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## Coral bleaching: the winners and the losers

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## Abstract

Sea surface temperatures were warmer throughout 1998 at Sesoko Island, Japan, than in the 10 preceding years. Temperatures peaked at 2.8 °C above average, resulting in extensive coral bleaching and subsequent coral mortality. Using random quadrat surveys, we quantitatively documented the coral community structure one year before and one year after the bleaching event. The 1998 bleaching event reduced coral species richness by 61% and reduced coral cover by 85%. Colony morphology affected bleaching vulnerability and subsequent coral mortality. Finely branched corals were most susceptible, while massive and encrusting colonies survived. Most heavily impacted were the branched *Acropora* and pocilloporid corals, some of which showed local extinction. We suggest two hypotheses whose synergistic effect may partially explain observed mortality patterns (i.e. preferential survival of thick-tissued species, and shape-dependent differences in colony mass-transfer efficiency). A community-structural shift occurred on Okinawan reefs, resulting in an increase in the relative abundance of massive and encrusting coral species.

## Keywords

Bleaching, coral, coral reefs, global warming, Okinawa, Japan.

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## INTRODUCTION

The bleaching or paling of corals, through the loss of their symbiotic algae (zooxanthellae) and/or their pigments, is a global phenomenon that is also possibly linked to global climate change and increasing ocean temperatures (Glynn 1991, 1993; Brown 1997a; Hoegh-Guldberg 1999; Strong *et al.* 2000). The first concerns regarding the impact of extensive coral bleaching on coral reefs were expressed more than 15 years ago (Glynn 1984). Recent reports of wide-scale coral bleaching from all the major tropical oceans of the world during 1997–98, and the unprecedented coral mortality that resulted (Wilkinson 1998), are a major concern among scientists and resource managers.

Coral bleaching may be a consequence of sudden environmental changes at and above the corals' acclimatization capacity. A variety of stressors have been invoked as being potentially responsible for causing coral bleaching (reviewed by Glynn 1993). Evidence is steadily accumulating for the role of specific factors (i.e. elevated or reduced sea water temperature, solar radiation including UV radiation, a combination of elevated temperature and solar radiation, reduced salinity, and bacterial infections) both in the field and in the laboratory (selected studies compiled by Brown 1997a). Coral bleaching may

also involve the gradual loss of pigmentation in the zooxanthellae, under stressful conditions (Hoegh-Guldberg & Smith 1989), without a reduction in zooxanthellae population densities (Fitt & Warner 1995; Kuroki & Van Woesik 1999). Higher than average sea surface temperatures (SSTs) under high solar radiation has been suggested as the primary causative agent of large-scale coral bleaching (Glynn 1993; Brown 1997a; Jones *et al.* 1998; Hoegh-Guldberg 1999). Elevated temperatures may also onset the virulence of coral associated bacteria that cause a reduction in endosymbiotic zooxanthellae densities (Kushmaro *et al.* 1996).

Jones *et al.* (1998) showed convincing evidence that the onset of coral bleaching begins by the impairment of CO<sub>2</sub> fixation under high temperature and high light intensity. They suggested that the toxic oxygen produced in zooxanthellae at high SSTs (Lesser 1997) coupled with high-light intensity could damage pigments and proteins, thus leading to the inactivation of photosynthesis. The inherent photo-protective capacities of carotenoids, produced by zooxanthellae, naturally quench oxygen radicals (Shick *et al.* 1996; Brown 1997a); however, under high temperatures the photo-protective properties of pigments within zooxanthellae may be inactivated. Mechanisms leading to this dysfunctionality are still under investigation.

In 1998, unprecedented worldwide coral bleaching coincided with some of the warmest sea surface temperatures (SSTs) on record. The year 1998 experienced the strongest El Niño on record. Consequently, very high water temperatures were observed in many parts of the oceans with SSTs up to 3–5 °C above normal. Bleaching reports spanning the World's three major oceans, from over 50 countries, bore witness to the global nature of the event (Wilkinson 1998; Wilkinson *et al.* 1999). Higher than average SSTs under high solar radiation has been suggested as the primary causative agent of coral bleaching (Hoegh-Guldberg 1999). Bleaching in Japan was evidenced from 33°30'N to 24°N; extending from Kushimoto in northern Japan to the Yaeyama Islands, near Taiwan, in the south (Yamazato 1999; Marine Park Center of Japan 2000).

