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Coral Reefs

Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia

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Abstract. Compared to the catastrophic impacts of various environmental disturbances and the subsequent recovery of scleractinian coral communities from these events, little is known about the early successional dynamics of coral communities following major volcanic eruptions. The 1988 volcanic eruption of Gunung Api, Banda Islands, Indonesia, provided a unique opportunity to study the rate at which a reef-building coral community develops on an andesitic lava flow. Coral colonization was studied at three locations varying in substrate characteristics. Five years after the eruption, the sheltered lava flow supported a diverse coral community (124 species) with high coral cover $\bar{x} = 61.6\% \pm 7.5$. Tabulate acroporids were a dominant component of the lava flow coral community, with some colonies measuring over 90 cm in diameter. Higher average coral diversity, coral abundance and cover were recorded on the andesitic lava flow than on an adjacent carbonate reef not covered by the lava, and on a substrate of unstable pyroclastic deposits located on the southwestern coast of the volcano. In some areas of high coral diversity and environmental stability, andesitic lava flows may create local hot-spots of coral diversity by providing a structurally complex, predator-free and stable substrate for the recruitment of coral species from the adjacent and regional species pools.

Introduction

Like many other ecosystems, coral reefs are subjected to a variety of biotic and abiotic disturbances that vary in intensity, frequency and duration (Pearson 1981; Huston 1985; Karlson and Hurd 1993). Recovery estimates of coral communities range from 10 to 70 years, depending on the type of disturbance and the initial conditions (Pearson 1981; Colgan 1987; Done et al. 1991; Dollar and Tribble 1993). Disturbance and recovery of coral communities following volcanic eruptions have received only scant attention (Grigg and Maragos 1974), yet volcanism has been recognized as a primary geological process that facilitated the dispersal of coral reefs throughout the tropics by creating new substrates (i.e., islands) for coral colonization (Darwin 1842; Dana 1872; Davis 1928).

On active volcanic islands, lava flows may cover entire reef tracts and destroy all benthic life in their path. Apart from large-scale geological disturbances (e.g., glaciation), other environmental perturbations such as tropical cyclones (Woodley et al. 1981; Mah and Stearn 1986; Van Woesik et al. 1991), short term sea-level anomalies (Loya 1976), El Niño events (Glynn 1984, 1990; Glynn and Colgan 1992), population explosions of coral predators (e.g. *Acanthaster planci*, Done 1985; Faure 1989; Done et al. 1991; *Drupella cornus*, Moyer et al. 1982) or mass mortality of invertebrate herbivores (*Diadema antillarum*, Lessios et al. 1984), do not destroy 100% of all benthic species within the impact zone, nor significantly alter the chemical composition of the reef matrix.

The Indonesian Archipelago is a tectonically active region containing some 17 000 islands, many of which are volcanic in origin (Hutchison 1989). These islands support some of the most diverse hermatypic coral reef assemblages in the world (Veron 1986). The Banda Islands (04°30′ S, 129°53′ E) are located in the eastern Banda Sea on the inner volcanic Banda Arc, and contain an active volcano named Gunung Api (Fig. 1). Gunung Api, with an altitude of 656 m, is one of the most active volcanoes in eastern Indonesia, and together with the adjacent islands of Banda Naira and Banda Besar is a remnant of a larger volcano (Kuenen 1935). According to Hutchison (1989), Gunung Api and Banda Naira (Fig. 1) form a tholeiitic basalt-dacite pair. Previous eruptions of Gunung Api were recorded in 1891, 1810, 1720 and 1614 (Kusumadinata 1979). After 97 years of dormancy, Gunung Api became active on 20 April 1988 and erupted on 9 May 1988 (Casadevall et al. 1989; Pardyanto et al. 1991).

The eruption released large quantities of viscous (acidic) andesitic lava (Casadevall et al. 1989; Van Bergen et al.

