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ABSTRACT

The mechanisms by which coral reefs recover from bleaching events are important to understand in the context of global climate change and predicted increases in both frequency and severity of such events in the future. Apo Island Marine Sanctuary is dominated by the massive scleractinian *Gardula fascicularis*. An estimated 90% of these colonies bleached in September 1998 during the ENSO event. A preliminary evaluation of the extent and nature of recovery two years after bleaching took place in November 2000. Rough estimates of living tissue cover were made on the entire population, and a detailed census of cover on 12 colonies was undertaken. Results showed that 65% of the colonies (n=112 colonies) contained <25% living *G. fascicularis* tissue, in isolated patches. Recovery from bleaching was evident in both the persistence of these patches and the presence of new coral recruits onto the dead coral skeleton. On censused colonies, tissue patches averaged 0.93 m³ ± 0.38 m³ (mean ± SE); roughly 10% of the original colony area. New colonies recruiting onto bare skeleton (mean = 6.7 recruits/colony) represented 15 genera, dominated by acroporids, and occupying an average of 0.002 m² per colony. Although recruits did not occupy a significant portion of the bare substrate at this early stage of growth, the diversity of the recruiting community is predicted to alter community structure of the Apo reef, by en-

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hancing both species and structural diversity. Regrowth of remaining patches of *G. fascicularis* may allow the species to persist on the reef, though future bleaching events will undoubtedly affect the persistence of these patches. The small amount of living tissue occupying the majority of these colonies two years after bleaching event suggests that recovery is slow if the reef is dominated by a highly susceptible species, even on relatively unstressed reefs.

**Key words:** community structure; coral bleaching; ENSO; mortality; recruitment

**INTRODUCTION**

Coral reef responses to mass bleaching are poorly understood at present, yet ENSO events that result in such bleaching are predicted to increase in both intensity and frequency (Hoegh-Guldberg 1999, Reaser et al. 2000). Concern regarding links between global climate change, bleaching events and reef death is growing (Souter and Linden 2000). Much of our current understanding of bleaching-related phenomena involves the physiological mechanisms of bleaching and zooxanthellae expulsion (Brown et al 1995, Fang et al. 1997), species-specific susceptibility to bleaching (Edmunds 1994, Marshall and Baird 2000), and world-wide patterns and extent of bleaching events (Done 1999, Wilkinson et al. 1999). Such post-bleaching responses as coral mortality and partial mortality, reef recovery rate, sources of recovery, and effects on community structure have rarely been examined for whole reefs. The global severity of the 1997-98 ENSO bleaching event has created an awareness among scientists that this gap in current understanding prevents reef workers from developing predictive power for the impacts of future events. A better understanding of how reefs respond to, and recover from, bleaching events may allow the formulation of mitigative steps and provide additional information for reef managers regarding how future events may impact particular reefs.

This paper presents the results of a preliminary survey of the ‘no-take’ sanctuary within the Apo Island Marine Reserve (Fig. 1) two years after major bleaching during the 1998 ENSO. The reef is relatively narrow, approximately 75 m wide from shoreline to drop-off, and the sanctuary area occupies a 0.45 km stretch (Russ and Alcala 1999). It is dominated by large massive colonies of the scleractinian *Galaxea fascicularis* (Linnaeus), which grow in an almost continuous band along the
Figure 1. Map of Apo Island Marine Reserve, showing the study site within the unfished sanctuary.
reef crest. This species is known to be a spatial dominant, sometimes to the exclusion of other corals (Veron 1986). In September 1998, an annual survey (Reef Check 1998) noted that 90% of these colonies were bleached along a permanent transect. Bleached tissue covered an average of 80% of each colony, suggesting that G. fascicularis is highly susceptible to the warmer water temperatures during this period. Annual surveys in subsequent years revealed that many of the previously bleached colonies contained large areas of bare skeleton, indicating high post-bleaching mortality and little recovery. Because of the spatial dominance of this species within the Marine Reserve, this response is likely to have a major impact on the reef community. Bare coral skeleton represents potential recruitment surfaces for benthic larvae. Theory predicts that an abrupt increase in the availability of suitable substrates may result in changes in community structure in the highly competitive benthic reef community (Dial and Roughgarden 1998, Hughes et al. 1999). We were interested in the extent and nature of recovery that had occurred over the two-year period following bleaching. Our objectives were as follows: 1) to quantify the impact of bleaching on G. fascicularis, two years after the event; 2) to assess the nature and extent of any recovery; and 3) to determine the relative contributions to reef recovery of the different sources of coral growth and/or recruitment.

