

Revisiting the winners and the losers a decade after coral bleaching

R. van Woesik^{1,*}, K. Sakai², A. Ganase¹, Y. Loya³

¹Department of Biological Sciences, Florida Institute of Technology, Melbourne, Florida 32901, USA

²Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, Motobu, 905-0227 Okinawa, Japan

³Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel

ABSTRACT: Over the past 3 decades, thermal stress events have damaged corals globally. Few studies, however, have tracked the recovery process or assessed whether winners in the short term are also winners in the long term. In the present study, we repeatedly sampled a coral assemblage over a 14 yr period, from 1997 to 2010, through 2 thermal stress events (in 1998 and 2001). Our goal was to examine the consistency of short-term winner and loser outcomes over the recovery period. Although species richness had recovered after 10 yr, the reef composition had changed, and few pocilloporids were to be found. The short-term winners were the thermally tolerant encrusting and massive coral morphologies (*Porites* and faviids) and *Acropora* colonies <5 cm in diameter. Long-term winners were revealed as (1) thermally tolerant, locally persistent colonies, (2) remnant survivors that rapidly regrew, and (3) regionally persistent colonies that recruited.

KEY WORDS: Coral bleaching · Climate adaptation · Temperature · Reefs · Recovery

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INTRODUCTION

Reef corals have recently experienced unprecedented thermal stress events (Glynn 1984, 1988, 1991, Hoegh-Guldberg 1999, Aronson et al. 2000, IPCC 2007). In many localities, extreme thermal stress has led to extensive coral bleaching, mortality and dramatic shifts in coral community structure (Marshall & Baird 2000, Loya et al. 2001, McClanahan 2004). Under such circumstances, corals with branched and corymbose growth forms, such as *Acropora*, *Pocillopora*, *Stylophora*, *Seriatopora* and branched *Porites* spp., are generally more susceptible to thermal stress than corals with massive and encrusting growth forms, such as massive *Porites* and faviids (Loya et al. 2001). Such findings are consistent throughout the Indo-Pacific region (Brown & Suharsono 1990, Marshall & Baird 2000, McClanahan 2004, McClanahan et al. 2007a,b). Thermal sensitivity of corals has been associated with high metabolic rates (Gates & Edmunds 1999), thin coral colony tissue thickness (Loya et al. 2001), low mass-transfer rates (Naka-

mura & van Woesik 2001), low concentrations of green fluorescent proteins (Bou-Abdallah et al. 2006), high light-absorbing capacities (Fabricius 2006) and intolerant symbionts (Baker 2001). Although thermal tolerance is clearly attributed to the properties of both the host coral and the resident symbionts (Baird et al. 2009), acclimation and adaptation to the local environment also plays a role in thermal susceptibility (McClanahan & Maina 2003, Smith-Keune & van Oppen 2006).

Over the next century, the climate is predicted to drive water temperatures to levels above those that have been experienced by coral reefs for over 400 000 yr (Hoegh-Guldberg et al. 2007), consequently increasing the risk of mass-bleaching events (Glynn 1993, Hoegh-Guldberg 1999, Donner et al. 2005, Hoegh-Guldberg et al. 2007). The oceans, however, are not homogenous and thermal stress events are not consistent over space and time (Wilkinson et al. 1999, McClanahan et al. 2007a,b). In the Pacific Ocean, some localities have historically experienced frequent thermal anomalies (every 5 to 6 yr), whereas other localities have experi-

*Email: rvw@fit.edu

enced anomalous temperatures only every 50 to 60 yr (Thompson & van Woesik 2009). For example, the southern islands of Japan, the Great Barrier Reef and Micronesia all historically show low-frequency return periods (~50 yr), whereas the Galapagos Islands and Kiribati historically show high-frequency return periods (~5 yr) (Thompson & van Woesik 2009). Not only are contemporary worldwide patterns in thermal anomalies similar to those in the past, but the localities that have shown high-frequency return periods in the past few centuries have also recently experienced the most severe thermal stress (Thompson & van Woesik 2009). If these patterns persist into the near future, then some localities will receive both more intensive and more frequent thermal stress than other localities.

Short-term studies suggest that some coral species are destined to become the 'winners', whereas others are destined to become the 'losers' (Loya et al. 2001). However, simply tolerating local thermal stress is not the only viable life-history strategy to persist through time. Ephemeral assemblages that are usually susceptible to local stress also survive regionally by being highly fecund and growing quickly (MacArthur & Wilson 1967, Loya 1976, Gates & Edmunds 1999). Regional persistence also depends on (1) the local survival of small fragments, which have an inherent capacity for regrowth, (2) whether corals on neighboring reefs survived through the thermal stress, (3) whether those neighboring corals have the capacity to supply recruits, (4) the survival of recruits from neighboring reefs, and (5) the return frequency and intensity of the thermal stresses.