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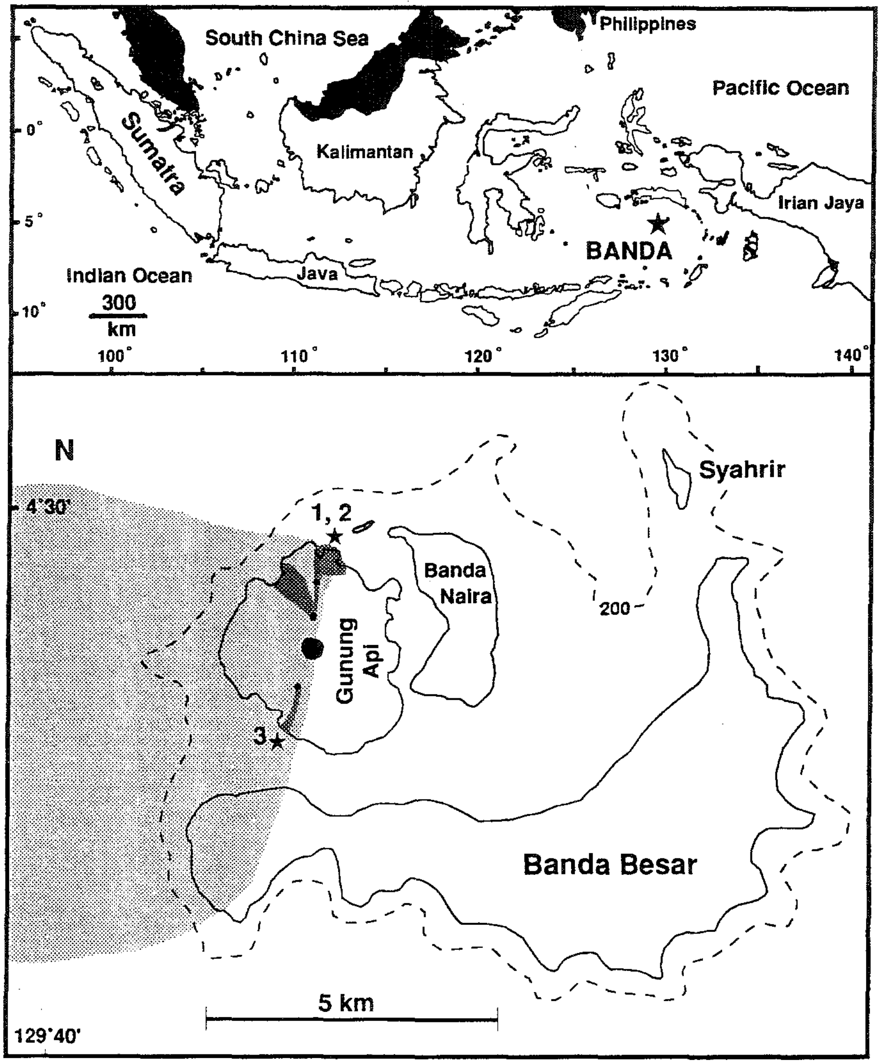

Fig. 1. Map of the Indonesian Archipelago showing the location of Banda Islands (upper), and the study locations (lower) surveyed in May 1993. A large black circle on Gunung Api represents the approximate location of the main crater. The northern and southern lava vents are indicated by small black circles. Lava flows are indicated by dark shaded areas. Air-fall tephra impact zone is indicated by the light shaded area. Dotted line represents the 200 m depth contour

1989; Pardyanto et al. 1991). The largest lava flow, with a volume of about $3.2 \times 10^6\,m^3$, originated from a north vent at an altitude of 200 m (Fig. 1). The lava entered the sea at 11:00 hours on 9 May 1988, and covered about $70\,000\,m^2$ (Casadevall et al. 1989) of a well-developed fringing reef (Sutarna 1990) to a depth greater than 50 m. The flow rate was estimated at $0.4 \times 10^6\,m^3 \cdot h^{-1}$ and continued for several days, accompanied by phreatic explosions (Casadevall et al. 1989). Because of the local topography, the lava flow split into two branches before reaching the reef, leaving an approximately 150 m wide 'island' consisting of the original reef matrix. Vegetation on the volcano's western slope suffered total decimation (Fig. 1) due to the accumulation of air-fall tephra, while the eastern slope was not affected mainly as a result of strong easterly winds during the eruption. Fringing reefs and non-reefal coral communities along the exposed southwestern coast were smothered by large quantities of pyroclastic deposits (i.e., tuffs and volcanic ash deposits).

