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REPORT

Is increased calcarinid (foraminifera) abundance indicating a larger role for macro-algae in Indonesian Plio-Pleistocene coral reefs?

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Abstract An important question in coral reef ecology is whether algal abundance in coral reef eco-systems is a natural phenomenon, or has increased as a result of coral reef degradation ultimately resulting in coral–algal regime shifts. Regime shifts, from coral to macro-algae dominated, alter the three-dimensional habitat structure in coral reef ecosystems. Surprisingly, few studies have looked at the effects for species that inhabit the reefs without being the architects of the three-dimensional structure. In this study the effects of a change in habitat characteristics on the community structure of large benthic foraminifera (LBF) is compared between an area with high (Kepulauan Seribu) and lower (Spermonde Archipelago) anthropogenic influence. The results indicate a general relationship between habitat and LBF assemblage structure. The largest difference was observed in shallow habitats. Habitats dominated by algae are inhabited by a specific group of LBF, the Calcarinidae, and domination of this group increases with higher algal prevalence. The fossil record of this group indicates that they evolved following a major change in settings of the central Indo-West-Pacific coral reefs from land detached platforms to fringing reefs, about 5 million years ago. Understanding the biotic response to this transition in reef morphology and the associated increase in terrestrially derived nutrients forms an excellent challenge to gain insights in present-day threats to coral reef ecosystems.

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Introduction

In the past decades, one of the general trends in coral reef ecosystem is the reduction in coral in favor of macro-algal cover. This phenomenon is most striking in the Caribean (e.g., Hughes 1994), but also prevails in Indo-Pacific reefs (e.g., Pandolfi et al. 2003; Bruno and Selig 2007). The processes leading to this trend are not fully understood, but are often related to decreased herbivory and increased nutrients, resulting in a reduced capacity to recover after disturbance (e.g., Mumby (2009) and references therein). The occurrence of groups of larger benthic foraminifera that are specifically associated with epiphytic habitats on fleshy macro-algae can contribute to our understanding of whether the occurrence of macro-algae on coral reefs is a natural phenomenon or always is a sign of degradation.

Coral–algal phase shifts are an important aspect of coral reef status, yet little is known about the effects it has on associated reef biota and habitat structure. The primary contributors to the three-dimensional structure on coral reefs are, by definition, scleractinian corals. However, many coral reefs fail to recover after disturbances and have undergone regime shifts (Done 1992; Bellwood et al. 2004; Hughes et al. 2007). Congruent sequences of degradation characteristically results in a transition from coral- to macro-algae-dominated reefs, frequently with some intermediate steps, such as an echinoid (especially *Diadema*)-dominated regime (Jackson et al. 2001; Bellwood et al. 2004). During such a regime shift, coral cover can be reduced to <5%, and macro-algae dominate with more than

90% cover (Hughes 1994). Studies on the effect of the resulting change in habitat structure have been biased toward the community structure of the strongly interacting corals, algae and herbivores (e.g., Done 1992; Edinger et al. 1998; Bellwood et al. 2004; Halford et al. 2004; Berumen and Pratchett 2006). On a coral reef, the slow-growing corals and the fast-growing algae compete for space, while the herbivorous fishes reduce algal abundance. If for some reason, for example, overharvesting of herbivorous fishes, disturbance events, or diseases, this balance is changed, the habitat structure of the reef is altered (Hughes 1994; Jackson et al. 2001). The effect this has on the assemblage structure of species with non-trophic interactions inhabiting this system is poorly understood.

The three-dimensional structure of coral reefs influences (micro) gradients in environmental parameters, such as, but not limited to, nutrient availability and composition (Rasheed et al. 2004, 2006), light (Kirk 1994), currents (van Duyl et al. 2006; Monismith 2007), and substrate type (Renema 2008), facilitating a diversified assemblage of plants and animals through a multitude of microhabitats and feedback systems (Lilly and Schiel 2006). Removal or replacement of dominant bioengineering species can result in a cascade of changes in the community structure (Steneck et al. 2002; Graham 2004). For example, in another marine ecosystem affected by regime shifts, kelp forests off the Californian coast, diversity decreased in all trophic levels in the kelp barren state (Steneck et al. 2002; Graham 2004). Following a regime shift in coral reefs, the three-dimensional structure of the environment is not dominated by corals, but by macro-algae. This is likely to affect environmental gradients within the benthic boundary layer.

