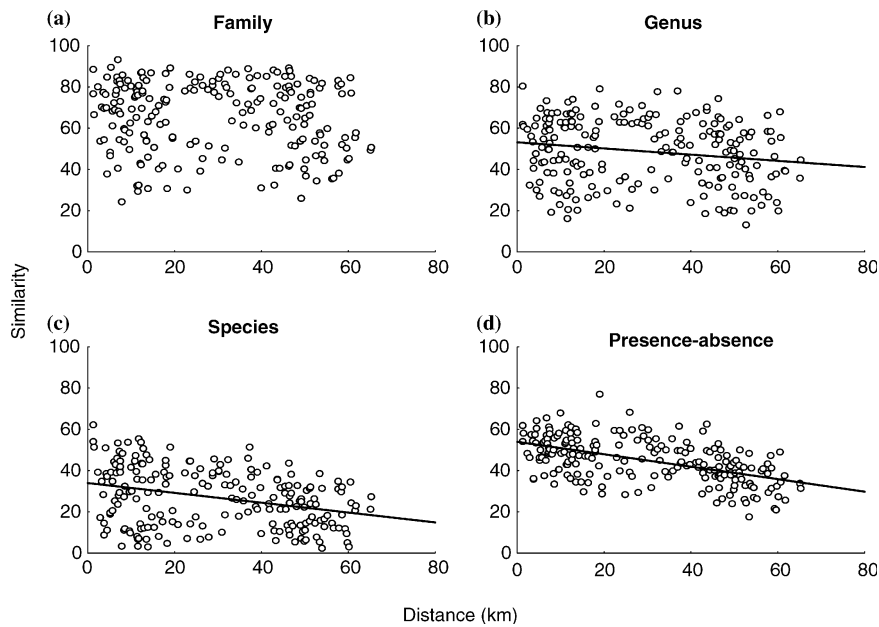


Figure 4. Relationship between similarity and distance between islands using (a) family level data, (b) genus-level data, (c) species-level data and (d) presence-absence data. Lines indicate a significant linear fit.

Table 3. Results of multiple forward nonparametric matrix regression analyses.

Dependent variable	Independent variable	Partial <i>b</i>	Partial <i>p</i>	Partial <i>R</i> ²
Cover	Shelf depth	0.611	0.001	0.374
	Island size	0.495	0.001	0.245
	Distance	0.169	0.004	0.025
	Total explained			0.644
Family	Shelf depth	− 0.556	0.001	0.309
	Island size	− 0.526	0.001	0.276
	Total explained			0.586
Genus	Shelf depth	− 0.665	0.001	0.442
	Island size	− 0.387	0.001	0.149
	Total explained			0.591
Species	Shelf depth	− 0.682	0.001	0.465
	Island size	− 0.358	0.001	0.128
	Total explained			0.593
Presence-absence	Shelf depth	− 0.597	0.001	0.356
	Distance	− 0.373	0.001	0.122
	Island size	− 0.105	0.020	0.011
	Total explained			0.490

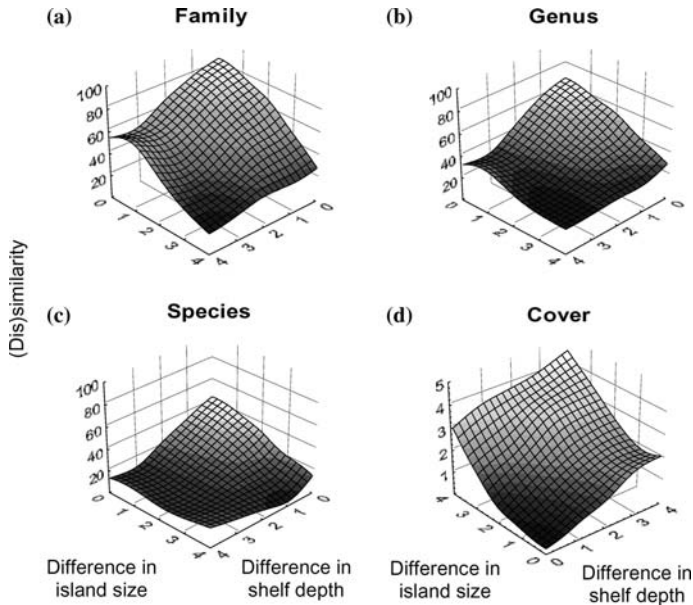


Figure 5. 3-D surface plot of the relationship of community similarity with difference in island size and difference in shelf depth (both using normalised Euclidean differences/distances) for (a) family level data, (b) genus-level data and (c) species-level data. 3-D surface plot of the relationship of (d) dissimilarity in live coral cover with difference in island size and shelf depth. The fitted plane was obtained with the distance-weighted least squares fitting option in Statistica for Windows 6.1. The shading in the plane indicates variation in the difference in species richness between pairs of transects. Dark shading indicates relatively little difference whereas light shading indicates pronounced differences.