METHODS

This preliminary survey took place in November 2000, approximately two years after major bleaching in August and September 1998. To obtain a rough estimate of the impact of post-bleaching mortality within the population of G. fascicularis, an ocular survey was made of all colonies within the reserve. Most colonies were found within a 20 m belt along the reef crest, and so were easily censused. Colonies within this area were visually examined, and categorized according to the amount of living tissue remaining on them, as follows: <25%; 25-50%; 51-75%; or >75% living tissue coverage. Line Intercept Transects (n=3, 20 m transects) were used to determine substrate composition within the sanctuary and the relative contribution of G. fascicularis to total live coral cover. Data from annual Reef Check surveys along permanent transects within the sanctuary were used to present changes in substrate composition over time from the ENSO bleaching event to the present.

It was immediately apparent that most colonies surveyed fell within the lowest category (i.e., <25% live tissue cover); those most se-
verely affected and containing the greatest amount of dead skeleton. Therefore, it was decided that a subgroup of these colonies would be selected for a detailed census. Twelve colonies (11% of the total population) were randomly selected within the reserve. On each colony, diameter and height were measured, and these measurements used with the standard formula for the surface area of a cone, to obtain overall colony surface area. All remaining tissue patches were measured by placing a grid with 1 cm² subdivisions over each patch, and counting the number of subdivisions occupied by living tissue. Lastly, each colony was scrutinized for new coral recruits. All recruits were identified to the genus level, and measured (maximum diameter and diameter perpendicular to maximum). These measurements were used to obtain colony surface area, using the formula for an oval. Data were subjected to descriptive statistics to obtain means and standard errors.

RESULTS

Figure 2 presents changes in dominant substrate composition along permanent transects within the reserve from 1998-2002 (Reef Check 1998-2002). Live hard coral continued to decrease through 2001, from 61% to 12%, but showed some recovery in 2002, particularly along the crest and seaward (cover had increased to 43% along deeper transects). Recently killed coral and rubble have remained stable. The major substrate increase is in the amount of soft coral, from 15% in 1998 to 44% by 2001, with a slight decrease in 2002, suggesting that bed-forming soft corals are replacing hard corals where substrate is available. This is particularly true on the reef flat, where patches of soft coral several meters in diameter continue to dominate (a mean of 54% in shallow transects).

G. fascicularis comprised 92% of the total coral cover along the reef crest, demonstrating spatial dominance of this reef community. A total of 112 colonies were counted within the surveyed area. Sixty-five percent of these colonies contained an estimated <25% living tissue, while only 25% of the censused colonies contained >75% surviving tissue. These figures indicate that G. fascicularis suffered high partial colony mortality as a result of the ENSO episode, and that few colonies fully recovered. Two years after bleaching, the majority of the reef was still dominated by bare coral skeleton, providing abundant recruitment surfaces for colonizing larvae, and suggesting very slow regrowth by G. fascicularis tissue.
Mean colony surface area was 9.3 m$^2 \pm 1$ m$^2$ for the 12 colonies censused in detail. Living tissue patches were predominantly small and isolated, surrounded by large areas of dead skeleton (Fig. 3; n=146 patches measured on 12 colonies). The number of live patches/colony ranged between 3 and 45 (mean ± SE: 16.8 ± 3.8), and patches were fairly uniform in size, averaging 0.11 m$^2 \pm 0.03$ m$^2$. Total live tissue per colony (obtained by adding all patches on each colony) averaged 0.93 m$^2 \pm 0.4$ m$^2$. Therefore, living tissue per colony averaged approximately 10% of the colony surface (see Fig. 4). There was no suggestion of any correlation between patch size and colony size (Fig. 4); variation in the amount of living tissue per colony was dictated by the number of remaining patches, rather than the size of the patch.