Large benthic foraminifera are unicellular organisms with a carbonate test. It is a polyphyletic group, which is largely defined on the size of the taxa (>0.5 mm) and the possession of symbionts. Large benthic foraminifera have been shown to be sensitive to variations in the ambient environment (Hallock et al. 2003; Schueth and Frank 2008; Uthicke and Nobes 2008). Autecological observations on the occurrence of species have demonstrated that substrate, depth, hydrodynamic energy, nutrient availability, and terrestrial influx are important, interrelated parameters attenuating the distribution of LBF in reef ecosystems (Hottinger 1983; Hohenegger et al. 1999; Renema and Troelstra 2001).

Large benthic foraminifera are dependent on the uptake of external nutrients, but are highly efficient recyclers. Although host-symbiont systems are particularly efficient in systems dominated by particulate organic carbon (POC) (Hallock 1985), the food sources are not clear (Lee 2006). All species of large benthic foraminifera occur within the benthic boundary layer of coral reefs, which has been shown to be depleted in POC and, especially at the base, enriched in dissolved nutrients relative to the surrounding water (Rasheed et al. 2004, 2006). The weighed proportion of symbiont-bearing foraminifera, irrespective of their composition and species specific properties, has been proposed and evaluated as a monitoring tool to evaluate whether the environment is conducive to coral reef growth (Hallock et al. 2003).

The calcareous tests of large benthic foraminifera are well preserved in the fossil record (Hallock et al. 2003). Their fossil record is one of the most complete for any of the organisms in coral reef ecosystems, especially corals, fishes and macro-algae (Renema et al. 2008).

In this study, I test the hypothesis that changes in the benthic boundary layer associated with a coral–algal phase shift is reflected in the assemblage composition in large benthic foraminifera. Alternatively, large benthic foraminifera can be hypothesized to reflect ambient water quality and are not sensitive to changes in the height and composition of the benthic boundary layer. The results are used to speculate on paleoecological changes in Pliocene–Pleistocene coral reefs, as indicated by changes in the assemblage structure of large benthic foraminifera.

Methods

Study areas

Spermonde archipelago (Fig. 1)

The Spermonde Archipelago is formed on a 40-km wide carbonate shelf and consists of a series of coral cay reefs formed on antecedent topography rimmed by a barrier (Renema and Troelstra 2001). The Jene Berang and Maros rivers discharge storm water and sewage from Makassar, with a population of 2 million people, into the Spermonde Archipelago.

Annual precipitation averages 2,500 mm distributed in a ‘wet’ season from December to March, during the northwest monsoon, and a ‘dry’ season from May to September, during the southeast monsoon. The wet season coincides with increased wave energy on the exposed (west) sides of the reefs.

Kepulauan seribu (Fig. 1)

The research sites are located in the Jakarta Bay and Kepulauan Seribu (Thousand Islands), extending 80 km to the northwest of Jakarta, Indonesia. Jakarta city has >12 million inhabitants, and several rivers with a combined catchment area of 2,000 km^2 discharge storm water and sewage into the central sector of the bay, as well as two flanking delta systems, with a combined catchment area of 6,000 km^2, which discharge peripherally. Annual precipitation averages