No visible erosion or break-up of the northern lava flow occurred during the five years following the 1988 eruption, since this part of the coastline is protected (by a headland and a small island) from seas generated during the northwest (December–March) and southeast monsoons (April–November). However, since much of the southwestern coast is fully exposed to swell and rough seas generated during the southeast monsoon, rapid erosion of the pyroclastic deposits and lava occurred soon after the eruption, resulting in a submarine topography characterized by an aggregate of unstable lava rock, large lava boulders and ash.

Colonization of lava flows by corals has been previously reported only from Hawaii (Grigg and Maragos 1974), a region with comparatively low coral richness (12 scleractinian genera and 44 species) (Grigg 1983; Dollar and Tribble 1993). Grigg and Maragos (1974) suggested that coral communities on sheltered lava slopes took over 50 years to recover (i.e., in terms of species richness, abundance, percent cover, and diversity), whereas those on exposed lava slopes took about 20 years. In this study, we provide evidence for rapid coral colonization rates (5 years) of a sheltered andesitic lava flow in terms of species diversity, abundance, and cover as well as rapid coral growth rates following the 1988 eruption. These results are in contrast to the Hawaiian study (Grigg and Maragos 1974), mainly because of differences in the frequency of disturbance by heavy seas (Dollar and Tribble 1993), differences in lava type (i.e. Hawaiian lavas are basaltic), biogeographic setting, the diversity of the local and regional species pool, and growth rates of constituent species (*Acropora* is not present at the Hawaii site).

Materials and methods

Study locations

The study was conducted in May 1993, five years after the eruption of Gunung Api. Three study locations were selected on the basis of substrate type. Location 1 was on the northern lava flow on the sheltered north coast of Gunung Api (Fig. 1). The andesitic lava covered the pre-eruption carbonate reef slope to a depth of about 50 m. Location 2 was on the original carbonate reef matrix, adjacent to the western branch of the northern lava flow. Location 3 was on the exposed southwestern coast of Gunung Api, where the substrate consisted of an unstable aggregate of pyroclastic deposits.

Sampling

Two permanent 20 m × 10 m sites (A, B) were established (50 m apart) at both locations 1 and 3. At each site, twenty 20 m line transects were laid parallel to the depth contour at 50 cm intervals down the slope, and the line transect method (Loya 1972, 1978) was used to quantify the coral community. Because of logistic and time constraints, location 2 was surveyed with a modified line transect method using an underwater video system consisting of a JVC GR-JX7 video camera in an Ikelite housing. At location 2, ten 20 m line transects were laid parallel to the depth contour at 1 m intervals down the slope. The video camera was slowly moved along each transect line approximately 30 cm above the substrate. Video footage was taken of the entire coral colony at each coral-transect intersect point, and close-up footage was taken of each intersect margin for length measurement. To facilitate species identification close-up footage was taken of each colony. The close-up option allowed a clear view of individual radial corallites of *Acropora* colonies, that greatly increased the accuracy of species identification on a TV monitor.

The most striking feature at location 1, when compared to locations 2 and 3, was the abundance and size of tabulate *Acropora* colonies. To obtain an approximation of horizontal skeletal extension rates of tabulate acroporids on a new substrate at location 1, maximum diameters of all tabulate colonies were measured to the nearest centimeter. Colonies were measured along sixteen and nineteen 20 m line transects at sites A and B respectively. The line transects were laid parallel to the depth contour at 50 cm intervals down the reef slope. Time constraints prevented a quantitative comparison with locations 2 and 3.

Data processing

Coral community structure among the three locations was compared using three community descriptors: (1) average number of species per transect; (2) average number of coral colonies per transect; and (3) average percentage of live coral cover per transect. A Shannon-Weaver index of diversity, $H' = -\Sigma pi \log 10\, pi$, was computed using both coral abundance ($H'n$) and percentage coral cover ($H'c$) data to compare coral community diversity among the three locations (Shannon and Weaver 1949; Pielou 1966; Tomascik and Sander 1987). Simpson's measure of concentration, $\lambda = \Sigma n_i(n_i - 1)/N(N - 1)$, was used to compare community dominance among the three locations (Brower and Zar 1977). λ was calculated from coral abundance ($\lambda'n$) and coral coverage ($\lambda'c$) data (Tomascik and Sander 1987). Relative abundance and relative cover were computed for 6 coral groups: (1) soft corals; (2) massive corals other than *Porites*; (3) *Porites* massive forms; (4) *Acropora* spp.; (5) branching corals other than *Acropora* spp.; and (6) encrusting corals.

