Biogeographic variation in coral species diversity on coral reefs in three regions of Indonesia

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Abstract. This paper assesses variation in coral species diversity within the Indonesian archipelago, and the influence of regional species pools, geomorphology and anthropogenic pollution on coral species diversity and occurrence. We obtained transects from 33 sites on 14 reefs in three regions of Indonesia: Ambon (Moluccas), South Sulawesi and the Java Sea. We determined the within-site species richness by using species-sampling curves. Cluster analysis and multi-dimensional scaling showed that land-based pollution was the primary determinant of coral species diversity and species occurrence on reefs. Relatively unaffected reference sites in eastern Indonesia were approximately 20% more diverse than Java Sea reference sites. Rare species formed a higher proportion of the coral fauna on eastern Indonesian sites, and eastern Indonesian apparent endemic species contributed approximately 25% of the total species pool sampled.

Between-site variation in species occurrence was lower on Java Sea reefs than on eastern Indonesian reefs. A larger species pool in eastern Indonesia than in the Java Sea probably accounted for most of the difference in within-site species diversity between eastern Indonesian and Java Sea reference sites. High fishing intensity in the Java Sea, including destructive fishing practices, may have also contributed to reduced within-site species diversity on Java Sea reference reefs. Despite the fact that the Java Sea was exposed during Pleistocene lowstands, and was recolonized by marine organisms only within the last 10 000 years, coral species diversity and assemblage composition on the Java Sea reefs was largely similar to open ocean reefs in eastern Indonesia.

Key words. Biodiversity, coral, epeiric seas, Indonesia, Java Sea, land-based pollution.

INTRODUCTION

Indonesia's importance to global terrestrial and marine biodiversity has long been recognized (Wallace, 1876; McManus, 1985; Wells, 1988; Gaston *et al.*, 1995; Paulay, 1997), as has the biogeographic division between eastern and western Indonesia, known as Wallace's Line (Wallace,

1876; Cox & Moore, 1993). Indonesia lies at the centre of biodiversity for corals (Veron, 1993), molluscs (Burgess, 1985), fish (Montgomery, 1990; Randall, 1998) and many other coral reef organisms (Gosliner *et al.*, 1996), and Eastern Indonesia is particularly diverse (Borel Best *et al.*, 1989; Pandolfi, 1992; Wallace, 1997; Wallace & Wolstenholme, 1998). The diversity of habitats in close geographical proximity, and their shifting mosaic through Plio-Pleistocene sea level changes, are important factors contributing to high marine biodiversity within the Indo-Malay archipelago (McManus, 1985; Paulay, 1997). While

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Indonesia's coral reefs have high biodiversity, they are also threatened by land-based pollution, overfishing, destructive fishing practices, oil spills and other forms of anthropogenic damage (Guzman *et al.*, 1991; Johannes & Reipen, 1995; Erdmann & Pet-Soede, 1996; Chou, 1997; Erdmann & Caldwell, 1997; Edinger *et al.*, 1998; see Ginsberg, 1994; Birkeland, 1997; for overviews).

Despite the early recognition of Wallace's line and the division in terrestrial faunas between eastern and western Indonesia, and a series of investigations of coral species diversity within various parts of eastern Indonesia (Moll, 1983, 1986; Moll & Borel Best, 1984; Borel Best & Hoeksema, 1987; Borel Best *et al.*, 1989; Wallace, 1996; Wallace & Wolstenholme, 1998), there have been very few comparisons of marine biodiversity among regions *within* Indonesia (Wallace, 1997; Hoeksema, 1997). Edinger *et al.* (1998) examined differences in within-site coral species richness associated with different types and intensities of reef degradation and noted an approximately 20% difference in within-site species diversity between relatively unaffected sites in the Java Sea and their counterparts in eastern Indonesia. This difference in α (within-habitat) diversity approximately matches patterns of *Acropora* (Oken 1815) and other coral species richness within Indonesia (Veron, 1993, 1995; Wallace, 1996, 1997; Hoeksema, 1997).

Three possible explanations may account for the greater within-site coral species diversity observed in eastern Indonesia than in the Java Sea:

1. larger species pool in eastern Indonesia than in the Java Sea (γ diversity; Veron, 1993; Cornell & Karlson, 1996; Fraser & Currie, 1996).
2. Greater variation in reef geomorphology in eastern Indonesia than in the Java Sea (enhancing β diversity; Bak & Hovel, 1989; Van Woesik & Done, 1997).
3. Anthropogenic effects related to high fishing intensity (limiting α diversity; Roberts, 1995; Erdmann & Pet-Soede, 1996) within the Java Sea.

To test these competing, but not mutually exclusive, hypotheses, we compare total species richness on individual reefs and within regions, then examine biogeographic patterns of apparent endemism between eastern and western Indonesian reefs sampled by Edinger *et al.* (1998). Finally, we use multivariate statistics to examine similarity of species occurrence among the 33 sites sampled,

in an attempt to disentangle biogeographic differences in species pools from geomorphological differences in habitat and anthropogenic effects from land-based pollution and mechanical damage.

METHODS

Study areas

We sampled 33 sites on 14 reefs in three regions of Indonesia: Ambon (Moluccas, four reefs, seven sites), Spermonde archipelago (South Sulawesi, four reefs, eight sites), and Central Java (six reefs, 18 sites). These reefs were chosen to represent different degradation regimes classified broadly as land-based pollution or mechanical damage (Edinger *et al.*, 1998), with at least one reference reef in each region (Table 1, Fig. 1). Reference reefs were operationally defined as the reefs in each region with least evidence of anthropogenic impact. Complete site descriptions are presented in Jompa (1996), Limmon (1996) and Edinger (1998).