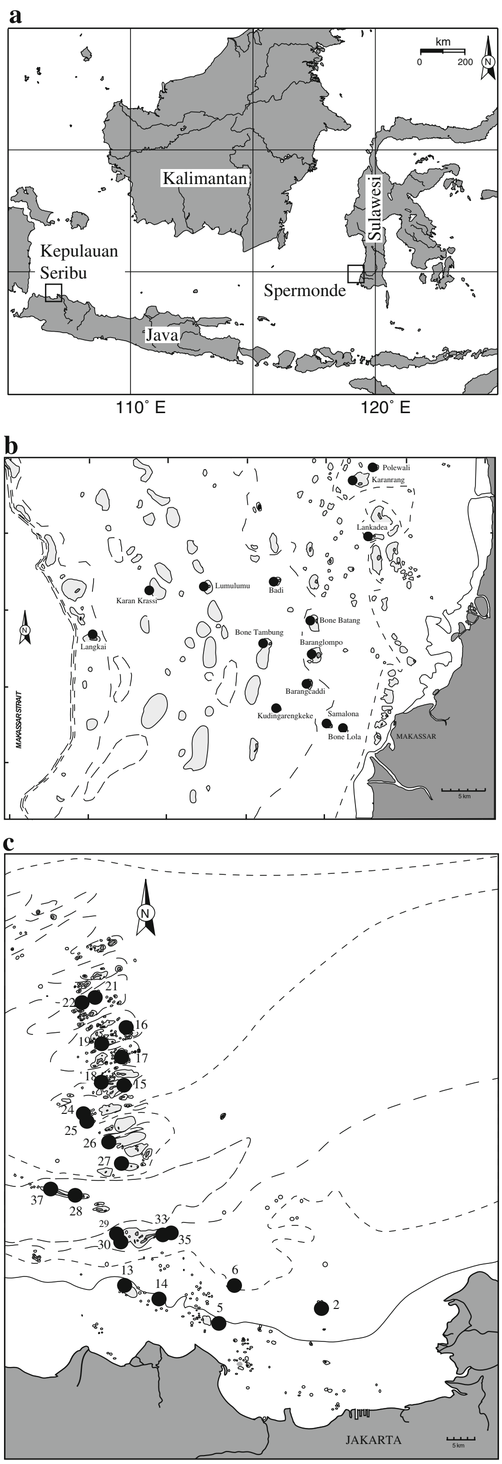

Fig. 1 **a** Indonesia with the research areas indicated (*squares*), **b** Spermonde Archipelago, **c** Kepulauan Seribu. Sample sites are indicated by *dots*. Reefs are indicated in *light gray*

1,700 mm distributed in a ‘wet’ season from November to March, during the northwest monsoon and a ‘dry’ season from May to September, during the southeast monsoon. In this study, the large benthic Foraminifera assemblages of 22 reefs have been assessed.

Reef geometry

In both the Spermonde Archipelago and Kepulauan Seribu, cay reefs developed on antecedent relief during the post-glacial transgression. The overall reef geometry is directly comparable and consists of a reef flat, reef crest and reef slope (Fig. 2). The reef flat is surrounded by a shingle rampart and can have islands on top. Shoals occur in both reaching only to 3–6 m water depth. They are topped by coral cover instead of a reef flat. The west side of these cays in the Spermonde Archipelago are exposed to oceanic swell and covered by coral, whereas the east side generally consists of carbonate sand with isolated coral patches. Corals grow all around the Kepulauan Seribu reefs, but cover is denser and extends deeper around their eastern and western tips. The coral cays in the southern part of the Kepulauan Seribu are larger than those in the Spermonde Archipelago.

Data collection

Foraminifera

Large variation in assemblage structure over small spatial scales is averaged out by sampling 11 reefs in the Spermonde and 15 reefs in the Seribu areas and applying multivariate statistics. In this study, I opted for replicate sampling at a fixed depth on multiple reefs; different benthic habitats (reef slope, reef crest and reef flat) between reefs or regions were sampled. In consequence, a sampling strategy was chosen that incorporated sampling multiple reefs along a gradient in water depth. At each reef, a depth transect starting at the reef base and going to the reef flat was sampled every 3 m in depth until the reef crest was reached. Further, samples on either side of the rampart, and at 25 and 50 m from the rampart on the reef flat, were included. A sample consisted of 1,000 cm^2 of seafloor, and all the substrate on it, in the Spermonde, and 100 cm^2 in the Kepulauan Seribu.

Environmental parameters

During sample collection, the substrate type at which the sample was taken was categorized in either of the following groups: rubble, rubble with sand (open spaces between rubble were filled with sediment), rubble with algae (foraminifera were both attached to rubble and to algae growing attached to the rubble), epiphytic (most if not all foraminifera were living attached to macro-algae, turf algae or sea grasses) and sand (Renema 2008). Simultaneously, macro-algal, turf-algal, live coral, dead coral, coral rubble and sand cover were visually estimated in the direct surrounding of the sample (Fig. 3). Where possible, these estimates were afterward checked using pictures