Few studies have examined the long-term recovery of coral assemblages following thermal stress. Here, we ask whether a winning species in the short term is also a winner in the long term. Previously we reported on the short-term effects of a severe thermal stress (~3°C above the seasonal average) on the coral populations of Sesoko Island (Okinawa) in 1998 (Loya et al. 2001), and a moderate thermal stress (1.8°C above the seasonal average water temperature) on islands 30 km southwest of Okinawa in 1998 (Roth et al. 2010). The present study tracked the coral populations in the lee of Sesoko Island, Japan, from 1997 to 2010, including nearly a decade of recovery during which the sea surface temperatures did not exceed seasonal averages (Fig. 1). Our primary objective was to assess the existence of any consistencies between short-term and long-term winners and losers.

MATERIALS AND METHODS

This study was undertaken on the southeastern reef of Sesoko Island, at the Sesoko Station of the Tropical Biosphere Research Center (University of the Ryukyus), Okinawa, Japan (26° 38' N, 127° 52' E). The reef flat is approximately 100 m wide and 2 m deep at high tide. The study site is a protected zone, regulated by the research station, and comprises an area of ca. 2500 m², as described and illustrated in Sakai & Yamazato (1984). Each year, 25 to 30 random 1 m² quadrats were surveyed using SCUBA. Sampling was carried out in 1997, 1999, 2000, 2001, 2004, 2007 and 2010. Each hard (stony) coral colony was identified to species and each soft coral colony was identified to genus. Only corals with their centers in the quadrats were measured (Zvuloni et al. 2008). For each colony in 1997 and 1999, colony length, width and height (to the nearest mm) was recorded. Projected surface area (A_{PS} ; cm²) of each colony was also estimated assuming an oval (i.e. elliptical) colony shape, using the equation $A_{PS} = (L/2)(W/2)$, where L is the length axis of a colony and W is the width measured perpendicular to the length axis (mm). From 2000 onwards, we only measured the diameter of each colony. The projected surface area of each colony was estimated by assuming that the colonies were approximately circular, using the formula πr^2 . We found little difference ($\pm 0.3\%$) in the projected surface area using the elliptical and circle formulae and therefore chose the more rapid field approach, by simply measuring each colony's diameter.

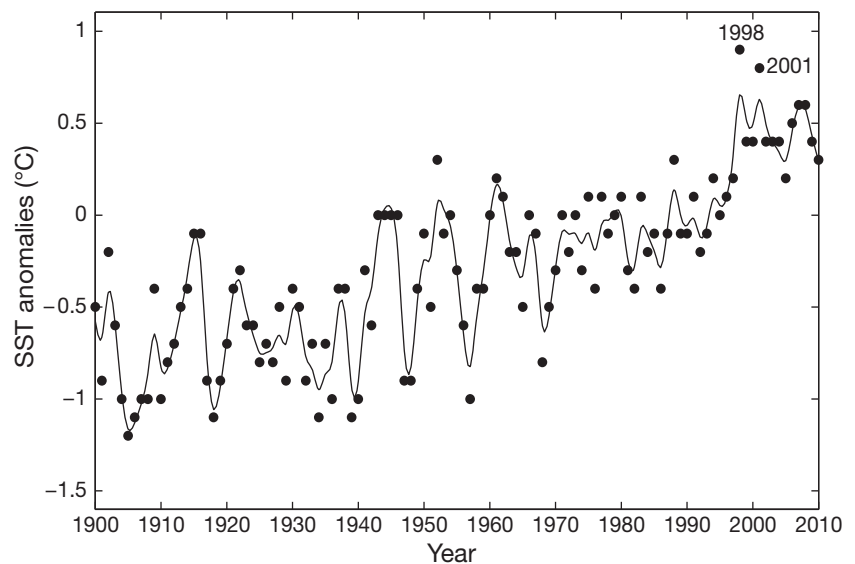


Fig. 1. One hundred and ten years of sea surface temperature (SST) anomalies for the South East China Sea region, where Sesoko Island is located. A smoothing spline (adj. $R^2 = 0.8324$) was fitted through the annual data (residual mean squared error = 0.1934); data were derived from the Japan Meteorological Agency (www.data.kishou.go.jp/db/nagasaki/nagasaki_warm/areaB_SST.txt)

A Wilcoxon matched-pair signed ranked test was used to determine whether there were discernable differences in absolute and relative percentage cover of each coral species through time. We were particularly interested in whether short-term effects were similar to long-term effects, and whether, and to what extent, the coral communities changed through time. In our 2001 publication, for each given species we summed the percentages across quadrats (Loya et al. 2001, their Table 1). In the present study, we calculated the relative contribution of each species in each quadrat relative to the contribution of that species across quadrats for each time period. More specifically, we compared the relative abundance and relative cover of each coral species in the following pairs of years (1) 1997 vs. 1999, (2) 1997 vs. 2000, (3) 1997 vs. 2010 and (4) 1999 vs. 2010. We were particularly interested in determining which species were short-term and long-term winners and losers. Therefore, we maintained the alpha value at 0.05 for each test in order to maintain power to detect meaningful ecological change through time (Rothman 1990).