All Ambon reefs were fringing reefs sampled on the exposed (windward) face, including the reef wall at Tanjung Setan, on the edge of the deep water Seram Strait. All Sulawesi reefs were coral cays on a carbonate shelf, including the reef wall at Kapoposan, on the edge of the deep water Makassar Strait. All but one of the Sulawesi reefs were sampled on the leeward side, which generally supports the highest coral growth and species diversity (Moll, 1983). The exception is Kayangan reef in Ujung Pandang harbour, which was sampled on the windward side, because the leeward (facing the harbour) side corals are all dead. The Java Sea reefs were mainly coral cays, and were sampled on both windward and leeward sides. The Java Sea fringing reefs at Bondo and Lagun Marican were sampled on their windward sides only.

Sampling methods

On each reef, we measured six replicate non-adjacent, non-overlapping 20-m line intercept transects (Risk, 1972; Loya, 1978) at 3 m and 10 m depth at each reef, for a total of 12 transects, or 240 m cumulative transect length per reef. For three reefs on which coral growth did not extend beyond 6 m depth (Wailiha, Bondo, L. Marican), transects were measured at 3 m only.

Table 1 Study site regions, names, morphologies and summaries of stresses. Code: two- or three-letter code for reefs and sites used in tables and figures. Java Sea coral cays divided into windward and leeward sites (e.g. PKW = windward, PKL = leeward). Geomorphology types include walls (reefs with steep drop-off into deep water), coral cay islands, submerged coral cays, exposed fringing reefs and protected fringing reefs. Max. depth: maximum depth of coral growth. Source of stresses summarizes impacts on each reef. More detailed descriptions of each reef can be found in Limmon (1996), Jompa (1996) and Edinger (1998)

Region	Reef name	Code	Reef morphology	Max. depth (m)	Source of stresses
Ambon	Tanjung Setan	TJS	Wall	40	reference sites (10 m, 3 m)
	Hila	HL	Exposed fringing reef	20	bombing, construction, rubble bottom
	Wayame	WM	Protected fringing reef	15	harbour, sewage, sedimentation
	Wailiha	WL	Exposed fringing reef	6	sediment, plywood factory
So. Sulawesi	Kapoposan	KP	Coral cay island/wall	50	unaffected (10 m), bombed (3 m)
	Barang Lompo	BL	Coral cay island	25	bombing, local sewage pollution
	Samalona	SL	Coral cay island	25	anchor damage, pollution from city
	Kayangan	KY	Coral cay island	11	harbour, industry, sewage, sedimentation
Karimunjawa	Pulau Kecil	PKW/PKL	Coral cay island	25	Java unaffected, overfishing
(Central Java)	Gosong Cemara	CMW/CML	Coral cay, submerged	20	Java unaffected, overfishing
	Pulau Burung	BRW/BRL	Coral cay island	25	storm damage (windward only)
	Lagun Marican	LM	Protected fringing reef (mangroves)	4	carbonate sedimentation
Jepara	Pulau Panjang	PPN/PPS	Coral cay island	8	sewage, sediment, aquaculture
(Central Java)	Bondo	BND	Exposed fringing reef	5	sedimentation, agricultural runoff
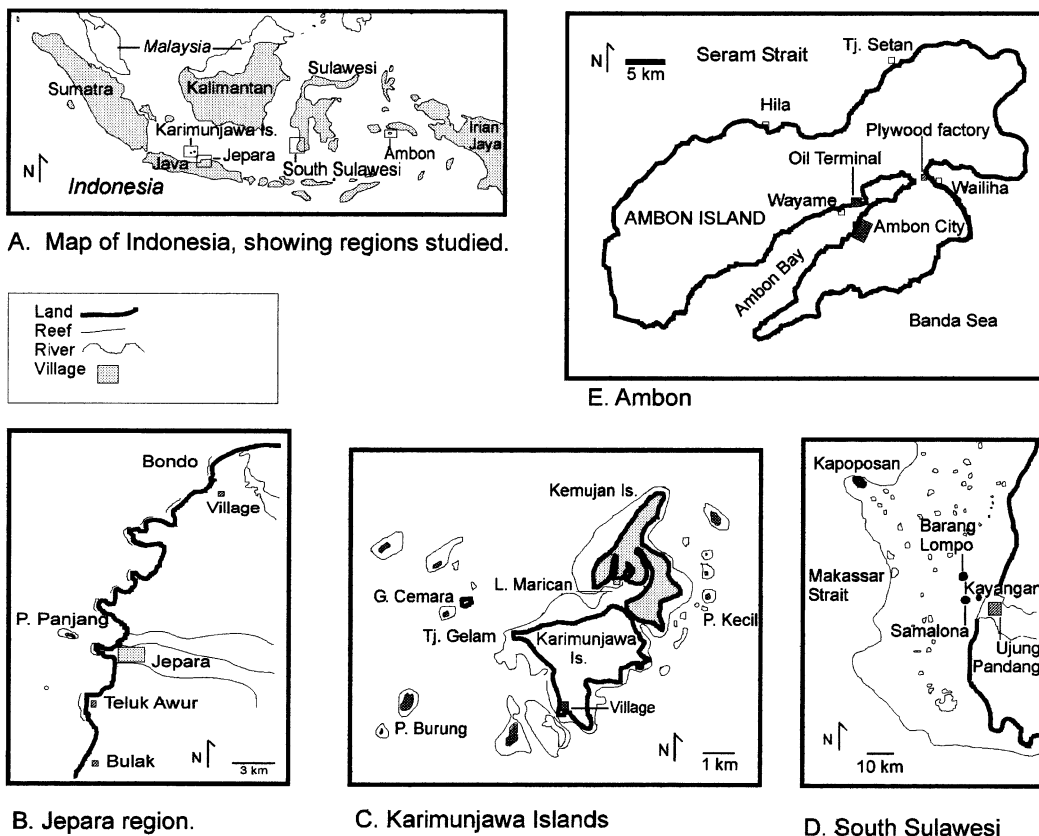
Fig. I Maps to study sties. (a) All Indonesia, showing regions studied, including Jepara (b), Karimunjawa (c), both in the Java Sea, and two areas in eastern Indonesia, the Spermonde Archipelago in South Sulawesi (d), and the island of Ambon (e), in the Moluccas.