Although coral bleaching was extensive in the southern Japanese islands, coral mortality was not absolute. There were considerable differences in the survival of colonies in accordance with taxa. Several researchers independently studied the coral reefs around Ishigaki Island (in the Yaeyama Islands, southern Japan). Most researchers suggest links to high SSTs (Fujioka 1999; Kayanne *et al.* 1999; Taniguchi *et al.* 1999). Fujioka (1999), working on two shallow reef flats on Ishigaki Island, reported that coral mortality due to bleaching reached 61–79%, in the most “thermally susceptible acroporids”. In contrast, the rate of bleaching was low and mortality was extremely low in some massive species of faviids and poritids. Kayanne *et al.* (1999) documented changes in living coral coverage before and after the 1998 bleaching event on two coral reef flats on Ishigaki Island (Shiraho and Kabira reefs). They showed that living coral coverage decreased by 50% following the bleaching event. Branching *Acropora* and *Porites* were most severely bleached and suffered high mortality. Bleaching was intermediate to high for massive *Porites*, although the frequency of their recovery was higher than for branched corals. Hasegawa *et al.* (1999) reported that extensive coral bleaching was first evident around Ishigaki Island in July 1998. They suggested that corals had already been severely damaged from red soil runoff during the previous rainy season, which recorded nearly twice as much rainfall as normal years. They further suggested that the high SSTs in the 1998 summer merely exacerbated the stress and caused extensive coral bleaching. Taniguchi *et al.* (1999) reported extensive coral bleaching around Akajima, approximately 30 km from Okinawa, which started in late July 1998. By the end of August, many pocilloporid and acroporid corals were bleached, but in contrast to the almost absolute mortality of bleached pocilloporid and acroporids at Okinawa, not all corals died on the offshore islands of Akajima.

There are numerous reports from a variety of geographical areas on wide-scale coral bleaching and resultant coral mortality, but only a few studies have presented detailed quantitative data on community structure and species diversity of corals before and after a bleaching event (Glynn 1988; Brown & Suharsono 1990; Gleason 1993; Kayanne *et al.* 1999). Hence, current information on changes to coral communities following coral bleaching is very limited and there are unclear or controversial projections concerning the long-term effects on coral community structures (Glynn 1993; Brown 1997a; Done 1999; Hoegh-Guldberg 1999).

The present study addresses this shortfall and quantitatively documents coral community changes in shallow water adjacent to the marine station at Sesoko Island, Okinawa from 1997 to 1999, one year before and one year after the bleaching event. We suggest two (not mutually exclusive) hypotheses that may explain, in part, the variance in coral mortality. (1) Preferential survival of thick-tissued coral species (i.e. mainly massive growth forms) suggests that such colonies are more likely to survive. (2) Under environmentally stressful conditions, high mass transfer facilitates survival of flat and encrusting corals over branched growth forms.

## METHODS

The study site was selected on the reef flat in front of the Tropical Biosphere Research Center (University of the Ryukyus) on the southern shore of Sesoko Island, Okinawa (26°38'N, 127°52'E). The reef flat is about 100 m in width (2 m deep at high tide). The study site was in the same area as that described and illustrated in Sakai & Yamazato (1984). Twenty-five random quadrats (1-m<sup>2</sup> each) were surveyed, using SCUBA, during the summers of 1997 and 1999, recording length and width (to the nearest mm) of all stony and soft coral colonies in the quadrats. In addition, a total of 30 1-m<sup>2</sup> quadrats along two belt transects (15 quadrats in each) were surveyed in the intertidal zone to document the unusual occurrence of juvenile *Acropora* species in this area. Each coral colony was identified and its PSA (projected surface area in cm<sup>2</sup>) was estimated assuming an oval (i.e. elliptical) colony shape, using the equation:  $PSA = \pi(L/2)(W/2)$ , where  $L$  is the length axis of a colony and  $W$  is the width measured perpendicular to the length axis (in mm). The PSA was divided by 10,000 cm<sup>2</sup>, which is the area within a 1-m<sup>2</sup> quadrat, to obtain the percentage estimates of coral cover.

Daily and monthly sea-surface temperatures were obtained during 1988–99 in the vicinity of Sesoko Island, from the Okinawa Prefecture Sea Farming Center, Motobu. Other meteorological information (i.e. air temperature, sunshine hours and rainfall) during this

period was obtained from the Okinawa Meteorological Observatory.

Fragments from 16 species of corals were randomly collected in summer 1999 from the shallow fringing reefs of Sesoko Island and nearby Bise Point, Okinawa. One fragment from each of five colonies of each species was removed using a hammer and chisel. Tissue thickness was measured on decalcified tissue and on histological sections. The fragments were fixed in 10% sea-water formalin for at least 24 h and then decalcified in 10% acetic acid plus 5% formalin solution. After decalcification, tissues were rinsed with fresh water and tissue thickness was measured with a caliper to the nearest 0.1 mm. Histological preparations were made through a graded series of ethanol concentrations. The tissues were embedded in paraffin wax, sectioned at 8  $\mu\text{m}$ , and stained with haematoxylin and eosin. Tissue thickness was measured using a calibrated ocular micrometer to the nearest 0.1 mm. Measurements resulting from caliper and ocular micrometer were almost identical and the mean from both was used for each colony.