We took a Bayesian approach (Gelman et al. 2003) to estimate the mean growth rates of corymbose *Acropora* species (which were mainly represented by *A. gemmifera*, *A. digitifera* and *A. nasuta*). We also compared the growth rates of corymbose *Acropora* at Sesoko Island with its growth rates at the same depth from reefs in the central Great Barrier Reef (Done et al. 2010). In both cases, we used a logistic growth model to predict the change in the mean colony diameter through time (d_t) using the equation:

$$d_t = L_{fin} / (1 + a \exp^{-bt}) \quad (1)$$

where L_{fin} is the diameter of corymbose *Acropora* colonies, which rarely exceeds 40 cm, and a and b are the fitted parameters of the logistic model over time (t). A normal likelihood function, θ , and normal priors for a and b , with a gamma prior of the precision, were used to calculate the posterior probabilities, $p(\theta|y)$, for colony growth data d_t . To obtain a useful posterior probability of growth rates, we used Markov chain Monte Carlo simulations employing Gibbs sampling. This method also determined the 95% credible intervals of the predicted growth rate parameters a and b . All models were implemented using WinBugs 1.4 (MRC Biostatistics Unit, available at www.mrc-bsu.cam.ac.uk/bugs/).

RESULTS

There was an immediate decrease in branching pocilloporids, branching *Porites* and all *Acropora* species >5 cm in diameter following the 1998 thermal stress event. By 2000, there was some hard coral recovery, evidenced by an increase in colony density and growth of survivors (Figs. 2 & 3). However, the thermal

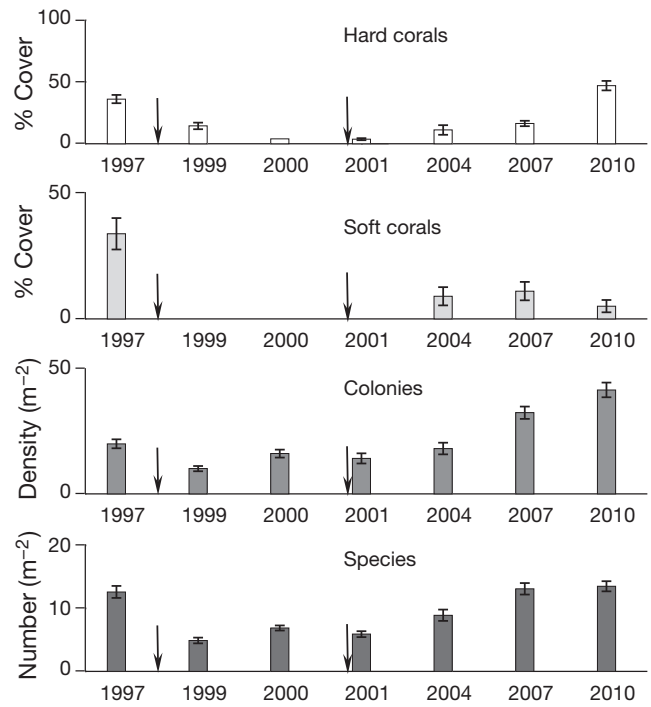


Fig. 2. Changes in percentage hard coral cover, percentage soft coral cover, density of hard coral colonies (m^{-2}) and coral species richness from 1997 to 2010 at Sesoko Island, Okinawa, Japan. Data are means \pm SE. The 1998 and the 2001 thermal stress events are indicated by arrows

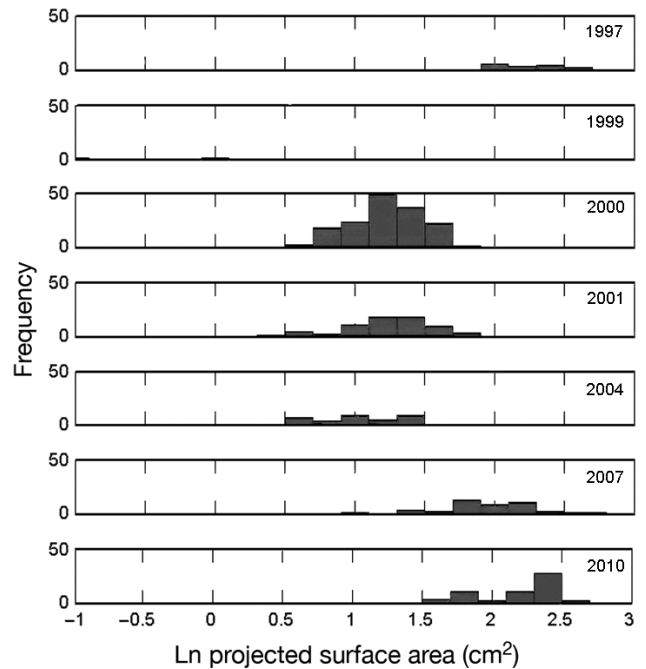


Fig. 3. Log_e-transformed size–frequency distribution of the projected surface area of corymbose *Acropora* colonies, from 1997 to 2010, at Sesoko Island, Okinawa, Japan