Statistical analyses

Prior to statistical analysis, the original data were tested for normality and homogeneity of variance using normal probability plot procedure in SYSTAT (Wilkinson 1989), and the $F_{\max}$ test, respectively (Zar 1984), and by plotting residuals against estimated values (SYSTAT–Wilkinson 1989). With the exception of $H'n$ and $H'c$, the results of the normality and homogeneity of variance tests indicated that data transformations were necessary. Accordingly, log 10(*x*) transformations were applied to the number of species, number of colonies and the Simpson's index of concentration data, while the ARCSIN(SQRT(*x*)) transformation was applied to the percentage coral cover data (Box et al. 1978; Zar 1984).

A single factor one-way analysis of variance (ANOVA) for unbalanced designs (i.e., true least squares program; Wilkinson 1989) was carried out on all data sets (i.e., number of coral species, coral abundance, percent coral cover, coral diversity and dominance) to test a general null hypothesis that there are no differences in coral community structure among the three locations. Bonferroni multiple comparison procedure was carried out to test for the significance of between-location differences (Wilkinson 1989).

Results

The coral community on the sheltered lava flow (location 1) had a statistically higher average number of coral species, percent coral cover, colony abundance and coral diversity (Fig. 2, Table 1) than either the adjacent reef substrate, not covered by the lava (location 2), or the unstable pyroclastic deposits on the exposed coast of the volcano (location 3). Locational differences in coral community structure may be a function of local environmental conditions and/or substrate type.

In terms of colony abundance, *Acropora* and other branching species were the most successful colonizers at locations 1 and 2 (Fig. 3). Encrusting species were more abundant at location 2 than at location 1. Coral cover at both locations 1 and 2 was dominated by *Acropora* colonies, followed by other branching and encrusting forms. In contrast, branching *Pocillopora* and encrusting *Montipora* and *Porites* colonies were the three most successful colonizers (in that order) at location 3.

A total of 1568 tabulate *Acropora* colonies were measured at location 1 ($\bar{x} = 44.8 \pm 9.4$ colonies/transect; $n = 35$), with an average diameter of 38 cm (STD ± 16 cm). The size frequency distribution of the tabulate acroporids was skewed, positively with colonies between 30 to 40 cm in maximum diameter being the most abundant size class (Fig. 4). Assuming that coral settlement was immediate, and based on the maximum diameter of the largest colony measured (i.e., 98 cm), the estimated maximum horizontal colony skeletal extension rates ($20\,\mathrm{cm \cdot y^{-1}}$, radial extension $10\,\mathrm{cm \cdot y^{-1}}$) of tabulate *Acropora* spp. are very high (cf. Done 1985). However, it is unlikely that coral colonization of the new substrate was immediate. Qualitative (video)