All coral species occurring on transects, from all depths and exposures, were recorded.

For each site within each reef, a species–sampling curve was generated by counting all species present in the first 5-m section of the first transect and then by adding previously unobserved species as they appeared in additional 5-m sections. These sections were ordered according to the number of new species they contributed to the species accumulation curve over a total distance of 40 m (except for Ambon, where the curve required 60 m before it approached horizontality). Species–sampling curves were log_{10}-transformed to calculate the slope of the species-log_{10}(sampling) line (Sokal & Rohlf, 1973) These slopes were then used to compare α diversity among sites and degradation regimes (Edinger et al., 1998). Average α diversity of unpolluted

reefs in each region was calculated as the average slope of the species-log_{10}(sampling) lines in Ambon (Tj. Setan, Hila, $n = 4$), Sulawesi (Kapoposan, Barang Lompo, Samalona, $n = 6$), and the Java Sea (G. Cemara, P. Kecil, P. Burung, $n = 12$).

All corals except *Acropora* were identified using Veron (1986). Field parties did not have sufficient experience in *Acropora* taxonomy to allow species identification underwater, and we were reluctant to collect large suites of specimens for later identification (cf. Salm, 1984). Rather, *Acropora* corals were identified to species group (Veron & Wallace, 1984) in the field, and *Acropora* species-groups were used to calculate species–sampling curves. Representative samples of each recognizable *Acropora* were collected for provisional identifications and subsequent verification by Dr C.C. Wallace. Individual *Acropora* species and *Acropora* species

groups are listed among the taxa identified. More rare *Acropora* species occurred on Eastern Indonesian sites than on Java Sea sites.

All samples collected and identified were archived in teaching collections at the local university in each region: UNPATTI (Pattimura University, Ambon, Moluccas), UNHAS (Hasanuddin University, Ujung Pandang, South Sulawesi) and UNDIP (Diponegoro University, Semarang, Central Java). Duplicate *Acropora* samples, identified by Dr C.C. Wallace, were archived at the Museum of Tropical Queensland, Townsville, Queensland, Australia.

Data analysis

Regional species pools, habitat heterogeneity, and similarity among regions

Species lists derived from transect data for each site helped to form composite regional species lists. Records from Kayangan reef at 10 m (KY10) were omitted from endemicity calculations because the very few coral species represented at this site were almost entirely different from other sites, probably as a response to extremely low light levels at 10 m on this polluted reef. The ratio of α diversity to γ diversity in each region was calculated as α/γ = [average slope of species-log(sampling) lines on unpolluted reefs/regional species pool]. Habitat heterogeneity in each region was inferred from the number of reef geomorphology types sampled in each region. Reef geomorphology types recorded were reef walls (sites dropping steeply into deep water), coral cays, exposed fringing reefs and protected fringing reefs (e.g. in mangroves). Percentage similarity was calculated among the three regions, Ambon–Sulawesi, Ambon–Java and Sulawesi–Java, as percentage similarity = [2(common spp.)/$(S_A + S_B)$], where S_A = species richness of site A and S_B = species richness of site B.

Local scale similarity

We calculated similarity among individual sites, followed by cluster analysis and ordination (multi-dimensional scaling) on the species presence–absence data. Cluster analysis and ordination used percentage disagreement and Ward's method, where percentage disagreement distance = 1% similarity, and was computed as the number of species not shared divided by the total number

of species on both sites, % disagreement = [(spp. not shared)/$(S_A + S_B)$]. Ordinations were performed using multi-dimensional scaling (MDS; Clarke, 1993). MDS was repeated sequentially, first on all species at all sites, then for common species only (species with < 3 occurrences eliminated) on all sites, and then for common species on sites not affected by land-based pollution.

RESULTS

Local species richness

One hundred and ninety-seven coral species were recorded in quantitative surveys of reefs (Table 2, Appendix 1 [the Appendix is published on-line at http://www.blackwell-science.com/products/journals/suppmat/ddi/ddi076/ddi076sm.htm]). The average species richness per reef on Java Sea reference reefs (Cemara, P. Kecil, Burung) was not significantly different from the per-reef species richness on eastern Indonesian reefs not subjected to pollution (Tj. Setan, Kapoposan, Barang Lompo, Samalona, Hila). Although two reference reefs, Tj. Setan (Ambon) and P. Kecil (Java Sea), were tied for the highest number of species recorded per reef (Table 2a), the slopes of species–sampling lines (Table 2b) on eastern Indonesian reference sites (TJS3, TJS10, KP10) were significantly greater than the slopes of species–area lines of leeward (the most diverse) Java Sea reference sites (*t*-test, $t = 9.94$, $P < 0.01$, $n = 7$). This indicates higher within-habitat (i.e. alpha) diversity of the eastern Indonesian reference sites (Edinger *et al.*, 1998).

Habitat heterogeneity

Three geomorphology types of reefs were sampled in Ambon (walls, exposed fringing reefs and protected fringing reefs) and in the Java Sea (coral cays, exposed fringing reefs, protected fringing reefs). Two geomorphology types were sampled in South Sulawesi (walls and coral cays). In addition, the coral cays in the Java Sea were sampled on both the windward and leeward sides.