Table 1. Structural shifts in the coral community from 1997 to 2010, with respect to relative abundance and relative percentage coral cover (both measures of mean \pm SE percent contribution to living population), at Sesoko Island, Okinawa. Winners were coral species that increase in their relative contribution to the total living cover, and losers were coral species that decreased in their relative contribution. ns: not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Absence indicated by (–)

Coral species	Growth form	Relative abundance (%)							
		1997	1999	1997 vs. 1999	2000	1997 vs. 2000	2010	1997 vs. 2010	1999 vs. 2010
STONY CORALS									
(a) Long-term winners									
<i>Acropora digitifera</i>	Branched	3.35 \pm 1.02	–	**	21.33 \pm 3.09	***	3.51 \pm 0.71	ns	***
<i>Acropora gemmifera</i>	Branched	0.20 \pm 0.20	–	ns	12.68 \pm 2.04	***	3.19 \pm 0.55	***	***
<i>Acropora hyacinthus</i>	Tabulate	1.18 \pm 0.71	–	ns	–	ns	0.72 \pm 0.31	ns	*
<i>Favites chinensis</i>	Massive	0.59 \pm 0.33	–	ns	0.86 \pm 0.48	ns	2.31 \pm 0.66	*	**
<i>Goniastrea aspera</i>	Massive	8.68 \pm 1.83	24.08 \pm 7.75	**	25.07 \pm 3.44	**	15.95 \pm 2.46	*	ns
<i>Leptastrea purpurea</i>	Encrusting	1.38 \pm 0.78	8.98 \pm 5.81	ns	0.58 \pm 0.58	ns	27.59 \pm 6.90	***	**
<i>Montipora altasepta</i>	Branched	0.20 \pm 0.20	–	ns	0.58 \pm 0.40	ns	1.99 \pm 0.61	**	***
(b) Short-term winners with no change in the long term									
<i>Leptastrea transversa</i>	Encrusting	3.16 \pm 1.27	10.20 \pm 3.63	*	–	**	5.66 \pm 1.95	ns	ns
Massive <i>Porites</i>	Massive	6.31 \pm 1.16	13.47 \pm 3.37	*	–	***	7.67 \pm 1.18	ns	ns
(c) Short-term losers, long-term winners									
<i>Montipora digitata</i>	Branched	1.78 \pm 0.80	–	*	–	*	3.27 \pm 0.61	*	***
(d) Neither winners nor losers									
<i>Acropora cerealis</i>	Branched	0.59 \pm 0.43	–	ns	2.31 \pm 0.79	*	–	ns	ns
<i>Cyphastrea chalcidicum</i>	Encrusting	0.79 \pm 0.47	0.41 \pm 0.41	ns	–	ns	0.24 \pm 0.13	ns	ns
<i>Cyphastrea microphthalmalma</i>	Encrusting	0.79 \pm 0.47	–	ns	–	ns	1.04 \pm 0.32	ns	**
<i>Favia fava</i>	Massive	1.38 \pm 0.61	2.04 \pm 1.67	ns	0.29 \pm 0.29	ns	2.71 \pm 0.82	ns	*
<i>Favia pallida</i>	Massive	2.56 \pm 1.28	–	ns	–	ns	0.32 \pm 0.19	ns	ns
<i>Favia speciosa</i>	Massive	2.17 \pm 0.86	1.22 \pm 0.68	ns	–	*	2.39 \pm 0.67	ns	ns
<i>Favites complanata</i>	Massive	1.38 \pm 0.67	0.41 \pm 0.41	ns	–	ns	0.16 \pm 0.16	ns	ns
<i>Favites halicora</i>	Massive	0.59 \pm 0.43	0.41 \pm 0.41	ns	–	ns	0.96 \pm 0.37	ns	ns
<i>Favites pentagona</i>	Massive	1.38 \pm 0.61	1.22 \pm 0.68	ns	–	*	1.12 \pm 0.68	ns	ns