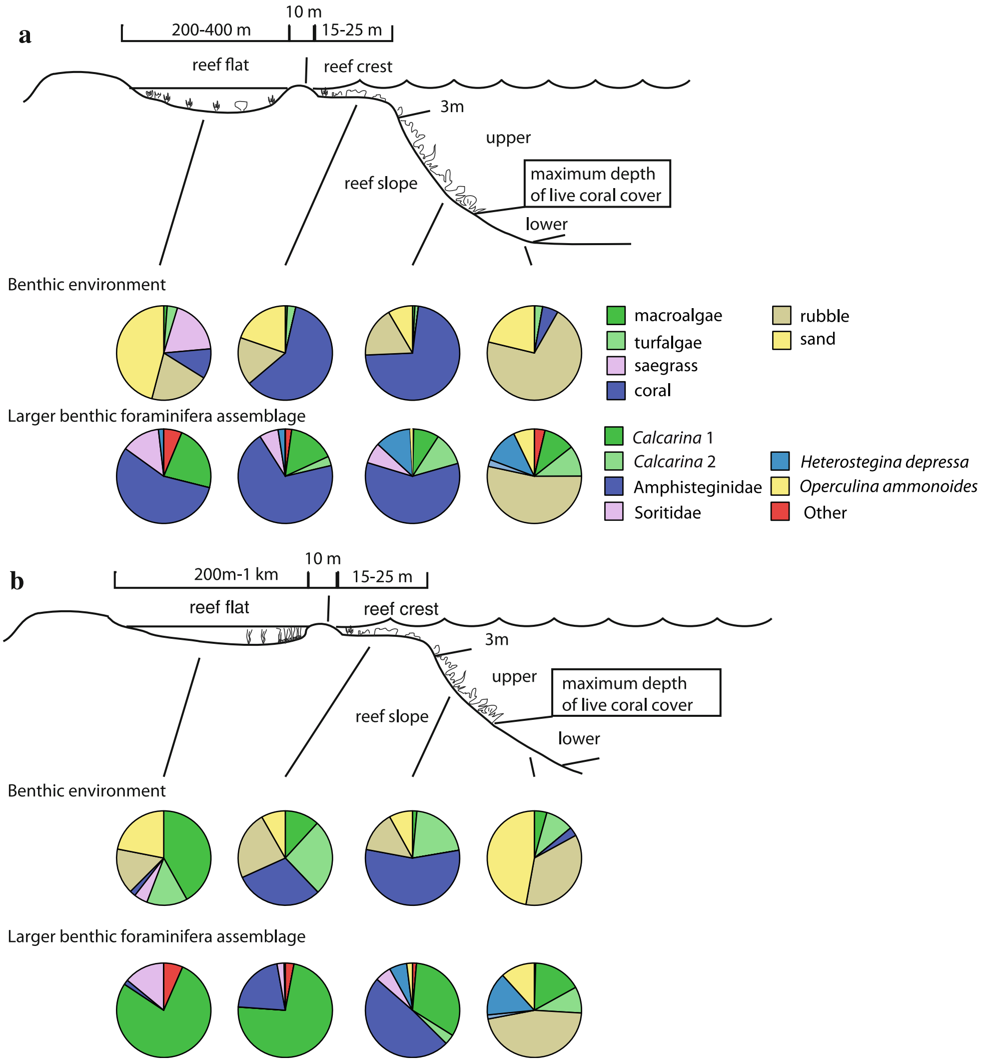

Fig. 2 Reef morphology and zonation of the reefs in the research area. The pie charts indicate the average frequency of the most important components of the benthic environment and the larger benthic foraminifera assemblage. **a** Spermonde Archipelago, **b** Kepulauan Seribu. Note the very comparable profile for the reef flat to reef lower reef slope environment, with the exception of the width of the reef flat which is much larger in the Kepulauan Seribu. The maximum depth of the reef slope increases offshore from 8 to 15 m in the Kepulauan Seribu and from 8 to 25 m in the Spermonde Archipelago

taken of the sampling sites. Additionally, for each sampling site, visibility was measured using a Secchi disk, and the maximum depth of live coral cover was estimated.

Data analysis

I utilized four analytical approaches to investigate habitat utilization of large benthic foraminifera in response to regime shifts in coral reef ecosystems: Analysis of Similarity (ANOSIM); non-metrical multidimensional scaling (NMDS); similarity percentage (SIMPER) analysis; and a Mantel-test (Appendix 1). A bootstrapping analysis has shown that a sample size of 50 specimens was enough to capture the variation in sample composition and that only the extremely rare species were potentially missed. NMDS and ANOSIM was performed on a log-transformed $[x_i = \log\ (\text{relative abundance}_i + 1)]$ species x sample matrix using Bray-Curtis similarity index. NMDS was used to graphically display the samples in a two dimensional plot. To relate the NMDS axis to environmental parameters, the correlation coefficient was calculated. Only correlation with a $r^2 > = 0.45$ are reported. Foraminifera assemblages were compared using analysis of similarities (ANOSIM) which, by analogy to ANOVA, compares variation in the similarity of species composition within and between groups of samples (Clarke 1993). Subsequently, the SIMPER test was used to identify which taxa accounted for any observed differences between assemblage groups. A Mantel test evaluated the correlation between the LBF abundance data matrix and a data matrix containing the environmental data at each site. NMDS and Mantel analyses were performed in PC-ORD v6, and ANOSIM and SIMPER analyses in Primer v6.1.6.