variation explained by these two variables was substantial, i.e., 59% at family, genus, and species level. Variation in shelf depth and island size also explained 64% of the variation in coral cover (Table 3). Although shelf depth and island size were the only significant variables in the multivariate model there were significant univariate relationships between coral similarity and other environmental variables. Coral species similarity, for example, was significantly related to rubbish abundance ($b = -0.285$, $p < 0.001$, $R^2 = 0.0810$), visibility ($b = -0.0557$, $p < 0.001$, $R^2 = 0.311$) and salinity ($b = -0.405$, $p < 0.001$, $R^2 = 0.164$) in addition to shelf depth and island size. This indicates the presence of a strong environmental gradient predominantly related to shelf depth from the relatively shallow inner Jakarta Bay to the deeper areas of the outlying Pulau Seribu islands.

There was significant congruence in similarity when different taxonomic levels were used to assess composition. Family-level similarity was significantly correlated with generic- ($r = 0.921$, $p < 0.001$) and species-level similarity ($r = 0.827$, $p < 0.001$) and with similarity obtained from presence-absence data ($r = 0.509$, $p < 0.001$). Genus-level similarity was significantly correlated

with species-level similarity ($r = 0.905$, $p < 0.001$) and similarity obtained from presence-absence data ($r = 0.620$, $p < 0.001$). Finally, species-level similarity was significantly correlated with similarity obtained from presence-absence data ($r = 0.702$, $p < 0.001$).

Discussion

We found no evidence of significant variation in rarefied taxon richness among zones or land-use types. The variation in richness that we could detect among islands was, however, severely limited by the very low coral densities in zone 1. Only 10 coral colonies were recorded using two 30 m transects at Ubi Besar island in zone 1, for example, compared to 216 colonies at Belanda island in zone 3. It is possible that a higher number of individuals per island in zone 1 would have allowed us to differentiate between zones but this would have required sampling a much larger area of zone 1 islands. Coral assemblages usually show lower species numbers near the shore in inshore-offshore gradients (Done 1982; Moll 1983; Hoeksema 1990). Another possibility is that despite the severe reduction in live coral cover in zone 1, that this has not yet affected richness. Richness, as opposed to community composition, tends to be a highly conservative measure of disturbance. Changes in species composition usually respond more rapidly to human activities than do changes in species and they affect ecosystems long before a taxon is threatened to extinction (Chapin et al. 2000). Brown et al. (2001), furthermore, showed that in three long-term studies there was a remarkable temporal constancy in species richness despite environmental changes that caused substantial alterations in species composition.

The species composition of the Pulau Seribu reef complex has been affected by severe bleaching that occurred on the shallow reefs in the Java Sea as a result of the 1982–1983 El Niño Southern Oscillation event. Sensitivity to excessive seawater warming varied significantly among coral species and within populations in relation to their bathymetric and spatial distribution (Brown and Suharsono 1990; Warwick et al. 1990; Hoeksema 1991). In 1985, the year of the present survey, not all species had fully recovered (Brown and Suharsono 1990; Warwick et al. 1990), and therefore the analysed species compositions have been affected by differing mortality rates.

In contrast to taxon richness we did find a significant gradient in live coral cover, which was highest in zone 3, intermediate in zone 2 and lowest in zone 1. Likewise, community composition differed significantly among zones, with the assemblages from zone 1 the most distinct. We failed to find significant variation in live coral cover or community composition among land-use types. This indicates that the primary mechanisms structuring coral assemblages in the Pulau Seribu are very large-scale environmental gradients and that local perturbations related to variation in human-habitation and land-use designation have very little measurable impact on coral communities, at least in

Pulau Seribu. The coral assemblages of the islands with a strict conservation status were generally similar to other islands in the same zone, even if these were used for residential or tourism purposes. This is a very clear indication that reef complexes, such as Pulau Seribu, need to be managed at large spatial scales as has been suggested in various studies (Margules and Pressey 2000; Bellwood and Hughes 2001). Despite Kelor Island being designated a strict nature reserve, it had only 5% live coral cover and a coral assemblage very similar to that of highly degraded reefs such as Bidari and Onrust. The severe degradation of reefs throughout zone 1 is the result of years of chronic and severe disturbance originating from its proximity to Jakarta. Zone 1 reefs are generally in such a bad state that various islands run the risk of eroding away and sinking below sea level, a fate that has already happened to Ayer kecil, Ubi kecil, and Nyamuk kecil (Ongkosongo 1986; Ongkosongo and Sukarno 1986; Stoddart and Brown 1986). Lack of proper management in Pulau Seribu means that the same destructive processes (e.g., dredging, sand and coral extraction) that have affected reefs in zone 1 will be repeated in outlying reefs in the run to exploit the remaining resources that have been virtually expended from zone 1 reefs.