## RESULTS

As shown in Fig. 1, SSTs were warmer throughout 1998 than in the 10 years preceding 1998, peaking at 2.8 °C above average during August (Fig. 1). In general, the weather conditions throughout the summer, until the beginning of September, were exceptionally calm, with low precipitation, high irradiation, and lack of disturbance by typhoons (Okinawa Meteorological Observatory, data not shown). In fact, 1998 was the warmest year since the start of temperature recordings, some 150 years ago, and the 1990s were the warmest decade recorded (NCDC 1999; Wilkinson *et al.* 1999).

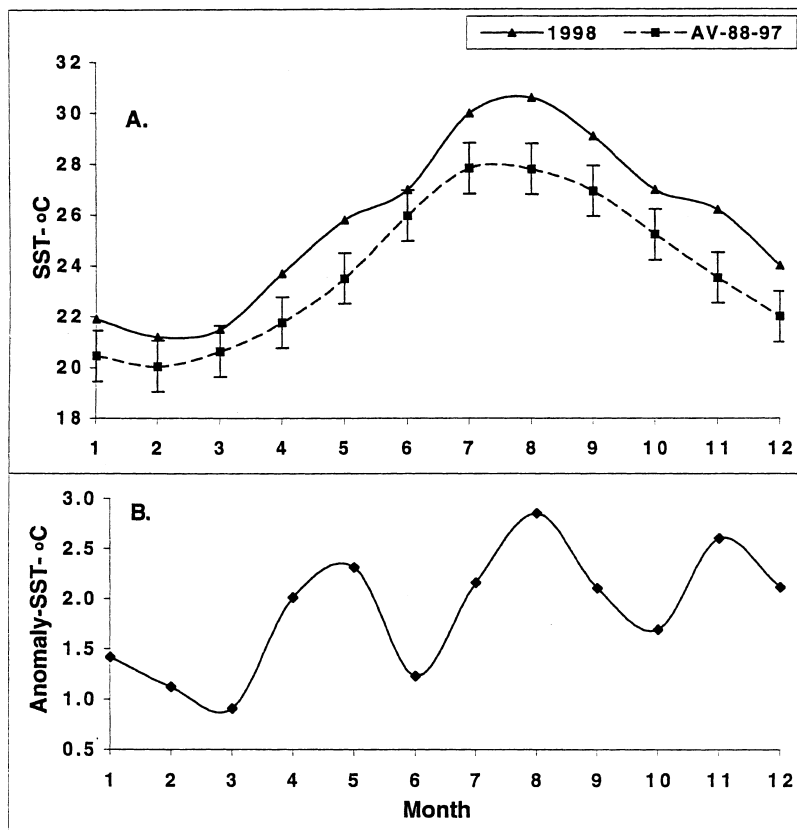
Quantitative documentation of the coral community structure (both stony and soft corals) in the shallow water adjacent to the marine station at Sesoko Island, during the summers of 1997 and 1999, one year before and after the bleaching, is provided in Fig. 2. Some coral species were “winners” and others were “losers”. Baskin (1998) used this terminology to describe differential survival of species leading to marked changes in species composition and community structure. Colony growth morphology affected bleaching vulnerability and subsequent coral mortality was species specific. Finely branched corals were most susceptible while massive and encrusting colonies survived (Table 1). Table 2 provides data on tissue thickness (in mm) of 16 coral species sampled in 1999, divided into two groups according to their growth form. It is evident that the massive colonies (group A, “winners”) supported significantly thicker tissue than the branched (group B, “losers”) colonies

(average of 3.9 mm vs. 1.2 mm, respectively; Mann–Whitney *U*-test,  $P < 0.001$ ).

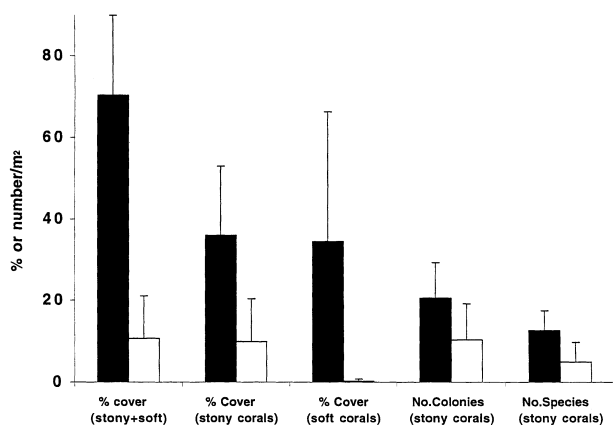
The observed bleaching event heavily impacted the branched *Acropora* corals at most locations around Okinawa Island (Van Woosik, personal observation). These corals were formerly the most prolific corals on Okinawan reefs. Other branched species suffered local extinction as shown in Table 1. Four branched pocilloporid coral species (*Stylophora pistillata*, *Seriatopora hystrix*, *S. caliendrum*, and *Pocillopora damicornis*), four branched *Porites* species (*P. sillimaniani*, *P. cylindrica*, *P. horizontalata* and *P. attenuata*) and the finely branched fire coral (*Millepora intricata*), abundant on the reefs prior to bleaching, showed local extinction (i.e. “losers”, Table 1) and no recruitment in 1999.