Results

A total of 21 species of larger benthic foraminifera were observed (Table 1). Species composition between the Kepulauan Seribu and Spermonde Archipelago is very

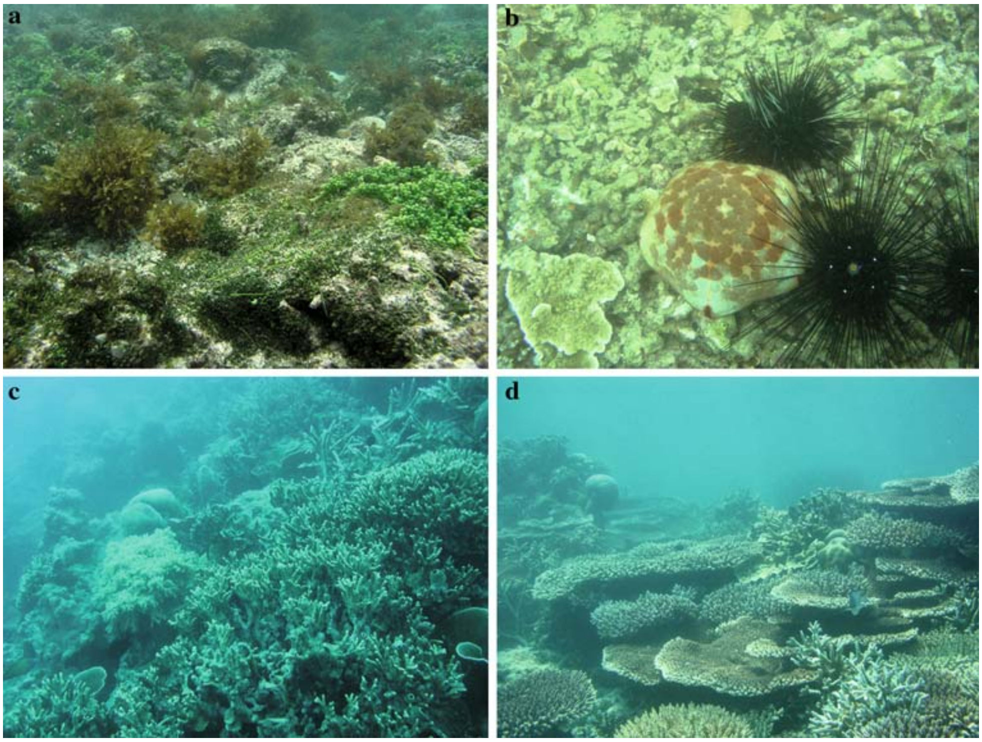

Fig. 3 Examples of habitat structures. **a** Reef flat with high algal cover, **b** reef flat with low algal cover, **c** upper reef slope with mixed algal and coral cover, **d** upper reef slope with high coral cover

similar. Twenty and 19 species were found in each of the areas, respectively (Renema and Troelstra 2001; Renema 2008). *Amphisorus* sp. was found only in the Spermonde Archipelago, and two species, *Calcarina defrancii* and *Borelis schlumbergeri*, only in the Kepulauan Seribu. Most species living at the reef slope occur at shallower depths along the reef slope with decreasing transparency of the water. This trend is most pronounced in the Spermonde Archipelago, where the samples were taken along a larger part of the turbid-clear water gradient (Fig. 2). The densities of LBF varied between 1 and 10 cm^{-2}. In the Spermonde, the average density ranged from 2 to 6 cm^{-2} from the reef crest to lower reef slope, with lower densities on the reef flat of 1–4 cm^{-2}. In the Kepulauan Seribu, average density on the reef slope was lower (1–5 cm^{-2}), while the density on the reef flat was higher (6–10 cm^{-2}). The six most abundant species in the Kepulauan Seribu were *Calcarina* sp. 2, *Amphistegina lessonii, A. lobifera, Heterostegina depressa, Calcarina* sp. 2 and *Baculogypsinoides spinosus*, while in the Spermonde Archipelago *Amphistegina lessonii*, *A. lobifera, A. radiata, Heterostegina depressa, Calcarina spengleri* and *Calcarina spengleri* (in descending order of abundance).

Average species richness ranged from 5.6 at the reef flat of the Spermonde to 7.8 in the lower reef slope of Kepulauan Seribu (Table 2). Overall average species richness was very similar between areas and environments. Species richness was highest at the reef crest and upper reef slope. Sample to sample heterogeneity, as measured by $\beta_{\mathrm{w},}$ was lowest in the lower reef slope and highest in the reef crest (Table 2).