Regional species pools and apparent endemicity

The most species-rich region was Ambon, while the Java Sea had the lowest number of species

Table 2a Total number of species recorded from each reef

Region	Site	Degradation type	No. of sites	S total
Ambon	Tj. Setan	Reference	2	99
Ambon	Hila	Rubble bottom	2	66
Ambon	Wayame	Harbour	2	63
Ambon	Wailiha	Sediment	1	42
Sulawesi	Kapoposan	Reference	2	75
Sulawesi	Barang Lompo	Bombing	2	70
Sulawesi	Samalona	Anchor damage	2	64
Sulawesi	Kayangan	Pollution + seds	2	45
Java Sea	G. Cemara	Reference	4	87
Java Sea	P. Kecil	Reference	4	99
Java Sea	P. Burung	Storm damage	4	79
Java Sea	P. Panjang	Pollution + seds	4	51
Java Sea	Bondo	Sediment	1	35
Java Sea	L. Marican	Mangrove	1	24

Table 2b Total number of species, and slope of species-log(sampling) line, number of rare species (occurring on < 3 sites), and percentage of rare species recorded from each site. Site codes follow Table 1. ww: windward; lw: leeward

Region	Site	Aspect	Depth	N spp.	Slope	No. rare	% rare
Ambon	TJS10	ww	10	71	38.6	9	13
Ambon	TJS3	ww	3	66	35.8	6	9
Ambon	HL10	ww	10	45	21.8	6	13
Ambon	HL3	ww	3	41	21.5	2	5
Ambon	WM10	ww	10	44	28.3	4	9
mbon	WM3	ww	3	38	28.3	2	5
Ambon	WL3	ww	3	42	22.7	3	7
Sulawesi	KP10	ww	10	62	37.8	8	13
Sulawesi	KP3	lw	3	28	16.1	4	15
Sulawesi	BL10	lw	10	56	32.5	6	11
Sulawesi	BL3	lw	3	33	19.4	1	3
Sulawesi	SL10	lw	10	55	30.6	0	0
Sulawesi	SL3	lw	3	30	18.3	5	17
Sulawesi	KY3	ww	3	42	23.9	3	7
Java Sea	CMW10	ww	10	48	25.6	0	0
Java Sea	CMW3	ww	3	37	21.6	0	0
Java Sea	CML10	lw	10	54	28.5	1	2
Java Sea	CML3	lw	3	50	28.3	1	2
Java Sea	PKW10	ww	10	46	23.2	2	4
Java Sea	PKW3	ww	3	48	26.8	2	4
Java Sea	PKL10	lw	10	51	29.2	0	0
Java Sea	PKL3	lw	3	55	29.2	3	5
Java Sea	BRW10	ww	10	36	20.7	1	3
Java Sea	BRW3	ww	3	28	17.1	0	0
Java Sea	BRL10	lw	10	51	24.5	6	11
Java Sea	BRL3	lw	3	40	22.7	1	3
Java Sea	PPN6	ww	6	24	15.1	0	0
Java Sea	PPN3	ww	3	22	12.7	0	0
Java Sea	PPS6	lw	6	22	12.7	0	0
Java Sea	PPS3	lw	3	29	17.1	0	0
Java Sea	BND3	ww	3	35	18.4	0	0
Java Sea	LM3	ww	3	24	13.2	0	0

Table 3 Total eastern and western Indonesian pandemic and apparent endemic species, all *Acropora* species counted

Region	Eastern Indonesia				
	Ambon	Sulawesi	All East	Java Sea	All regions
Total spp.	145	136	182	135	197
No. of pandemics	119	113	120	120	120
% pandemics	82	83	66	92	61
No. of app. endemics	26	23	62	15	77
% app. endemics	18	17	34	8	39
No. of reefs	4	4	8	6	14
No. of sites	7	7	14	18	32
Mean α diversity	29.4	25.8	27.2	24.8	—
(unpolluted reefs)	($n = 4$)	($n = 6$)	($n = 10$)	($n = 12$)	

Table 4 Similarity analyses of Ambon, Sulawesi, and Java Sea corals (percentage similarity)

Comparison	Ambon–Sulawesi	Ambon–Java	Sulawesi–Java
No. of spp. Area A	145	145	136
No. of spp. Area B	136	135	135
Common sp.	99	106	100
No. of spp. Area A only	46	39	36
No. of spp. Area B only	37	29	35
Percentage similarity	71	76	74

(Table 3). The Java Sea had as many species as occurred in Sulawesi alone, 90% of the species pool of Ambon, and 77% of the species pool of all eastern Indonesian sites combined (Ambon + Sulawesi). The ratio of average α diversity/γ diversity was 0.18 in the Java Sea, 0.19 in South Sulawesi, and 0.20 in Ambon.

The majority of species (120) were pandemics, occurring both in the Java Sea and in the Eastern Indonesian sites. Of the remainder, the great majority, 62, were recorded in Eastern Indonesia only and a much smaller number, 15, in the Java Sea only. The two genera with the highest number of apparent endemics were *Acropora* and *Fungia* (Lamarck 1801).

Twelve fungiid corals sampled in eastern Indonesia were not recorded in the Java Sea. The abundant records of fungiids in Eastern Indonesia came mainly (5/12) from Hila, the site on a rubble bottom, where fungiids were particularly common and diverse.

Forty-eight of 62 (77%) of the apparent eastern Indonesian apparent endemics were rare species (occurring on only one or two sites). Rare species formed a significantly greater part of the coral fauna recorded on eastern Indonesian sites than on Java Sea reference sites (Table 2b; ANOVA, $F = 8.17$, $P < 0.0025$, d.f. = 23). Within each region, rare species formed a smaller percentage of the fauna on polluted reefs than on reference reefs (Table 2b; Java: *t*-test, $t = 3.17$, $P < 0.005$).