<i>Galaxea fascicularis</i>	Massive	2.56 \pm 1.07	0.82 \pm 0.57	ns	–	*	0.40 \pm 0.17	*	ns
<i>Goniastrea pectinata</i>	Massive	2.17 \pm 0.81	3.27 \pm 1.53	ns	–	*	0.88 \pm 0.29	ns	ns
<i>Leptastrea pruinosa</i>	Encrusting	0.79 \pm 0.47	2.04 \pm 1.32	ns	0.29 \pm 0.29	ns	0.72 \pm 0.72	ns	ns
<i>Millepora exaesa</i>	Encrusting	1.38 \pm 1.01	1.22 \pm 1.22	ns	–	ns	0.96 \pm 0.29	ns	ns
<i>Millepora platyphylla</i>	Plate-like	0.99 \pm 0.64	0.41 \pm 0.41	ns	–	ns	–	ns	ns
<i>Porites rus</i>	Encrusting	1.38 \pm 0.45	4.08 \pm 1.95	ns	–	**	0.88 \pm 0.57	ns	*
<i>Platygyra ryukuensis</i>	Massive	0.99 \pm 0.49	0.41 \pm 0.41	ns	–	ns	0.40 \pm 0.20	ns	ns
<i>Platygyra sinensis</i>	Massive	0.59 \pm 0.43	2.45 \pm 1.35	ns	0.29 \pm 0.29	ns	0.24 \pm 0.13	ns	ns
<i>Platygyra yaeyamaensis</i>	Massive	0.99 \pm 0.40	–	*	–	*	1.20 \pm 0.34	ns	**
(e) Short-term losers with no change in the long term									
<i>Goniastrea retiformis</i>	Massive	2.56 \pm 0.81	–	**	0.86 \pm 0.48	*	1.44 \pm 0.52	ns	**
(f) Long-term losers									
<i>Platygyra lamellina</i>	Massive	0.20 \pm 0.20	–	ns	–	ns	–	ns	ns
<i>Porites horizontalata</i>	Branched	1.18 \pm 1.18	–	ns	–	ns	–	ns	ns
<i>Porites nigrescens</i>	Branched	0.99 \pm 0.99	–	ns	–	ns	–	ns	ns
<i>Millepora dichotoma</i>	Branched	0.99 \pm 0.49	–	ns	–	ns	–	ns	ns
<i>Porites aranetai</i>	Branched	0.20 \pm 0.20	–	ns	–	ns	–	ns	ns
<i>Montipora aequituberculata</i>	Foliose	1.58 \pm 0.47	–	**	–	**	–	**	ns
<i>Millepora intricata</i>	Branched	5.13 \pm 1.19	–	***	–	***	–	***	ns
<i>Montastrea curta</i>	Massive	1.78 \pm 0.56	–	**	–	**	0.40 \pm 0.28	*	ns
<i>Millepora tenella</i>	Branched	1.38 \pm 0.61	–	*	–	*	–	*	ns
<i>Porites cylindrica</i>	Branched	2.96 \pm 1.24	0.41 \pm 0.41	*	–	*	–	*	ns
<i>Pocillopora damicornis</i>	Branched	2.56 \pm 0.91	–	*	–	*	0.24 \pm 0.18	*	ns
<i>Porites lichen</i>	Encrusting	1.58 \pm 0.62	–	*	–	*	–	*	ns
<i>Platygyra pini</i>	Massive	3.94 \pm 1.14	–	**	–	**	0.72 \pm 0.28	**	*
<i>Seriatopora hystrix</i>	Branched	1.58 \pm 0.55	–	*	–	*	–	*	ns
<i>Stylophora pistillata</i>	Branched	4.14 \pm 0.97	–	**	–	**	–	**	ns
<i>Porites attenuata</i>	Branched	0.99 \pm 0.40	–	*	–	*	–	*	ns
<i>Porites sillimaniani</i>	Branched	1.18 \pm 0.43	–	*	–	*	–	*	ns
SOFT CORALS									
<i>Lobophytum</i> spp.		80.77 \pm 13.23	4.76 \pm 4.76	***	50.00 \pm 50.0	**	50.00 \pm 20.76	ns	*
<i>Sarcophyton</i> spp.		3.85 \pm 3.85	–	ns	50.00 \pm 50.0	ns	30.00 \pm 30.0	ns	ns
<i>Sinularia</i> spp.		15.38 \pm 9.09	95.24 \pm 62.99	ns	–	ns	20.00 \pm 13.90	ns	ns