Other corals also common at Sesoko Island in 1997 were absent in 1999 (Table 1), causing a 73% decrease in total living cover of stony corals (Fig. 2). Consequently, some corals with low to moderate cover per  $\text{m}^2$  in 1997 showed no significant change in their average cover per  $\text{m}^2$  in 1999 (Wilcoxon Matched-pair Signed Ranked test,  $P > 0.05$ , data not shown), but showed a marked increase in their *relative* contribution to the total impoverished coral cover in 1999 (i.e. “winners”, Table 1). Massive and encrusting coral species were among the coral “winners” of the 1998 bleaching event. ‘Winners’ among the encrusting coral species included *Leptastrea purpurea* and *L. transversa*, which increased their relative contribution to the total abundance by 4.6- and 3.3-fold; while “winners” among the massive species included *Porites lutea*, *P. lobata* and *Goniastrea aspera* which increased their relative contribution to the total abundance by 3.4-, 2.1-, and 2.8-fold, respectively (Table 1). *Porites lutea*, for example, increased its relative contribution to the total living cover of stony corals from 16.3% in 1997 to 43.8% in 1999, and its relative contribution to the total abundance increased from 3.3 to 11.2%. It should be noted that the marked increase in relative contribution of some coral species to the total abundance of the 1999 stony coral community (i.e. “winners”) was a result of partial colony mortality due to bleaching and resultant colony fission (*sensu* Hughes & Jackson 1980) and was definitely not due to recruitment.

The coral community structure at Sesoko Island changed drastically following the 1998 bleaching event as is illustrated graphically in Fig. 2. The total number of species recorded in the quadrats decreased from 81 in 1997 to 40 in 1999. The combined stony coral and soft coral living cover decreased dramatically by 85% (from 70.5% in 1997 to 10.8% in 1999). Indeed, a rotting odour, caused by the decaying coral tissue, was evident for weeks, during the summer of 1998, at the marine laboratory on Sesoko Island. In the stony coral community, the mean



**Figure 1** (A) Monthly means of surface sea water temperatures, SSTs ( $^{\circ}\text{C}$ ), during 1998 and the 10 preceding years (1988–97) in the vicinity of Sesoko Island, Okinawa, Japan. Values are means  $\pm$  SD. (B) Anomalies in 1998 monthly SSTs ( $^{\circ}\text{C}$ ) compared with the mean SSTs of the 10 preceding years (i.e. 1988–97).



**Figure 2** Community descriptors of stony corals and soft corals: number of species, number of colonies, and percent living cover per  $\text{m}^2$  in the reef moat. Values are means  $\pm$  SD; black bars, 1997; empty bars, 1999.

living cover, number of species and number of colonies per  $\text{m}^2$  decreased by 73%, 61%, and 50%, respectively.

The widespread bleaching of the soft coral community resulted in mass mortality and a near localized elimination of their living cover from an average of 34.4% in 1997 to 0.2% in 1999, which is more than a 99% decrease in living soft coral cover (Fig. 2). The most abundant soft coral

*Lobophytum* sp. (which prior to the bleaching event dominated the soft coral community, contributing 91% of total soft coral cover) decreased in 1999 to 10% living cover out of the remaining depauperate soft coral community. However, *Simularia* sp., the second most abundant species among the soft corals in 1997, was much more resistant to bleaching and replaced *Lobophytum* sp. as the most abundant soft coral at Sesoko Island (Table 1). Many small colonies were recorded as aggregates in a few quadrats, having resulted from partial mortality and fission of a few large colonies.