Two major gradients captured most of the variance in the foraminifera assemblages, the first two dimensions containing 64 and 14%, respectively, of the information in the total dataset (Fig. 4). The first gradient corresponds to the depth gradient from shallow to deep. The second gradient corresponds to a gradient in benthic cover from algae to coral dominated.

The Mantel test rejected the null—hypothesis of no correlation between the foraminifera assemblage and environmental parameter data matrices ($r = 0.52$, $p < 0.001$). Correspondingly, significant differences were observed between habitats in the Spermonde Archipelago and Kepulauan Seribu (ANOSIM; global $R = 0.542$, $p < 0.001$). Pairwise comparison shows that the R-value of the between habitat comparisons is highest between the reef flat (ANOSIM; $R = 0.885$, $p < 0.001$) and decreases for the deeper habitats (reef crest, $R = 0.576$, $p < 0.001$; upper reef slope, $R = 0.362$, $p < 0.001$; lower reef slope, $R = 0.077$, $p = 0.036$).

The SIMPROF analysis showed that 7 out of 13 of the species contributing mostly to the dissimilarities between the Spermonde and Kepulauan Seribu belong to the Calcarinidae. *Calcarina* sp. 1, *C.* sp. 2 and *Baculogypsinoides spinosus* dominated the Kepulauan Seribu, while *Calcarina*

Table 1 Foraminifera taxa observed, including a reference to a published picture demonstrating the interpretation of the taxa, substrate preference and the group in which they are represented in Fig. 2

Species	Figured	Substrate preference	Group
Amphisteginidae			
Amphistegina lessonii d'Orbigny 1826	Renema et al. (2001: pl. 10g, f)	No preference	Amphisteginidae
A. lobifera Larssen, 1976	Renema (2003: Fig. 9)	Rubble	
A. radiata (Fichtel and Moll, 1798)	Renema et al. (2001: pl. 10g)	Rubble	
Calcarinidae			
Baculogypsinoides spinosus Yabe and Hanzawa, 1930	Renema et al. (2001: pl. 15c)	Macro-algae	Calcarinidae
Calcarina defranci d'Orbigny 1839	Renema (2008: Table 1) Renema (2003: Fig. 19)	Macro-algae	Calcarinidae
C. mayori (Cushman, 1924)	Renema (2008: Table 1) Renema and Hohenegger (2005: Pl. 1, Figs. 20–24)	Macro-algae	Calcarinidae
C. sp. 1	Renema (2008: Table 1)	Macro-algae	Calcarinidae
C. sp. 2	Renema (2008: Table 1)		Calcarinidae
Calcarina spengleri (Gmelin, 1791)	Renema (2008: Table 1) Renema and Hohenegger (2005: Pl. 1, Figs. 1–10)	Macro-algae	Calcarinidae
Neorotalia calcar (d'Orbigny, 1839)	Renema et al. (2001: pl. 10e)	Macro-algae	Calcarinidae
Nummulitidae			
Heterostegina depressa d'Orbigny, 1826	Renema et al. (2001: pl. 20a)	Rubble	*Heterostegina depressa*
Operculina ammonoides (Gronovius, 1781)	Renema et al. (2001: pl. 20b, c)	Rubble with sand	*Operculina ammonoides*
Soritidae			
Parasorites sp.	Renema et al. (2001: pl. 7g, h) (as *P. Orbitolitoides*)	No preference	Soritidae
Amphisorus spec	Renema et al. (2001: pl. 10c, d) (as *A. hemprichii;* see Cevasco and Lee (2007)	Rubble and reef rock	Soritidae
Sorites orbiculus (Forskal, 1775)	Renema et al. (2001: pl. 10a, b)	Seagrass and macro-algae	Soritidae
Laevipeneroplis malayensis (Hofker, 1952)	Renema et al. (2001: pl. 7e, f) (as *L. proteus*)	No preference	Other
Alveolinellidae			
Borelis schlumbergeri (Reichel, 1936)	McCulloch (1977: pl. 101 Fig. 11) (as *B. clarionensis*)	No preference	Other

spengleri was more important in the Spermonde Archipelago reef slope assemblages.