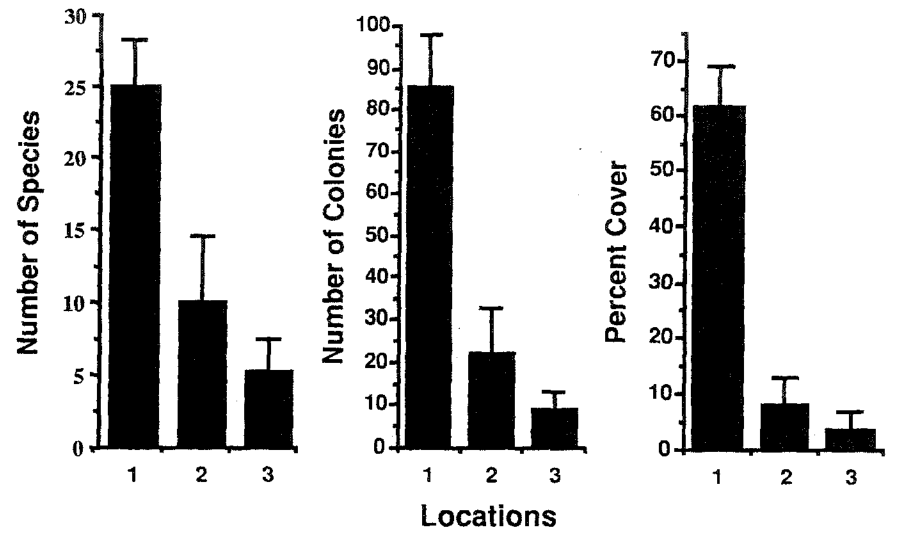

Fig. 2. Results for the comparison of coral community descriptors, species (species richness) abundance, coral colony abundance and percent live coral cover, among the three study locations on Gunung Api. Values represent means per transect, error bars represent standard deviations. For location 1 and 3: $n = 40$; for location 2: $n = 10$. Results of one-way ANOVAs for location between differences for each community descriptor indicated statistically discernible differences ($P < 0.001$). All Bonferroni multiple comparison tests (Wilkinson 1989) for pairwise differences between location means revealed statistically discernible differences at $P < 0.001$

Table 1. Coral community characteristics at the three study locations on Gunung Api where ($\bar{x}$) and standard deviation (SD) per transects are given and n is the number of transects sampled. $H'n$ and $H'c$ are Shannon-Weaver's diversity indices based on coral abundance and percent coral cover data respectively $\lambda'n$ and $\lambda'c$ are Simpson's measure of concentration indices based on coral abundance and percent coral cover data respectively $\lambda'n$ and $\lambda'c$ were $\log_{10}(x)$ transformed. Results of one-way ANOVA for between location differences are indicated by P values. Tests show the results of the Bonferroni multiple comparison test (Wilkinson 1989) for statistically discernible (at least at $p < 0.05$) pair-wise-differences between location means.

Location[a]	n	$H'n$		$H'c$		$\lambda'n$		$\lambda'c$	
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1	40	1.176	0.084	1.111	0.084	0.095	0.031	0.118	0.033
2	10	0.816	0.224	0.785	0.211	0.166	0.099	0.218	0.110
3	40	0.616	0.240	0.547	0.235	0.168	0.165	0.310	0.169
P		0.001		0.001		0.05		0.001	
Tests		1 > 2 > 3		1 > 2 > 3		3, 2 > 1		3 > 2 > 1	

[a] Locations as for Fig. 1

observation of the lava flows in 1988, 1989, 1990, and 1991 as well as the size frequency distribution (Fig. 4) indicate that major coral recruitment took place between 1990–1991, suggesting that the maximum growth rates of tabulate *Acropora* spp. could have been as high as $30\,\mathrm{cm \cdot y^{-1}}$ (radial extension $15\,\mathrm{cm \cdot y^{-1}}$).

Discussion

This study documents a rapid rate of coral community development (i.e., colonization) on an andesitic lava flow following a major volcanic eruption. Five years after the eruption, the northern lava flow of Gunung Api supported a diverse coral community consisting of 124 species, which is roughly 40% of all recorded (synonymized) coral species in eastern Indonesia (i.e., Moluccas) (Best et al. 1989). High species richness was accompanied by high coral cover (i.e., $\bar{x} = 61.6\% \pm 7.5$; $n = 40$). There was a striking difference between the colonization rates of the sheltered (location 1) and exposed (location 3) slopes, as well as much slower recovery on the adjacent carbonate reef not covered by the northern lava flow (location 2).

The northern lava flow provided a complex and initially predator-free platform. Intermittent creation of novel substrates in high diversity areas may potentially increase the abundance of rare or uncommon coral species (becoming local 'hot-spots'), particularly if the new substrates present optimal habitats for such species, and if they are used as staging areas for dispersal. Indeed, 35% of the coral species that settled on the northern lava flow are considered as either rare or uncommon members of coral communities (Veron 1986), while 47% are common and 18% are abundant. *Acropora* species were the most successful colonizers on the northern lava flow in terms of abundance and cover. The coral community on the lava flow contains one of the most diverse *Acropora* assemblages from a single location described in Indonesian waters (cf. Moll 1983). Of the 76 synonymized *Acropora* species recorded in Indonesia (Moll 1983; Best et al. 1989; C.C. Wallace and J. Wolstenholme, personal communication) 45 were recorded on the northern lava flow. This diverse *Acropora* assemblage has