Paradoxically, juvenile *Acropora* colonies survived in the intertidal zone despite being exposed to high irradiance and desiccation during summer midday low tides. The percentage size distribution of 17 *Acropora* species recorded from 389 colonies measured in 30  $1\text{-m}^2$  quadrats in 1999 is presented in Fig. 3, and the mean projected surface areas (PSA in  $\text{cm}^2$ ) of the nine most abundant species is presented in Fig. 4. It is apparent from the *Acropora* size frequency distribution that colonies with PSAs of 10–20  $\text{cm}^2$  (3–5 cm in diameter) were the most abundant colonies in 1999 (Fig. 3). The frequency of large colonies was very low, and no colony larger than  $\approx 9$  cm in diameter was found in this area (i.e. approximately 65  $\text{cm}^2$ ). Repeated censuses of the same quadrats, throughout

**Table 1** Structural shift in the coral community following the 1998 bleaching event: (A) “winners”, coral species increasing their relative contribution to total living cover and abundance in 1999 compared to 1997; (B) “losers”, coral species absent in the 1999 survey. Percentage contribution to living cover and abundance was calculated separately for the stony and soft coral populations.

Coral species	Growth form	Cover (%)		Abundance (%)	
		1997	1999	1997	1999
Stony corals					
(A) “winners”					
<i>Porites lutea</i>	Massive	16.3	43.8	3.3	11.2
<i>Porites lobata</i>	Massive	6.1	13.5	2.1	4.4
<i>Leptastrea transversa</i>	Encrusting	3.6	11.3	3.1	10.4
<i>Goniastrea aspera</i>	Massive	3.5	3.9	8.6	24.0
<i>Goniastrea pectinata</i>	Massive	1.2	1.7	2.1	3.3
<i>Leptastrea purpurea</i>	Encrusting	1.0	1.7	2.0	9.2
<i>Platygyra ryukuensis</i>	Massive	0.9	2.5	1.0	0.4
<i>Porites rus</i>	Massive	0.9	3.4	1.4	3.2
<i>Favites halicora</i>	Massive	0.5	3.4	0.6	2.0
<i>Favia fava</i>	Massive	0.3	1.3	1.4	2.8
Total percentage contribution		34.3	86.5	25.6	70.9
(B) “losers”					
<i>Millepora intricata</i>	Branched	6.4	0.0	5.1	0.0
<i>Millepora dichotoma</i>	Plate-like	2.4	0.0	1.0	0.0
<i>Acropora digitifera</i>	Branched	2.3	0.0	3.3	0.0
<i>Porites attenuata</i>	Branched	2.3	0.0	1.8	0.0
<i>Porites sillimaniani</i>	Branched	2.1	0.0	1.2	0.0
<i>Stylophora pistillata</i>	Branched	1.9	0.0	4.1	0.0
<i>Porites cylindrica</i>	Branched	1.9	0.0	2.1	0.0
<i>Montipora aequituberculata</i>	Plate-like	1.7	0.0	1.6	0.0
<i>Porites nigrescens</i>	Branched	1.5	0.0	1.0	0.0
<i>Pocillopora damicornis</i>	Branched	1.4	0.0	2.5	0.0
<i>Millepora platyphylla</i>	Plate-like	1.4	0.0	1.0	0.0
<i>Porites aranetai</i>	Branched	1.3	0.0	1.0	0.0
<i>Porites horizontalata</i>	Branched	1.3	0.0	1.2	0.0
<i>Seriatopora hystrix</i>	Branched	0.6	0.0	2.0	0.0
Total percentage contribution		28.5	0.0	28.9	0.0
Soft corals					
<i>Lobophytum sp.</i>		91.1	10.0	80.7	3.5
<i>Sinularia sp.</i>		7.5	76.6	15.3	68.9

the 1999 summer and the 2000 winter, indicated that almost all of these juvenile colonies survived.

## DISCUSSION

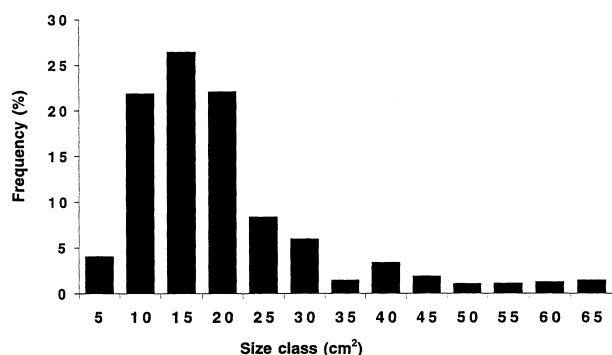
The high SSTs recorded at Sesoko Island and the unusual calm and clear weather conditions of the 1998 summer affected the coral colonies over a range of time scales, from immediate bleaching of the zooxanthellae within *Stylophora pistillata* colonies in July/August, at the onset of the higher than average SSTs (Kuroki & Van Woelk 1999), to cessation of *Porites* colony growth for up to 6–7 months (Suzuki *et al.* 2000). Reports from Australia have also shown adverse effects on coral reproduction the year following bleaching (Ward 2000). We quantitatively

documented the coral community structure, of both stony corals and soft corals, in the shallow water adjacent to the marine station at Sesoko Island, during the summers of 1997 and 1999, one year before and after the bleaching event. Some coral species were “winners” and others were “losers” (*sensu* Baskin 1998). Colony growth form and tissue thickness appeared to influence coral vulnerability.