Table 1 (continued)

		Relative cover (%)					
1997	1999	1997 vs. 1999	2000	1997 vs. 2000	2010	1997 vs. 2010	1999 vs. 2010
2.31±0.67	–	ns	17.47±3.16	***	7.62±2.12	*	***
0.12±0.12	–	ns	8.86±1.78	***	9.92±2.07	***	***
0.83±0.49	–	ns	–	ns	4.62±2.57	*	*
0.83±0.49	–	ns	12.33±11.62	ns	1.73±0.65	ns	**
3.54±0.73	0.52±0.28	***	27.07±6.51	***	1.93±0.30	ns	***
1.00±0.56	0.05±0.03	ns	0.41±0.41	ns	4.45±1.28	**	***
0.23±0.23	–	ns	0.25±0.18	ns	3.95±1.21	**	***
3.58±1.50	9.55±8.52	ns	–	*	6.15±2.44	ns	ns
22.71±6.35	44.84±17.25	ns	–	***	18.62±5.11	ns	ns
1.14±0.50	–	*	–	*	7.18±2.01	**	***
0.13±0.12	–	ns	1.39±0.58	*	–	ns	ns
3.05±2.76	0.02±0.02	ns	–	ns	0.73±0.58	ns	ns
0.34±0.24	–	ns	–	ns	1.13±0.39	ns	**
0.92±0.43	0.02±0.02	*	0.21±0.21	ns	0.67±0.21	ns	***
1.55±0.79	–	ns	–	ns	0.11±0.06	ns	ns
2.17±0.93	0.31±0.26	ns	–	*	1.18±0.52	ns	*
1.20±0.48	0.02±0.02	ns	–	ns	0.03±0.03	ns	ns
0.56±0.40	8.53±8.53	ns	–	ns	0.26±0.09	ns	ns
0.85±0.37	0.21±0.21	ns	–	*	0.25±0.15	*	ns
0.90±0.50	0.01±0.01	*	–	*	0.43±0.26	ns	*
1.22±0.48	0.06±0.04	*	–	*	0.63±0.21	ns	**
0.58±0.32	0.09±0.09	ns	0.07±0.07	ns	0.27±0.27	ns	ns
0.61±0.42	0.01±0.01	ns	–	ns	0.57±0.23	ns	**
1.42±0.84	–	ns	–	ns	–	ns	ns
0.90±0.41	2.05±1.65	ns	–	*	0.39±0.29	ns	ns
0.90±0.43	–	ns	–	ns	0.10±0.05	ns	ns
0.49±0.34	–	ns	0.13±0.08	ns	0.10±0.06	ns	ns
1.18±0.50	–	*	–	*	0.23±0.09	ns	**
1.34±0.51	–	*	2.32±1.59	ns	0.77±0.24	ns	**
0.21±0.21	–	ns	–	ns	–	ns	ns
1.33±1.33	–	ns	–	ns	–	ns	ns
1.55±1.55	–	ns	–	ns	–	ns	ns
2.36±1.28	–	ns	–	ns	–	ns	ns
1.33±1.33	–	ns	–	ns	–	ns	ns
1.73±0.60	–	**	–	*	–	*	ns
6.08±2.01	–	***	–	**	–	***	ns
1.19±0.38	–	*	–	*	0.04±0.03	*	ns
0.94±0.41	–	*	–	*	–	*	ns
1.90±0.85	–	*	–	*	–	*	ns
1.44±0.49	–	*	–	*	0.01±0.01	*	ns
1.02±0.50	–	*	–	*	–	*	ns
3.18±0.87	–	**	–	**	0.20±0.09	**	*
0.61±0.21	–	*	–	*	–	*	ns
1.93±0.45	–	**	–	**	–	**	ns
2.30±1.26	–	*	–	*	–	*	ns
2.06±0.85	–	*	–	*	–	*	ns
91.08±19.25	23.78±23.78	**	92.16±92.16	**	89.14±49.61	ns	*
1.40±1.40	–	ns	7.84±7.84	ns	2.14±2.14	ns	ns
7.53±4.49	76.22±43.69	ns	–	ns	8.72±6.06	ns	ns

stress events in 2001 caused another decrease in coral cover (Figs. 2 & 3). Hard coral cover increased from 3% in 2001 to 47% in 2010, whereas soft coral cover never exceeded 10% after 1998 (Fig. 2). Change in coral colony densities followed the same trend as coral cover, increasing steadily through time (Fig. 2). By 2007, species richness had recovered to ~13 species m^{-2} , which was similar to species richness in 1997, although the species composition had undergone change (Table 1).

The most common corals on Sesoko Reef in 2010, in terms of both relative percentage cover and relative abundance, were *Goniastrea aspera*, massive *Porites*, *Leptastrea purpurea*, *L. transversa*, *Montipora digitata*, *Acropora gemmifera*, *A. digitifera* and *Favia favus*. These coral populations, however, took different trajectories over the 14 yr study period. The first 2 species were thermally tolerant and increased in relative abundance through time (Table 1a). *Leptastrea purpurea* increased in relative abundance through the thermal stress events and continued to increase (Table 1a), whereas *L. transversa* increased in relative abundance through the thermal stress and remained constant thereafter (Table 1b). Massive *Porites* were short-term winners, but did not increase overall over time (Table 1b). The branched *Montipora* species, especially *M. digitata*, declined in 1998 to only a few remnant survivors, but had recovered by 2010 (Table 1c). Thirteen faviids were neither winners nor losers through time (Table 1d). Indeed, species that did not change through time were mainly the massive colonies. *Sinularia* spp. were the most resistant soft corals to the initial thermal stress, and increased in relative abundance and cover in 1999. By 2010, *Sinularia* spp. had returned to the same relative cover and abundance as in 1997. In contrast, *Lobophytum* spp. and *Sarcophyton* spp. initially decreased in 1998, but had returned to similar relative cover and abundance by 2010 (Table 1).