Similarity analysis

Similarity analyses among the three regional faunas (Ambon, Sulawesi and Karimunjawa) using *Acropora* species groups revealed similar faunas, with similarities among all three groups exceeding 70% (Table 4). Site scale cluster analysis of the entire dataset yielded two primary groupings of sites (Fig. 2). Group 1 contained the relatively unaffected Java Sea sites (CM, PK, BR) plus the Ambon reference site (TJS) and
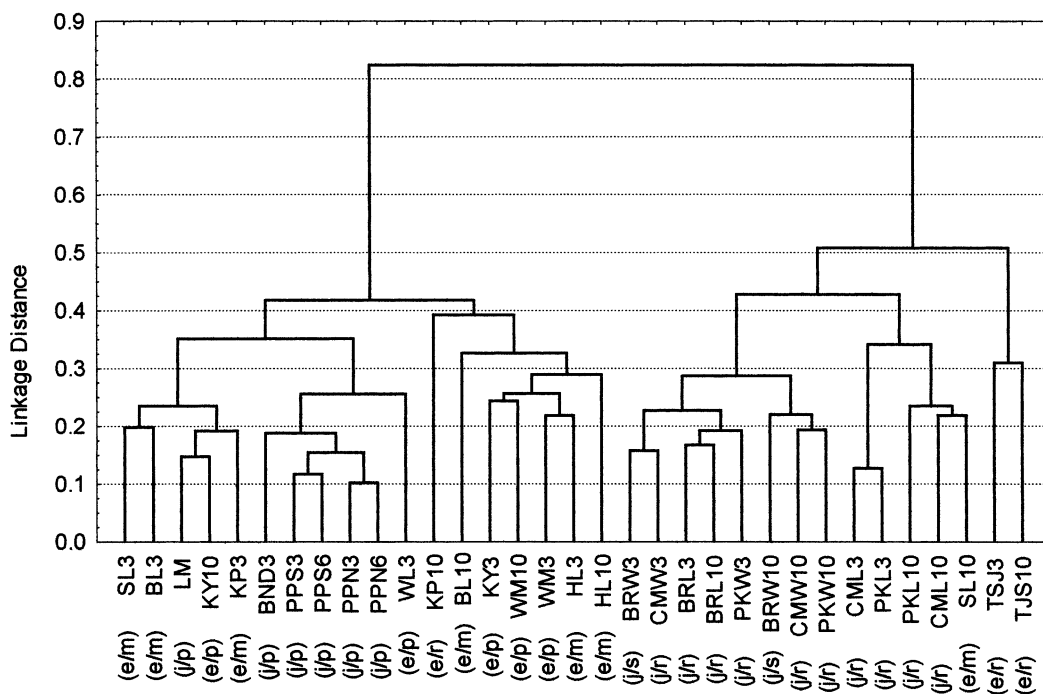
Fig. 2 Cluster analysis results. All species, all sites. Land-based pollution exerts the primary influence on position of sites in cluster analysis, overriding biogeographic differences. Site codes as in Tables 1, 2b. Region codes: e: eastern Indonesia; j: Java Sea. Anthropogenic effects codes: m: mechanically damaged, p: polluted, r: reference.

the Sulawesi anchor damaged site at 10 m (but not at 3 m) depth. Group 2 contained all the sites affected by land-based pollution (PP, BND, KY, WL, WM), the mangrove fringing reef (LM), and all the sites subject to anthropogenic mechanical damage (HL, SL3, BL3, KP3), including the anchor damaged site at 3 m. Most fishing boats in Indonesia anchor in less than 5 m water depth. Group 2 also contained two of the 10-m sites on reefs subject to mechanical damage (BL10, KP10). Further clustering mixed biogeographic regions among the anthropogenically affected sites, but left biogeographic groups intact among the relatively unaffected sites.
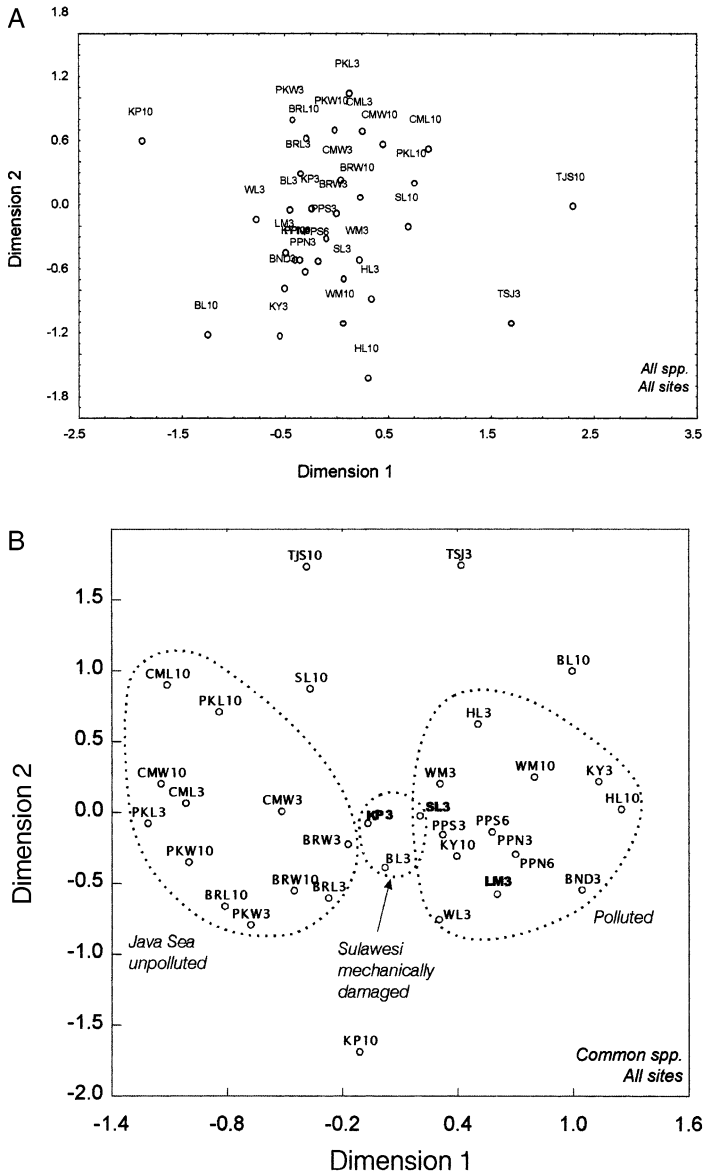
Ordination: multi-dimensional scaling
Initial multi-dimensional scaling of reef sites, based on all records at all sites (Fig. 3a), yielded a dense cluster of sites affected by land-based pollution, close to a slightly more dispersed cluster of relatively unaffected Karimunjawa