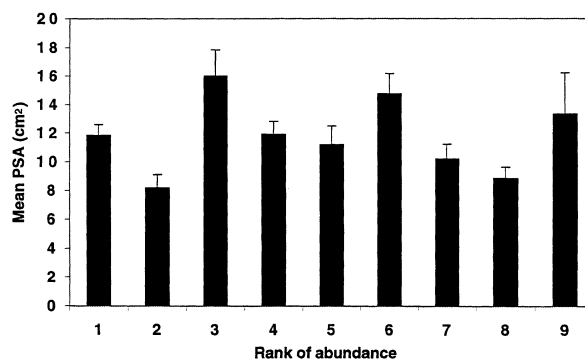
Done (1999) outlines four possible scenarios for coral reef systems under growing stresses. They range from (a) physiological tolerance of extant corals with no changes to community structure; (b) faster turnover of populations resulting in younger age structure of the community; (c) strategy shifts—a move to more ephemeral (*r*-selected) coral species; and (d) phase shift transition to a well adapted but functionally different group (e.g. macro-

**Table 2** Tissue thickness (mm  $\pm$  SD) of massive and branching corals ( $n = 5$ ).

Coral species	Growth form	Tissue thickness (mm)
Winning species		
<i>Porites lutea</i>	Massive	2.6 $\pm$ 0.009
<i>Goniastrea aspera</i>	Massive	3.6 $\pm$ 0.006
<i>Platygyra ryukyuensis</i>	Massive	4.0 $\pm$ 0.096
<i>Porites rus</i>	Massive	1.9 $\pm$ 0.300
<i>Favites chinensis</i>	Massive	9.4 $\pm$ 0.174
<i>Goniastrea retiformis</i>	Massive	2.8 $\pm$ 0.196
<i>Favia pallida</i>	Massive	3.1 $\pm$ 0.011
Mean		3.9 $\pm$ 0.110
Losing species		
<i>Porites cylindrica</i>	Branched	1.3 $\pm$ 0.180
<i>Pocillopora damicornis</i>	Branched	0.9 $\pm$ 0.043
<i>Porites sillimaniani</i>	Branched	1.3 $\pm$ 0.135
<i>Stylophora pistillata</i>	Branched	1.5 $\pm$ 0.279
<i>Pocillopora verrucosa</i>	Branched	0.4 $\pm$ 0.006
<i>Montipora digitata</i>	Branched	0.9 $\pm$ 0.006
<i>Acropora gemmifera</i>	Branched	1.9 $\pm$ 0.018
<i>Acropora digitifera</i>	Branched	1.9 $\pm$ 0.105
<i>Acropora aspera</i>	Branched	1.0 $\pm$ 0.329
Mean		1.2 $\pm$ 0.120

**Figure 3** Percent size distribution for several size classes (PSA in cm<sup>2</sup>) of 17 juvenile *Acropora* species in the intertidal zone in 1999 ( $n = 389$  colonies).

algae, soft corals, etc.). Although phase shifts in coral community structure have been reported, they have been mostly in association with eutrophication (Smith *et al.* 1981), *Acanthaster planci* outbreaks (Done 1992), and overfishing (Hughes 1994), but rarely in association with coral bleaching (Glynn 1988 and most recently by Ostrander *et al.* 2000). On Okinawan reefs we witnessed a different outcome, a “community-structural shift,” the result of differential survival of coral species leading to marked changes in species composition and community structure. Baskin (1998) used the terminology, “winners” and “losers” to describe such differential selective pressures and consequent outcomes.

**Figure 4** Mean projected surface area (PSA in cm<sup>2</sup>) of the nine most abundant juvenile *Acropora* species in 1999 in the intertidal zone ( $n = 345$  colonies in 30  $\times$  1-m<sup>2</sup> quadrats). Number of colonies of each species in parenthesis: 1, *A. digitifera* (98); 2, *Acropora* spp. (72); 3, *A. aspera* (44); 4, *A. latistella* (39); 5, *A. gemmifera* (26); 6, *A. hyacinthus* (20); 7, *A. tenuis* (19); 8, *A. cerealis* (14); 9, *A. nasuta* (13).