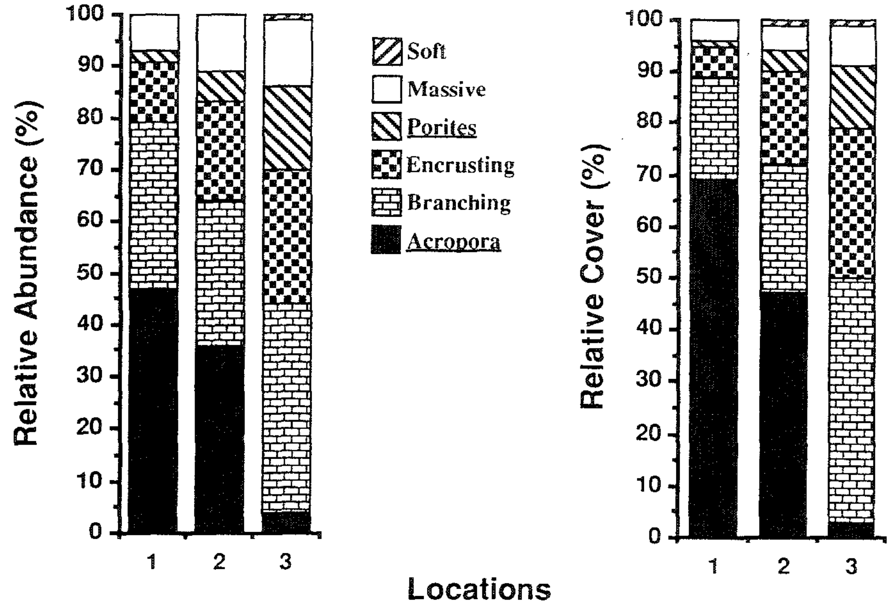

Fig. 3. Relative abundance and relative cover of six major coral groups at the three study locations on Gunung Api. Soft corals; massive: all massive corals other than *Porites*; *Porites*: massive growth forms of *Porites*; encrusting: all encrusting corals; branching: all branching corals other than *Acropora* spp.; *Acropora*: all *Acropora* species *sensu* (Done et al. 1988)

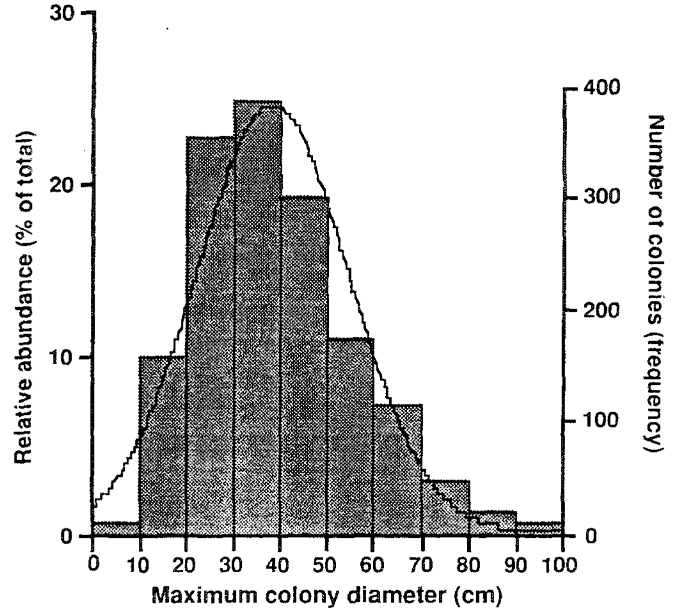

Fig. 4. Size frequency distribution and normal curve for tabulate *Acropora* spp. at location 1 based on maximum colony diameters. The distribution is positively skewed ($\bar{x} = 38.0$ cm; median = 36.0 cm; $n = 1568$; skewness $(g_1) = 0.733$). The null hypothesis H_0: $g_1 = 0$ is rejected at $P < 0.002$ (Zar 1984)

a high proportion (i.e., 45%) of either rare or uncommon species (Moll 1983; Veron 1986), including a previously undescribed species, *Acropora desalwii*, (Wallace 1994) as well as 5 forms being currently described (C.C. Wallace and J. Wolstenholme, personal communication).