sites, and surrounded by five widely dispersed and highly diverse eastern Indonesian sites. This pattern implies that the most polluted sites contain and are dominated by a core subset of species, which are also found in nearly all of the more diverse unpolluted sites.

Eliminating rare species from the analysis allowed a somewhat clearer division of polluted vs. non-polluted reefs, but otherwise had little influence on the MDS results. MDS analysis with rare species eliminated (Fig. 3b) yielded two clusters of approximately equal disparity. The first cluster contained all the polluted sites (PP, BND, LM, KY, WM, WL) and the rubble bottom reef (HL). The second cluster contained all the Java Sea unpolluted sites (CM, PK, BR). The mechanically damaged Sulawesi sites at 3 m depth (BL3, SL3, KP3) formed a tight cluster which plotted immediately between the two larger clusters. The five remaining reefs, including the Ambon reef walls (TJS), Sulawesi

Fig. 3 Multi-dimensional scaling results. (a) All species, all sites. Polluted sites fall in the centre of the ordination field, and are surrounded by more diverse nonpolluted sites. Most Java Sea unpolluted sites form a distinct cluster. Most diverse eastern Indonesian reference sites (KP10, TJS3, TJS10) are highly disparate. Site codes as in Tables 1, 2b. (b) Rare species excluded, all sites. Polluted sites (PPS3, PPS6, PPN3, PPN6, LM3, BND3, KY3, WM3, WM10, WL3) form a cluster distinct from Java Sea unpolluted sites, and close to a cluster of shallow mechanically damaged sites from South Sulawesi (KP3, SL3, BL3). Site codes as in Tables 1, 2b. (c) Rare species excluded, polluted sites excluded. Sites KP3, SL3, BL3 are mechanically damaged shallow sites from south Sulawesi. Remaining eastern Indonesian sites are widely disparate. Site codes as in Tables 1, 2b.
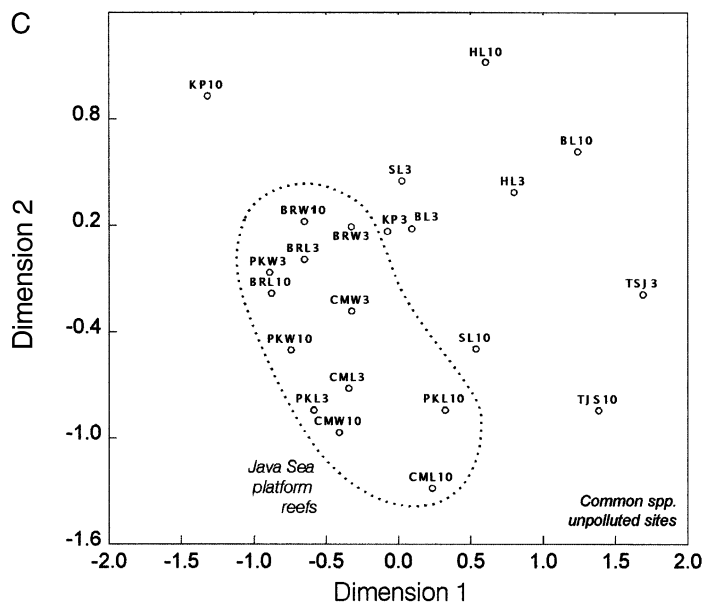
Fig. 3 *continued*

platform reefs at 10 m (BL10, SL10) and the Sulawesi reef wall (KP10), were widely dispersed.

Only with polluted reefs removed from the analysis were biogeographic patterns apparent. A final MDS analysis, with rare species eliminated (Fig. 3c), but retaining only those sites that were not subject to land-based pollution (i.e. sites PP, BND, LM, MJ, WM, WL and KY were eliminated), yielded one fairly compact cluster of the Java Sea unpolluted sites (CM, PK, BR) and a broadly dispersed cluster of eastern Indonesian platform and fringing reefs (BL, SL, HL). The three reef walls (TJS, KP10) remained distinct, with Ambon (TJS) and Sulawesi (KP10) reef walls highly dissimilar.

DISCUSSION

The primary division in species occurrence among sites was associated with pollution or disturbance regime. Polluted reefs had a core set of species common to most reefs sampled, and polluted reefs were all very highly similar to each other, regardless of biogeographic region. When rare species were removed from the analysis, polluted sites formed a cluster separate

from reference and mechanically damaged sites. These analyses suggest that land-based pollution was the primary determinant of species occurrence on the reefs we sampled (cf. Edinger *et al.*, 1998).