At Sesoko Island, the most obvious “losers” during the 1998 summer bleaching event were the branched pocilloporids (i.e. *Stylophora pistillata*, *Pocillopora damicornis*, *Seriatopora hystrix*, *S. caliendrum*) branched *Porites* species (*P. sillimaniani*, *P. cylindrica*, *P. horizontalata*, and *P. attenuata*) and the finely branched fire coral *Millepora intricata* (Table 1). In 1997, these corals were locally dominant. However, no colonies of these species were found after extensive searches throughout the study site in 1999. Clearly, they had become locally, if only temporarily, extinct. The obvious “winners” were massive and encrusting colonies, including the species *Leptastrea purpurea*, *L. transversa*, *Porites lutea*, *P. lobata*, and *Goniastrea aspera*. Although their total percent cover did not change significantly in 1999, their relative contribution to abundance had increased in 1999 by several fold (see Table 1), a result of partial mortality and subsequent fission of previously large colonies. The soft coral community also showed a dramatic change. Not only was the percentage of soft coral cover reduced by 99%, but there was also a community-structural shift in soft coral dominance from *Lobophytum* sp. to *Sinularia* sp.

Differential susceptibility of corals to bleaching in Okinawa was clearly linked to colony morphology and possibly tissue-thickness (Table 2). In reports mainly for Indo-Pacific corals, branched coral species were among the first to bleach and die (Yamazato 1981; Fisk & Done 1985; Harriott 1985; Oliver 1985; Glynn 1988, 1993; Brown & Suharsono 1990; Hoeksema 1991; Gleason 1993; Hoegh-Guldberg & Salvat 1995; Fujioka 1999; Kayanne *et al.* 1999; Taniguchi *et al.* 1999). One hypothesis suggests that bleaching vulnerability depends on the genetic constitution of the symbiotic algae (Rowan

*et al.* 1997). More extensive genetic studies are necessary at the zooxanthellae level to contest this hypothesis. Fujioka (1999) suggested that acroporids with higher ratios of surface area per volume of skeleton were thermally more susceptible than acroporids with lower ratios. Fujioka, however, did not provide a mechanism. We offer two further hypotheses. The first, suggested by Hoegh-Guldberg (1999), involves differential tissue thickness (depth). He speculated that thick-tissued colonies may be more likely to survive because of the photo-protective capacity of the tissue (*per se*). Brown (1997b) suggested that expansion and contraction of tissues provide a rapid and flexible means of regulating radiant flux reaching zooxanthellae. In a retracted state, the algal cells become self-shading. Hence, in thick-tissued species, retraction of tissues and self shading is probably more effective than in thin-tissued species. We clearly show that the massive and encrusting coral species have, on average, thicker (deeper) tissue (Table 2). The relatively high abundance of thick-tissued species (i.e. *Favites chinensis*, *Platygyra ryukyuensis* and *Goniastrea aspera*, Table 2) in the intertidal zone of Sesoko, exposed to the air, high irradiance, and desiccation during summer midday low tides (Loya *et al.* unpublished data), may be explained by this hypothesis. The large size of many of these colonies (up to more than 100 cm in diameter) may also indicate that they are more tolerant to this harsh environment, as also recently suggested for corals on the reef flat in Phuket, Thailand (Brown *et al.* 2000). The “experience-mediated tolerance” hypothesis, suggested by Brown *et al.* (2000), cannot explain the surprisingly high abundance of the juvenile *Acropora* in this area. Perhaps the high abundance of these juvenile colonies may be partially due to the fact that most of them were found in shaded crevices created by the bioerosion activity of the sea urchin *Echinometra mathaei*, which is extremely abundant in this area. Nonetheless, some colonies were found exposed to maximal solar irradiance, yet in good condition, on the surface of the intertidal carbonate. Other locations surveyed on Okinawa also showed a high survivorship of juvenile *Acropora*, and survivorship was not depth dependent (Van Woesik, unpublished data).

Our second hypothesis involves differential mass transfer in accordance with coral morphology. We hypothesize that under environmentally stressful conditions high mass transfer facilitates survival. Patterson (1992) showed that mass transfer varies in accordance with the shape of a marine invertebrate. Here we link this theory to coral bleaching. Since high SSTs and high solar irradiation cause the accumulation of superoxides and other oxygen radicals in coral colonies (Lesser 1997; Jones *et al.* 1998), removing these by-products may be an essential process to ensure colony health. Patterson (1992)

predicted mass transfer exponents relating body shape to metabolic rate. He showed that the mass transfer of flat organisms was higher than the mass transfer of thinning cylinders under laminar or turbulent flow. Patterson’s theoretical work suggests that under a unit-flow regime, flat colonies should have a higher mass transfer than branched colonies. This theory suggests that small *Acropora* colonies, which are often flat for up to 2 years, before they begin to branch and form 3-dimensional structures (Van Woesik, personal observation), should (theoretically) have higher mass transfer than large 3-dimensional *Acropora* colonies, and hence preferentially survive over larger colonies. The size distribution of the juvenile *Acropora* colonies (Figs 3 and 4) suggests that they had settled in the intertidal zone before the 1998 bleaching event and survived, while large *Acropora* colonies died. If the data are back transformed one year, to 1998 when the bleaching occurred, mean size would not exceed 3–4 cm in diameter, the size at which *Acropora* colonies still exhibit a relatively flat growth form, before they start to branch and become 3-dimensional.