Discussion

Differences in assemblage composition between coral and macro-algae-dominated reefs

Interarea differences reported in this study demonstrate the large benthic foraminiferal faunal differences between reefs in macro-algae and coral-dominated regimes. Regime shifts alter the habitat structure, not only of the highly interacting corals and algae, which dominate the habitat structure, but also herbivorous fishes that maintain the low algal densities in the coral-dominated phase. The phase shifts affect the substrate type availability to large benthic foraminifera as well as the structure and height of the benthic boundary layer. The increase in algal cover resulted in the increase of species preferring a macro-algal substrate.

In the Spermonde Archipelago, the assemblages were dominated by species preferring coral rubble with interstitial space between the rubble (open rubble). These differences probably respond to changes in micro-scale gradients within the habitat. In open rubble, there are more possibilities to shelter from high light levels and to find the optimal concentrations of nutrients, while these options are not available in rubble with sand filling the interstitial space.

Table 2 Species diversity of larger benthic foraminifera in the two study sites and four environments

	N	Average *S*	β_w	*S*
Total	275	7.3 (1.8)	1.9	21
Spermonde	126	7.1 (1.9)	1.7	19
Seribu	149	7.5 (1.9)	1.7	20
Reef flat	37	6.6 (1.7)	1.6	17
Spermonde	15	5.6 (1.6)	1.3	13
Seribu	22	7.2 (1.4)	1.1	15
Reef crest	62	7.0 (2.2)	1.9	20
Spermonde	25	7.0 (1.8)	1.6	18
Seribu	37	6.9 (2.3)	1.6	18
Upper reefslope	109	7.5 (1.8)	1.7	20
Spermonde	63	7.2 (1.8)	1.2	16
Seribu	46	7.6 (1.8)	1.5	19
Lower reefslope	67	7.7 (1.8)	1.3	18
Spermonde	23	7.5 (1.9)	0.9	14
Seribu	44	7.8 (1.7)	0.9	15

N number of samples; *Average S* average number of species in a sample, standard deviation in brackets; β_w Whittaker's β = S/average S−1; *S* total number of species in an aggregate

One family of large benthic foraminifera is characteristic for algal-influenced coral reefs

Contrary to other studies, in which the assemblages of degraded habitats are dominated by generalist species that are able to deal with the degraded habitat (Attrill et al. 2000; Hauser et al. 2006; Jackson et al. 2001), in large benthic foraminifera, a number of taxa, predominantly belonging to the Calcarinidae, are more prominent in the algal phase. Within the Calcarinidae, a distinction between at least two functional groups of taxa can be made. One group, represented by *Calcarina spengleri* in this study, lives in openly structured coral rubble covered by crustose coralline algae and, more rarely, articulated calcified algae. The other species of *Calcarina*, *Neorotalia calcar* and *Baculogypsinoides spinosus* have a preference for rubble covered by turf algae, or corticated and leathery macrophytes (Hohenegger 2004; Hohenegger et al. 1999; Renema 2008). All calcarinids have canaliculated spines that are adaptations to strongly attach to macro-algae by a protoplasm plug. Five out of six of the species that illustrate the difference between the two areas belong to this second group of algae-associated calcarinids.