Biogeographic effects on species diversity and occurrence could be discerned only after polluted sites were removed from the dataset. Rare species contributed a large amount of the enhanced coral species diversity on eastern Indonesian reefs, and Java Sea reference reefs contained a subset of the coral species found on eastern Indonesian reefs. The variation in coral species occurrence was much greater among eastern Indonesian reefs than among Java Sea reefs, whether or not rare species were included.

The species richness and apparent endemicity patterns reported here, using *Acropora* species groups, and species of all other corals, were broadly similar to previous maps of Indo-Pacific coral species distributions (Veron, 1993, 1995) and to recent findings on biogeography and diversity of Indonesian *Acropora* corals (Wallace, 1997). Among *Acropora*, the south-west region of Indonesia (Sumatra and Java) was the least diverse of five Indonesian regions, with 28

Acropora species, and no endemics. The other sampled regions, all parts of eastern Indonesia, had more than 50 *Acropora* species, including one or more endemic *Acropora* species. More *Acropora* were recorded from all parts of Sulawesi than from the Moluccas, in contrast to the diversity pattern presented here. Wallace cautions, however, that the reefs of Sumatra are relatively poorly sampled (Wallace, 1997).

Although the Java Sea was only re-flooded 10 000 years ago (Tjia, 1980), α diversity on the Java Sea reference reefs was 80% of the diversity of Eastern Indonesian reference reefs, and the Java Sea species pool was 77% of the combined eastern Indonesian species pool. Similarly, recent surveys of seagrasses in the Karimunjawa islands (Java Sea) found 10 of 12 known Indonesian seagrass species (G. Llewellyn, personal communication 1998), again indicating the high similarity of Java Sea and eastern Indonesian marine flora and fauna. These data suggest that marine invertebrate species diversity on a recently re-flooded continental shelf can approach that of open ocean regions, if that shelf is well connected to a high diversity open ocean area (Veron, 1995). Further, our data indicate that most coral species are able to reoccupy recently flooded habitats on a time scale below the limits to resolution of the fossil record (Kowalewski, 1996).

Possible explanations of regional variation in biodiversity

Three non-mutually exclusive explanations may account for the greater within-site and total coral species diversity observed on eastern Indonesian reference reefs than on the Java Sea reference reefs: (1) a smaller initial species pool in the Java Sea (Veron, 1993; Wallace, 1997); (2) geomorphological differences related to reef growth in a recently re-flooded epeiric sea; and (3) more common destructive fishing practices and more intense non-destructive fishing, in the Java Sea than in eastern Indonesia. The first two of these are consequences of Pleistocene sea-level fluctuations, during which the Sunda Shelf was repeatedly drained and exposed (Wyrtki, 1961; Tjia, 1980). Our analyses suggest that an enhanced species pool in eastern Indonesia was the primary factor influencing geographical vari-

ation in within-habitat species diversity and occurrence, after pollution effects were eliminated.

1. Enhanced species pool

The total species occurrence and apparent endemicity data (Table 3) suggest that eastern Indonesia is inherently more diverse than the Java Sea, corroborating the patterns seen in other datasets (Wallace, 1997). The ratio of average α diversity to γ diversity in each region was approximately constant, suggesting that differences in the regional species pools were a primary determinant of lower within-site diversity on Java Sea than eastern Indonesian reefs (Cornell & Karlson, 1996). Furthermore, the Java Sea reefs held fewer apparent endemic coral species than did eastern Indonesian reefs. Similarly, no endemic *Acropora* species have been reported from western Indonesia, but western Indonesia contains *Acropora* species that are either pan-Indo-Pacific or of Indian Ocean origin (Wallace, 1997). All parts of eastern Indonesia contain some mix of pandemics, Indian Ocean species, Pacific Ocean species and endemic *Acropora* species. Their greater diversity is attributed to this mixing (Wallace, 1997).

Rare species formed a greater portion of the fauna on Eastern Indonesian than on Java Sea reefs (Table 2b), but were probably not responsible for the differences in diversity between the two regions. The average number of *common* species on eastern Indonesian reference sites (59 species per site) was still greater than the average *total* species richness on Java Sea sites (52.5 spp./site, leeward sites only). Rare species probably account for less than half of the 20% reduced within-site diversity on unpolluted reefs in the Java Sea.

2. Geomorphology

A greater range of reef geomorphology types represents a difference in β (between-habitat) diversity, rather than the α (within-habitat) diversity measured by species–sampling curves, and might contribute to increased α diversity principally by increasing regional species pools (Huston, 1994). The most diverse sites in the dataset are the eastern Indonesian reef walls (Tanjung Setan 3 m, 10; Kapoposan 10 m). Furthermore, the within-site diversity of Java Sea reference reefs was very similar to that of the 10-m deep South Sulawesi platform reef sites that are affected by

mechanical damage in shallow water (Edinger *et al.*, 1998).

While eastern Indonesia as a whole may have a greater range of geomorphologically determined reef habitat types than the Java Sea (cf. Bak & Hovel, 1989), we sampled from an equal number of reef geomorphology types in Ambon (3) and the Java Sea (3), more than in Sulawesi (2). Furthermore, the ratio of average α diversity to γ diversity in each region was approximately equal. Differences in habitat diversity probably did not contribute to the observed difference in within-habitat species diversity between eastern Indonesia and the Java Sea.

All three MDS analyses grouped sites according to pollution regime or biogeography, but eastern Indonesian sites were not grouped along geomorphological lines. These analyses suggest that geomorphology had relatively little influence on species occurrence, compared to species pool and anthropogenic effects. A few species, such as the azooxanthellate corals *Tubastrea micrantha* (Ehrenberg 1834) and *T. coccinia* (Lesson 1829), were only recorded on reefs subject to strong currents, including both wall reefs and exposed fringing reefs, and were also observed on coral cays elsewhere.