Recruitment onto bare skeleton was evident and the recruiting community was very diverse (Table 1). Algae covered all surfaces not occupied by corals and other encrusting fauna, though the abundance of herbivorous fish (*Ctenochaetus* spp. and *Acanthurus* spp.) and invertebrates on this reef kept the algal community from becoming dense (unpubl. data, A. Maypa). The soft coral *Cespitularia* sp. occasionally formed mats several centimeters in diameter, though generally soft corals were not major space occupiers of bare skeleton on these colonies. A total of 100 coral recruits were observed on 9 colonies. Most coral recruits were approximately 2 cm in diameter, and probably settled during the spawning season subsequent to bleaching (the following April-May-June). This new community was dominated by *Acropora*, *Porites* and *Euphyllia* were also common (Table 1). This recruiting coral community will not be spatially or structurally dominant for many years; it still occupied an average of 0.002 m$^2 \pm 0.008$ m$^2$ per colony at this early stage. The number of recruits per colony varied greatly, but was not correlated with colony size (Fig. 5). It was interesting to note, however, that colony #12, containing the most recruits (Fig. 5), was located farthest on the reef periphery and extended over the drop-off. Most recruits were also located on the seaward-facing side of the colony, suggesting a pattern of larvae being transported toward the reef from open water and settling on the first contacted suitable substrate. Corallivory, however, likely accounts for high recruit mortality; several fresh bite marks were visible on various colonies during sampling, and corallivores (*Scarus* spp.) are abundant within the reserve.
Table 1. Composition of the recruiting community onto bare skeleton of *G. fascicularis* colonies.

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<td>Non-coral fauna</td>
<td>Encrusting sponges Soft corals: <em>Xenia</em> sp., <em>Cespitularia</em> sp. ascidians</td>
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**DISCUSSION**

This preliminary survey showed that the Apo Island Marine Sanctuary, a well-managed and relatively pristine reef, was severely impacted by the 1997-98 ENSO event. Evidence suggests this was primarily due to the susceptibility to bleaching and post-bleaching mortality of the spatial dominant on the reef, the scleractinian *Galaxea fascicularis*. *G. fascicularis* comprised 92% of the hard coral fauna along the reef crest, and 65% of these colonies had an average of 10% coverage by living, healthy tissue two years after bleaching. White (2002) presents data on substrate composition changes within the sanctuary at 10-year intervals from 1982 to 2002. This time period encompassed two major ENSO events: 1982-83 and 1997-98. Hard coral cover increased steadily from 1982 (34.7%) to 1992 (47.9%) to 2002 (56.6%), while soft coral generally decreased, from 22.7% to 9.4%. Although surveys conducted on haphazardly-placed transects at 10-year intervals do not allow the discrimination that annual surveys along permanent transects can achieve, it is elucidating to compare shorter-term results with long-term data sets. Twenty-year data show less dramatic changes in substrate composition over a longer time frame, suggesting an intrinsic resiliency in the coral community’s response to stress.
Raymundo and Maypa: Reef recovery after ENSO event

Figure 2. Changes in substrate composition over a five-year period along permanent Reef Check transects in Apo Island Sanctuary (n=4x20 m transects at two depths; 4 m and 12 m).