A qualitative comparison can be made with a 1986 pre-eruption survey of seven reef sites in the Banda Islands (Sutarna 1990). Each site in the 1986 study was surveyed with one 100 m line transect, laid parallel to the depth contour at a depth of less than 6 m. All coral species intersected by the line transect were recorded and identified to species level. A total of 86 coral species were recorded from the seven 1986 study sites ($\bar{x} = 32.9 \pm 16.9$; $n = 7$) (Sutarna 1990). One of the 1986 sites was apparently located about 300 m to the east of locations 1 and 2 of the present study. According to Sutarna (1990), the coral community, consisting of 41 hermatypic coral species, was dominated by massive forms of *Porites lutea* and *Diploastrea heliopora*. Scleractinian corals accounted for 36.7% of the total substrate cover (24.3% by massive forms alone), while soft corals covered 18.5% of the substrate (Sutarna 1990). In 1993, we recorded a total of 45 hermatypic coral species on the old carbonate substrate (location 2), which is roughly comparable to the 1986 value. However, the 8.3% coral cover is well below the 1986 value. Soft corals were almost totally absent from the 1993 community.

Based on anecdotal information and observations during the eruption (D. Alwi, personal communication), it is probable that corals at location 2 suffered high mortality because of thermal stress, leaving an area of bare substrate consisting of dead coral colonies and loose coral rubble (personal observations) as well as a few surviving colonies of *Porites lobata* and *Diploastrea heliopora*. Since the northwest branch of the lava flow and the adjacent section of the old reef were under approximately the same environmental conditions (i.e., illumination, exposure and hydrography) and exposed to the same incoming larval pool, it is probable that the differences in coral community structure between locations 1 and 2 may be primarily a function of the physical and chemical composition of the substrate. These results indicate that given similar environmental conditions, coral planulae may exhibit a strong preference in settlement, or survive more readily, on andesitic lava substrates.

High nutrient concentrations may be one explanation for the rapid skeletal extension rates on the sheltered lava flow (Belda et al. 1993). The effusion of geothermal fluids from numerous shallow-water hydrothermal vents around

Gunung Api may be a significant source of nitrogen and phosphorus (Pringle et al. 1993). As a result of submarine topography, this area is also under the influence of daily tidally-induced upwelling events (personal observations) that may significantly influence the nutrient budget of the reef. High ambient nitrate concentrations may be one explanation for the recently demonstrated N-15 enrichment of *Porites* spp. tissue samples collected from the lava flow (J. Heikoop, personal communication).

Although the three locations were at the same temporal stage of succession (where May 1988 can be considered as $t = 0$), they now differ markedly in terms of post-disturbance substrate stability. Since the eruption, the northern lava flow has provided a stable substrate. High coral cover and diversity, combined with low dominance values, indicate that competitive exclusion through shading, overgrowth or aggressive interactions (Connell 1978), has so far not been a major factor in structuring the new coral community. In comparison, the pyroclastic deposits on the southwestern slope have been subjected to frequent slumping and heavy wave action (personal observations). The coral community has been subjected to frequent local disturbances that have maintained the community at an early successional stage. This environmental instability is reflected in the high within-site variability of coral diversity and dominance coefficients (Table 1). In comparison, high variability in community characteristics on the old reef matrix (location 2) may be a function of greater substrate heterogeneity (i.e., a mixture of coral rubble and large coral heads) when compared to the more uniform, but complex, substrate composition of the lava flow (location 1).

Intermittent disturbance, either through biotic (Porter 1972) or abiotic (Grigg and Maragos 1974; Grigg 1983) processes, has been suggested as a mechanism for enhancing coral species richness (Connell 1978). The inverse relationship between coral diversity (i.e., species richness) and coral cover used as one measure of the intermediate disturbance hypothesis (Connell 1978; Rogers 1993), has been demonstrated by Porter (1972) in the tropical eastern Pacific and by Grigg (1983) in Hawaii. The inverse relationship may be a function of long-term physical stability as well as hydrological conditions that favor resource monopolization by a few competitively superior species. The results of this study illustrate a coral community in a relatively early stage of ecological succession on a sheltered lava flow, which is characterized by high coral cover and species richness.

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