Our sampling of the two Sulawesi platform reefs found 25% fewer coral genera compared to a 1980 study (Moll, 1983) of the same reefs (Edinger *et al.*, 1998). This further suggests that anthropogenic effects may be responsible for the approximately equal diversity we observed between Sulawesi platform reefs at 10 m and Java Sea platform reefs. Because we were not able to sample eastern Indonesian platform reefs free from anthropogenic disturbance, it is impossible to test this hypothesis with our current data. Coral species diversity data from the reef walls at the eastern edge of the Sunda shelf (cf. Roberts *et al.*, 1987, 1988) may help to clarify the contribution of geomorphology to observed differences in species diversity.

3. Influence of fishing

The reduced within-site species diversity reflected in Java Sea species–sampling curves may reflect biotic effects associated with intense fishing activity within the Java Sea, particularly in the Karimunjawa Islands, where all the Java Sea reference reefs are located. Overfishing may reduce local scale habitat heterogeneity, leading to reduced within-habitat diversity (Roberts, 1995).

The Karimunjawa islands are one of the principal fishing grounds in the Java Sea for peri-reefal pelagic fish and, increasingly, reef fish. In the course of more than 80 dives in the Karimunjawa islands no fish larger than 0.5 m in length were observed, but fish traps were abundant. Fishing boats were observed operating in all zones of the marine park, regardless of protection status. Blast fishing and cyanide fishing occur here and in the Spermonde Archipelago (South Sulawesi), but cyanide fishing for the lucrative live fish trade is increasingly common in the Java Sea (Edinger & Browne, 2000). Fishing pressure by traditional (non-destructive) means appears to be more intense in the Java Sea than in eastern Indonesia, but blast and poison fishing are more common in certain parts of eastern Indonesia (Erdmann & Pet-Soude, 1996). The effect of these fishing activities on coral species diversity in Indonesia require further study.

Implications for the fossil record

This study may have important implications for geographical variation in biodiversity in the fossil record. The Java Sea is one of the modern world's rare tropical epicontinental seas, and has been suggested as a modern analogue for epeiric sea facies in the fossil record (Friedman, 1988; Edinger & Risk, 1998). First, epeiric sea facies in the fossil record typically had lower species diversity than contemporary open ocean regions, although their relative diversity fluctuated with changing environmental factors (e.g. Oliver, 1977; reviewed by Meyerhoff *et al.*, 1997). Our results suggest that species diversity in reef communities on broad shallow shelves may approach that of open ocean reefs, if the shelf areas are well connected to adjacent high diversity regions (Veron, 1995). Secondly, all marine species occurring in the Java Sea necessarily immigrated into the Java Sea within the last 10 000 years (Paulay, 1997). Our results suggest that most marine invertebrates can colonize recently flooded shelves on time scales below the resolution of the fossil record (Kowalewski, 1996), and such immigration would appear instantaneous in geological time.

Thirdly, far fewer apparent endemic corals occurred in the Java Sea than in eastern Indonesia, and there are no known true endemic coral species in the Java Sea (Hoeksema, 1997; Wallace, 1997). Endemic coral species would not be expected on a broad continental shelf that was repeatedly exposed during Pleistocene sea-level lowstands, and that was only re-flooded within the past 10 000 years (Tjia, 1980). Morphological features of newly described endemic *Acropora* species from deep reef habitats of the Togian islands, north-eastern Indonesia, suggest that these species are not newly evolved (Wallace, 1997), implying that the current flooding of the Sunda shelf occurred too recently for endemic coral species to have evolved in the Java Sea. By contrast, the Devonian epicontinental seas of north America were home to a diverse and largely endemic rugose coral fauna at sea level lowstands, which became more cosmopolitan at highstands, when greater migration between epeiric seas and open ocean regions was possible (Oliver, 1977).

We caution that comparisons between the Java Sea and the stable epeiric seas of the Palaeozoic are limited because the Java Sea is much smaller than most Palaeozoic epeiric seas (e.g. Johnson, 1987). Moreover, the Sunda shelf was repeatedly and completely drained and reflooded during the Pleistocene glaciations (Wyrtki, 1961; Tjia, 1980), to a greater extent and on a faster time scale than the transgressive–regressive cycles recorded in Palaeozoic epicontinental sedimentary basins (Ross & Ross, 1985). Last, the larval and dispersal biology of modern scleractinian corals and Palaeozoic tabulate and rugose corals may have differed considerably.

CONCLUSIONS

Within-site coral species diversity on eastern Indonesian reefs was 20% higher than that of Java Sea reefs. Differences in regional species pools are the best explanation for higher within-habitat species diversity on unpolluted eastern Indonesian reefs than on their Java Sea counterparts. More intense fishing pressure in the Java Sea than in eastern Indonesia may have enhanced the inherent biogeographic differences in diversity by reducing habitat complexity within Java Sea reefs.

Land-based pollution was the primary determinant of species occurrence patterns. Polluted reef sites contained a core set of eurytopic species common to most of the reef sites in the study. Biogeographic patterns in species occurrence were evident only when polluted reefs were removed. There was more variability in species occurrence among eastern Indonesian sites than among Java Sea sites.

Nearly two-thirds of the coral species recorded were pandemics, occurring in both eastern and western Indonesia. Approximately 25% of the species recorded on eastern Indonesian reefs were apparent endemics, occurring only in the east, while only 8% of Java Sea species were apparent endemics. Despite being re-flooded within the last 10 000 years, the Java Sea held 75% of the coral γ diversity recorded in eastern Indonesia. Corals and other marine invertebrate species recolonized the Java Sea within a geologically instantaneous period of time.

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