In order to avoid this fate, proper large-scale management, including effective protection, is required. One important aspect of this management is the development of efficient monitoring schemes using indicator taxa (Noss 1990; Zorn et al. 2001). In the present study, we have identified a number of indicator taxa at three taxonomic levels that can be used to ascertain whether reef assemblages are regenerating to healthy levels. In the present study, indicator species of zone 3 such as *A. tenuis* and *A. brueggemanni* are probably most representative of the pre-disturbance community, although disturbance has to some extent already, affected the whole Pulau Seribu complex.

By identifying indicator taxa, we should not overlook the possibility of a sampling bias in favour of zone 1. Zone 1 taxa may not be recorded in the shallow transects of zones 2 and 3, but since the water is clearer in these offshore zones and the depth range is more extended, it is possible that these taxa occur at greater depths. The ecological preferences of taxa should be understood in order to ascertain whether they function as indicator taxa for particular zones or for just the shallow transects in those zones. The status of *O. crispata* as the major indicator species for zone 1 (Table 2) remains undisputed since it usually occurs in turbid water near river mouths or in sheltered bays (Ditlev 1978; Cope and Morton 1988; Veron and Marsh 1988; Lam 2000; Yamashiro 2000; Hoeksema pers. obs.). *Turbinaria peltata*, which ranks 3rd for zone 1 (Table 2) and has also been recorded as an inner-reef coral at the Great Barrier Reef Done (1982), occurs in loose sandy substrate in a wide depth range (Veron and Pichon 1979; Scott 1984; Coles 1996; Hoeksema pers. obs.). Hence, among shallow habitats this species may be indicative of near-shore reefs, such as in zone 1, but this does not rule out a deeper distribution in zones 2 and 3. A role of indicator species should, therefore, be limited to shallow reef habitats.

The use of effective and easy to identify taxa, such as coral genera, should be promoted in order to effectively monitor the greater Pulau Seribu reef ecosystem. Even family-level studies may yield important information. At very large spatial scales, Bellwood and Hughes (2001), for instance, found that the community composition of reef fishes and corals across the Pacific and Indian oceans was constrained within a surprisingly narrow range of configurations. Deviations at depauperate sites appeared to have a biological basis. Acroporids, for example, are underrepresented at disturbed sites whereas faviids are over-represented. This is congruent with findings that acroporids are less resilient to environmental stress than faviids. In the present study, the Acroporidae is a very good indicator of the lesser disturbed zones 2 and 3 reefs ($IV = 92.69$) and was virtually absent from the perturbed zone 1 reefs where the only significant indicator family was the Dendrophylliidae, but with an IV of only 37.50.

In line with various terrestrial and marine studies we found that assemblages appeared to be primarily structured by environmental processes as opposed to purely stochastic (spatial) processes. Distance accounted for very little variation in the community similarity of stream fish assemblages in Seix, Portugal (0% out of 58%; Magalhaes et al. 2002), bird assemblages in South Africa (1.7% out of 27%; Githaiga-Mwici et al. 2002) or tree assemblages in Panama (7% out of 41%; Duivenvoorden et al. 2002). Likewise, environmental variables proved much better descriptors of benthic faunal assemblages off the Norway coast than distance alone (Ellingsen 2002). In the Caribbean, Pandolfi (2002) showed that there was a high degree of variance in estimates of community similarity at multiple spatial scales in Caribbean coral communities indicating that distance *per se* was not driving community patterns.

The prevalence of environmental over spatial processes in this study is predominantly related to a combination of human- and natural-induced disturbance. Rees et al. (1999) noted the existence of a very strong environmental gradient with higher temperatures and lower salinity near-shore in zone 1 and lower temperatures and higher salinity further offshore. Shelf depth also increases in this general direction and the distance offshore from Jakarta is a strong determinant of pollution levels. It is unclear to what extent environmental factors may have been predominant in the predisturbance community of Pulau Seribu.

Conclusions

Coral assemblages in the Pulau Seribu complex, Java Indonesia were primarily structured by large-scale environmental gradients as opposed to local environmental differences among islands related to land-use designation. Near-shore reefs located in Jakarta Bay were in particular, characterised by very low coral cover and markedly different composition. Umbgrove (1947) suggested that reduced visibility caused by suspended terrigenous sediments and

phytoplankton blooms due to increased nutrient concentrations in the Jakarta Bay led to the disappearance of functional coral reefs that were present in 1939. Rees et al. (1999) noted key nearshore stress factors such as sediment and nutrient loading or organic contaminants such as oils and other hydrocarbons. Clearly, monitoring of coral reefs in Jakarta Bay and the Pulau Seribu complex should be combined with environmental assessments, particularly in relation to potential key stress factors such as algal blooms. The prevalence of the large-scale nature of the phenomena affecting Jakarta Bay and the Pulau Seribu reef complex is also a clear indication that these coral reefs need to be managed over very large spatial scales. Monitoring of the reefs is also crucial in order to identify compositional changes and relate these to changing environmental conditions.

Acknowledgements

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