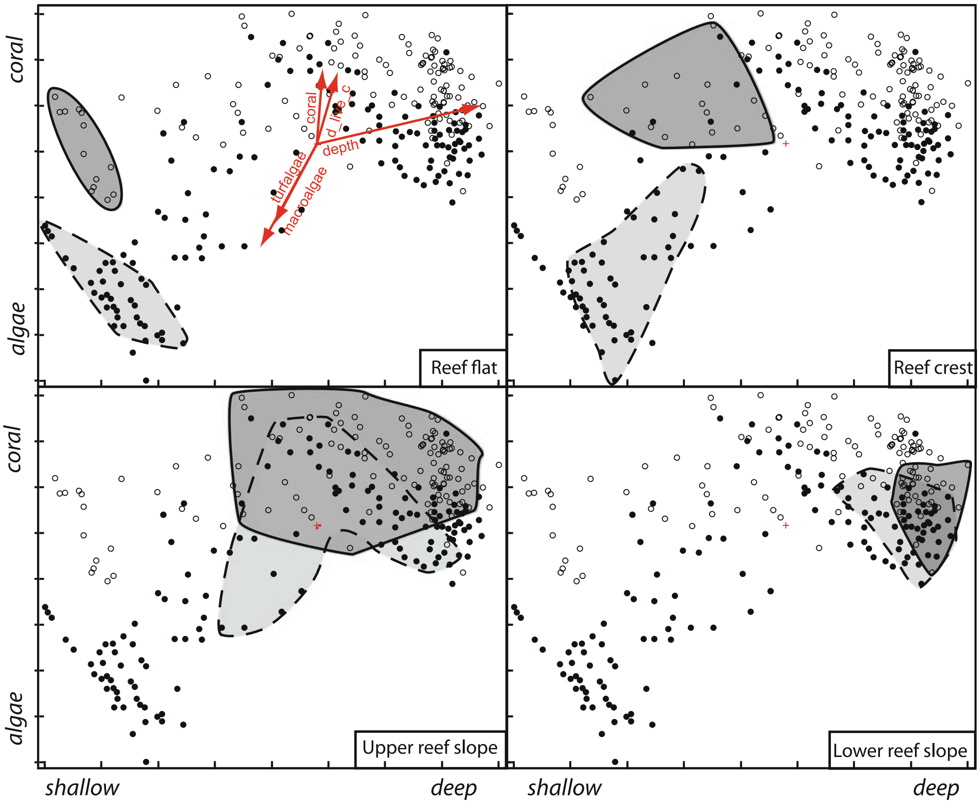

Fig. 4 Multidimensional scaling ordinations (residual stress = 0.1309) of Bray Curtis similarity between log-normalized samples. The *four panels* show the different habitats. Note the decrease in distance and the increase in overlap from shallow to deep habitats. The environmental parameters that correlate strongest with the ordination axes are indicated along the axes in *italics*. *Dark gray* = Spermonde Archipelago, *light gray* = Kepulauan Seribu

An extended history of macro-algal influence on Indo-Pacific coral reefs?

One of the big challenges in coral reef conservation is to predict when reef ecosystems are unstable and on the verge of a transition to an algal-dominated phase. The present study indicates a general relationship between regime shifts in reef ecosystems and large benthic foraminifera assemblage structure and provides quantitative evidence that macro-algae dominance directly influences assemblage structure. There has been a lively debate on top down (grazing) and bottom up (nutrients) control on algal dominance in reef ecosystems (e.g., Szmant 2002; Mumby et al. 2006; Mumby 2009; Sotka and Hay 2009). Algal dominance has, in both of these scenarios, been linked to anthropogenic disruptions of the ecosystem (Bruno and Selig 2007; Pandolfi et al. 2003), by either overfishing or increased terrestrial run-off. The present study cannot contribute to this discussion, but another important question is whether algal abundance in coral reef eco-systems is a natural phenomenon or has increased as a result of coral reef degradation.

The dominant group in the Kepulauan Seribu reefs, the calcarinids, increase in abundance in the fossil record in the Pliocene, some 5.0–2.5 million years ago (Renema 2007). *Calcarina* is rare in Middle-Late Miocene deposits, but radiates into a number of lineages during the Pliocene. Most strikingly is the increase in frequency of deposits dominated by calcarinids. This increase is coincident with a change in the regional tectonic setting related to the onset of the collision of the Australian plate to the island arcs resulting in the large scale uplift in the Papua New Guinea–Indonesia–Philippine region (Hall 2002; Renema et al. 2008). This instigated a change in reef morphology from platform, present at least since the Early Miocene, to fringing reef domination (Wilson 2008) and increased exposure to terrestrial run-off on the reefs. Calcarinidae are limited in their geographic distribution to the Indo-West Pacific (Langer and Hottinger 2000). More specifically, the species groups indicative of algal abundance are restricted in their distribution to the south western rim of the Pacific Ocean, i.e., Papua New Guinea, Indonesia, the Philippines and southern Japan. This is the region most affected by the aforementioned change in tectonic setting (Hall 2002).

The observed increased in abundance and diversity in large benthic foraminifera associated with macro-algae can be hypothesized as a response to this change in reef type, and an increased abundance of rubble, especially macro-algae on the reef flats and reef slopes in Pliocene-Quaternary reefs (e.g., Billmann and Kartaadiputra 1974; pers.obs. in reef terraces at Kalimantan, Sulawesi, Sumba, Timor and Papua New Guinea). A similar congruence in change in tectonic setting, response in geomorphological change and benthic foraminiferal assemblage structure has been observed in the Caribbean as well (Collins et al. 1996).

No data are available yet that document the effect of the recent coral–algal phase shift in that region on LBF assemblage structure. However, it has been shown that Amphisteginidae, found to be more abundant in the coral-dominated Spermonde, are sensitive to reduced water quality (Hallock et al. 2003).

This increase was prior to increased exploitation of coral reefs by humans. Understanding the biotic response to this transition in reef morphology and the associated increase in terrestrially derived nutrients forms a challenge to gain insights in present-day threats to coral reef ecosystems.

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