Only one species (*Goniastrea retiformis*) was a short-term loser but showed no change in the long term (Table 1e). Twelve hard coral species showed a significant decrease in both relative percentage cover and abundance through time (Table 1f); 5 species (*Platygyra lamellina*, *Porites horizontalata*, *Porites nigrescens*, *Porites aranetai* and *Millepora dichotoma*), uncommon in 1997, did not show a significant decline through time but were no longer recorded in the Sesoko Island area in subsequent surveys (Type II error). Most of the species that were losers in 1999 remained losers throughout the 14 yr study, particularly the pocilloporids (*Stylophora* spp., *Pocillopora* spp., and *Seriatothya* spp.). Twelve of the 17 long-term losers showed no recovery (e.g. *Seriatothya hystrix* and *Stylophora pistillata*), and *Pocillopora* colonies were still uncommon in 2010. Branching *Porites* suffered a similar fate, and were also not found at the study site in 2010 (Table 1f).

Although most *Acropora* colonies >5 cm died in 1998, the corymbose *Acropora* populations had recovered slightly by 2000, and declined again in 2001 during the thermal stress event. The size–frequency distribution of corymbose *Acropora* species changed from a log-normal distribution in 1997 to a right-skewed distribution in 1999 and back to a log-normal distribution in 2001. Following the second thermal stress, there was a steady increase in colony size from 2004 to 2010 (Fig. 3). The mean growth rate of the corymbose *Acropora* colonies, after the 2001 thermal stress, followed an S-shaped logistic function. Mean growth was slow in the first few years after recruitment, at just over 1 cm yr⁻¹. Growth rates increased to ~3–4 cm yr⁻¹ at 7 yr, and then decreased thereafter (Fig. 4). The growth rates of corymbose *Acropora* on the Great Barrier Reef followed a remarkably similar pattern to those of the corymbose *Acropora* at Sesoko Island.

DISCUSSION

Short-term winners

Most of the massive *Porites* (*P. lutea* and *P. lobata*) and the faviids survived the 1998 thermal stress, including *Leptastrea purpurea*, *L. transversa*, *Goniastrea*

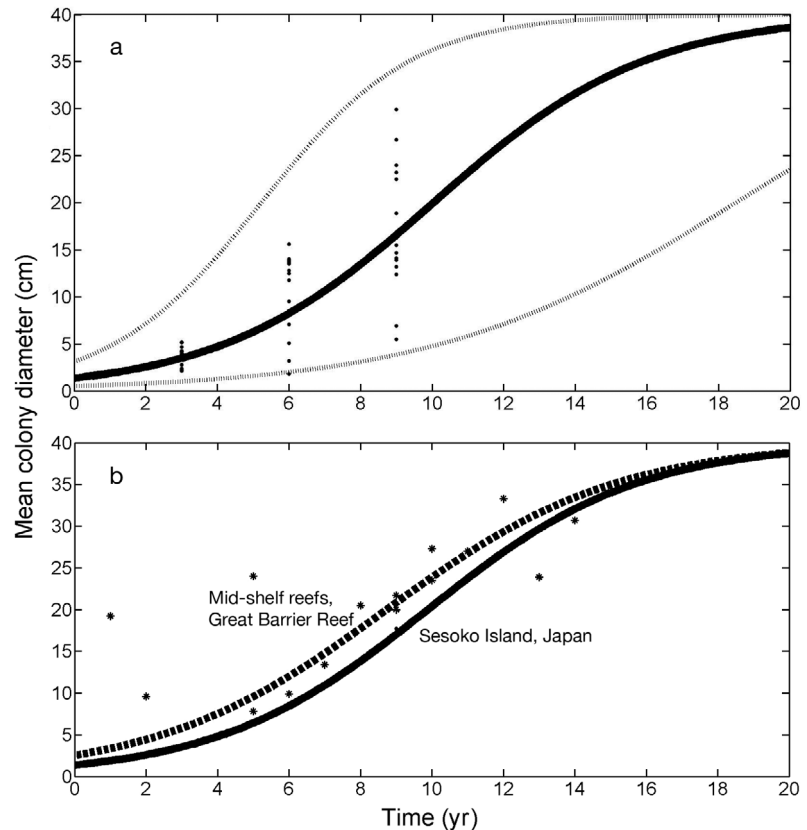


Fig. 4. (a) Mean diameter of corymbose *Acropora* colonies from 2004 to 2010 at Sesoko Island (raw data are filled circles), fitted (solid line) to the logistic growth equation, $d_t = L_{\text{fin}}/(1+a\exp^{-bt})$ with 95% Bayesian credible intervals (broken lines), where a was predicted as 28.59 (95% credible intervals = 11.88 and 78.64) and b was predicted as 0.339 (95% credible intervals = 0.23 and 0.47). (b) Comparison of mean diameter of corymbose *Acropora* colonies through time at Sesoko Island (solid line) with the mid-shelf reefs of the Great Barrier Reef (dashed line) (Done et al. 2010). Asterisks indicate data from the Great Barrier Reef. Both data sets were fitted to the logistic growth equation. Predictions for Sesoko Island are given above; for the Great Barrier Reef, a was predicted as 21.27 (95% credible intervals = 2.56 and 115.50) and b was predicted as 0.2725 (95% credible intervals = 0.12 and 0.56)

aspera and *Favia fava* (Table 1). However, the perennial question remains: What biological or physical traits allow some corals to resist thermal stress, whereas other corals bleach and die (van Woesik et al. 2004)? Bleached corals that rely exclusively on metabolites from symbionts are likely to die rapidly when their nutrient source is removed, whereas feeding on plankton, when depleted of symbionts, will facilitate colony survival (Grottoli et al. 2006). Similarly, thin-tissued corals have limited resources and may die rapidly after bleaching (Loya et al. 2001).