To reiterate, the massive colonies supported thicker tissue than the branched colonies, which should, in principle, protect some underlying zooxanthellae from severe light intensities. Some photo-protection may allow photosynthesis to continue, thereby processing otherwise toxic radicals. Small, encrusting, and thick-tissued colonies may preferentially survive abnormal environmental conditions (i.e. higher than average SSTs under high solar irradiance), both through their high mass-transfer capacity and through the protective capacity of their tissue. During the 1999 summer we performed qualitative surveys by skin-diving at numerous additional sites around Okinawa. The surveys showed a similar pattern of mortality. The only place where we recorded a relatively high survivorship of large *Acropora* species was at Bise point ( $\approx$  6 km north-east of Sesoko Island, depth greater than 8 m). Very strong currents typify this site. Such observations concur with our mass transfer hypothesis (detailed in Nakamura & Van Woesik, in press), because high current velocities promote enhanced mass transfer (Baird & Atkinson 1997). This can be understood with reference to Newton’s law of viscosity, which states that a small increase in water-flow speed enhances shear stress by its square. Shear stress in turn allows the passive diffusion of metabolites or heat across the boundary between organisms and the ambient environment. It may be argued that strong currents upwell cooler, oceanic waters. This may indeed be the case at some locations, yet recent experimental evidence shows high coral survival under high flow and low coral survival under low flow, in the same SST conditions (Nakamura & Van Woesik, in press).

Coral survival was also high on offshore reefs, 15–30 km from Okinawa. This spatial difference in survival provides a unique opportunity to test the recent contention that marine systems are not particularly open, and larval exchange between neighbouring reefs may have been overestimated in the past (Barber *et al.* 2000; Cowen *et al.* 2000). Cowen *et al.* (2000) modelled the downstream advection of larvae in a group of reefs in the Caribbean. They showed that larval mortality in the plankton has been overlooked. A mortality exponent dramatically changes the degree of reef connectivity, even when modelled as low. The alternative process of larval retention near local populations may be more important in the maintenance of marine populations and for the management of marine resources (Jones *et al.* 1999; Swearer *et al.* 1999; Barber *et al.* 2000).

The surviving juvenile *Acropora* colonies at Sesoko Island may allow the recovery of local *Acropora* populations. But whether the connection between nearshore and offshore reefs is adequate to sustain, and indeed restock, the once abundant pocilloporid populations requires testing. Subsequent reinvasion and recovery will depend on recruitment from neighbouring reefs, for example from the Kerama Islands, some 30 km west of Okinawa, where high survival of coral was apparent. If recovery of *P. damicornis*, *S. pistallata*, *S. hystris*, and *S. caliendrum* is slow, connectivity can be assumed to be limited; however, their quick recovery will provide good evidence for considerable connectivity among reefs. Complicating such simplistic predictions are the different life-history strategies of acroporid and pocilloporid colonies. On the one hand, *Acropora* colonies are renowned broadcast spawners, dispersing gametes and subsequent larvae over large distances (Harrison & Wallace 1990). Pocilloporid colonies, on the other hand, are regarded primarily as brooders, where brooded larvae are most likely retained within reefs (Hughes *et al.* 1999). Indeed, molecular evidence supports this conjecture. Adjeroud & Tsuchiya (1999) recently conducted a baseline study on the genetic variation of *Pocillopora damicornis* in the Ryukyu Islands, including Sesoko Island. Their study showed significant genetic differentiation in accordance with location, suggesting only moderate gene flow between reefs in the Ryukyu Islands. This leads to the prediction that the pocilloporid populations may not regain their previous high abundance on the Okinawan reefs. Thus, a transition in community structure may be occurring, where hardier corals (i.e. massive and encrusting thick-tissued species) will eventually replace less hardy corals (mainly branched, thin-tissued species).

Analyses presented by Gates & Edmunds (1999), examining the ability of scleractinian corals to survive predicted global environmental changes via physiological

mechanisms of acclimatisation, corroborate our prediction. They suggested that corals with low growth rates and high metabolic rates, such as massive species, acclimatise more effectively than those with high growth rates and low metabolic rates, characteristic of branched species. Whether the recolonisation of pocilloporid corals is rapid (or even evident) at Sesoko Island, and how the changes in species composition will affect long-term stability of the reefs, will only be determined by long-term monitoring.

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#### BIOSKETCH

Research interests focus on coral reefs and stony corals including: Population and community structure, ecology and evolution, conservation and management, life history strategies, global climate change and its effect on coral-reef communities, bleaching, sclerochronology.

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