Figure 3. Living tissue patches relative to colony size in sampled G. fascicularis colonies (n=12). Total recruit surface area generally insignificant; greatest surface area per colony indicated at arrows on graph.
Figure 4. Living tissue patch size plotted against *G. fascicularis* colony size on sampled colonies (n=12).

Figure 5. Colony surface area versus recruit surface area on bleached *G. fascicularis* colonies (n=9 colonies and 100 recruits).
Recovery from post-bleaching mortality was obvious from two sources: survival and possible regrowth of remaining *G. fuscircularis* tissue patches, and recruitment of new colonies from settled larvae. Remaining tissue patches were scattered over most of the colonies; few colonies were completely devoid of living tissue. However, these patches were small and isolated, and it could not be determined during a single survey whether the patches were regrowing over the dead skeleton. *G. fuscircularis* reproduces asexually via extratentacular budding of peripheral corallites (corallites surrounded by living tissue do not bud). Because the corallites are large and only loosely connected to each other, buds are fairly visible. Few signs of extratentacular budding around the periphery of tissue patches were noted during our survey, suggesting that regrowth over dead skeleton is a slow process. Regrowth may be further reduced by post-bleaching stress; growth inhibition has been found to be a long-term effect of bleaching in surviving colonies (Goreau and MacFarlane 1990, Meesters and Bak 1993). In addition, only 2 of the 100 new recruits on the censused colonies were noted to be *Galaxea*, so that little recovery of this species is likely to occur via larval production and settlement. Szmant and Gassman (1990) found that energy allocated for sexual reproduction was greatly reduced after bleaching related stress; lower fecundity may be a long-term effect. Raymundo and Maypa (unpub. data) also noted decreased larval output in the brooder *Pocillopora damicornis* during the months of maximum larval production the year following the ENSO event. It seems reasonable to suspect that colonies of *G. fuscircularis*, stressed by bleaching, may also be experiencing a prolonged depression in gamete production. However, acroporids, also observed to have bleached during the ENSO event and known to be bleaching-susceptible, were the most abundant recruits. The impact of bleaching on sexual reproduction, therefore, requires further investigation.

Recruitment of new colonies from settled larvae was also evident as a source of reef recovery. The diversity of this community suggests that both structural and species diversity of the marine reserve may increase, should these young colonies survive and recruitment continue to replace much of the surface area formerly occupied by *Galaxea*. However, this process is also expected to be slow; coral growth rates are generally slower than other sessile, colonial invertebrates, and corallivory accounts for an unquantified mortality rate among recruits. Two years after bleaching, live coral cover from new recruits accounted for less
than 1% of the available surface area on the bare substrates previously occupied by *G. fascicularis* corallites.

Preliminary data suggest that the Apo reef sanctuary community may be in the process of a community shift as a result of the bleaching episode. The high post-bleaching mortality of *G. fascicularis*, and evidence of its very slow recovery from regrowth and recruitment, suggests that this species may be in the process of being replaced. It seems unlikely that it will be completely eliminated, given that many colonies and tissue patches continue to persist, but future bleaching episodes are likely to have a continued impact on recovery. Bleaching of remaining colonies was observed during the 2001 Reef Check survey (R. Pavia, pers. obs.), while very little bleaching was observed in other species within the reef. Therefore, it is likely that different species recruiting onto the substrate made available by *G. fascicularis* death will result in a community that is both species and structurally more diverse.

This study, on the response of a relatively small reef to a severe bleaching episode, raised several questions of concern to reef managers. It is evident that reef responses to stressors may be dictated not only by the state of health of the reef prior to the onset of the stress (the Apo reef is healthy and relatively unstressed), but also by the composition of the reef community and abundance of susceptible species. Furthermore, the time scale over which such responses are examined must also be considered; relatively dramatic changes in coral cover following a bleaching event reflect immediate effects of species-specific mortality and partial mortality. Longer-term effects on the reef community may be less drastic and may reflect a larger-scale resiliency to stress.

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LITERATURE CITED


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