Nevertheless, the physical properties of corals (including shape, size and height), which influence gas and metabolite exchange across boundary layers, in turn affect thermal susceptibility (Nakamura & van Woesik 2001). However, the interactions between

such mass transfer and irradiance are not straightforward. Because the tips of coral branches receive the highest irradiance, thus increasing photoinhibition (van Woësik & Koksai 2006), they also receive the highest flow (i.e. mass transfer), which sequesters thermal stress (Nakamura et al. 2003). Our previous study also revealed that *Acropora* colonies >5 cm were not resistant to thermal stress on a local scale, whereas juveniles <5 cm did survive such thermal stress (Loya et al. 2001). Survival of these small *Acropora* colonies in 1998 had become obvious by 2000, when *A. gemmifera* and *A. digitifera* substantially contributed to relative coral abundance (Table 1) only to again suffer a decline in 2001, when those small colonies had increased in size. Theoretically, small colonies have higher mass transfer rates than large colonies (Nakamura & van Woësik 2001), but *Acropora* recruits also have conspicuously higher concentrations of green fluorescent protein than large colonies (Papina et al. 2002), which have strong antioxidant properties (Bou-Abdallah et al. 2006). Such complexities exemplify the need for controlled experiments that partition these variables, enabling more precise predictions of differential survival based on biological and physical traits.

Short-term losers but long-term winners

In 1999, only a few *Montipora digitata* and *M. alta-septa* were recorded in our quadrats. We noticed (K. Sakai pers. obs.) that these remnant branches grew rapidly and fragmented each typhoon season. By 2010, both branched species occupied a considerable proportion of the substrate (Table 1). It thus seems that the recovery of branched *Montipora* was largely by means of remnant survival and rapid regrowth rather than recruitment.

The gradual recovery of some species of *Acropora* suggests that the ecosystem was still able to absorb the thermal stressors without undergoing change to a less desirable state (Holling 1973, Scheffer & Carpenter 2003). There is a high level of genetic connectivity between the *Acropora* populations in the Kerama Islands, 30 km southwest of Okinawa, and Sesoko Island (Nishikawa et al. 2003, Nakajima et al. 2010). Moreover, neighboring reefs in the Kerama Islands continued to support *Acropora* colonies throughout the thermal stress events (Roth et al. 2010). Therefore, it is highly likely that the Kerama Islands facilitated *Acropora* recovery on Sesoko Island by supplying recruits. Similarly, *Acropora* populations had fully recovered 7 yr after an extreme thermal-stress event in Palau (Golbuu et al. 2007); and in the Arabian Gulf, Riegl & Purkis (2009) showed that *Acropora* assem-

blages could recover from thermal-stress cycles occurring every 15 yr.

Acropora recovery is illustrated in Fig. 4, which offers a useful baseline for researchers examining disturbance and recovery periods. If corymbose *Acropora* populations at specific localities do not closely reflect these recovery trajectories, then the locality of interest may be suffering from stress. A slowing of the rates may also represent the approach of a critical threshold indicating a less desirable state, beyond which recovery is more difficult (van Nes & Scheffer 2007). Nonetheless, predicting population recovery is complex. Recovery also depends on a number of variables, including the spatial scale of a species' distribution, its fecundity, how the neighboring sites fare through stress events and their capacity to supply recruits, and the intensity and frequency of the disturbance (Dayton 1971, Sousa 1979).

Adult *Acropora* are extremely fecund (Wallace 1985), grow quickly and are susceptible to most physical anomalies (Loya et al. 2001). Such life-history traits most often induce an ephemeral existence locally, but allow regional persistence. The rate and degree of *Acropora* recovery also depend on the density of nearby adult colonies (Hughes et al. 2000). On the Great Barrier Reef, for example, Done et al. (2010) contended that the dense aggregation of reefs, well connected oceanographically to a source of adult *Acropora* populations, facilitated rapid *Acropora* recovery following *Acanthaster planci* disturbance. The genus *Acropora*, however, is comprised of over 100 species. By 2010, there was a proliferation of *Acropora gemmifera* and *A. digitifera* at Sesoko Island (Table 1, Fig. 4), whereas other species, such as *A. hyacinthus* and *A. cerealis*, were less common in 2010 (Table 1).

If *Acropora* populations are subjected to more intensive and frequent thermal anomalies, will the Indo-Pacific coral reefs eventually become devoid of *Acropora*? Côté & Darling (2010) recently suggested that the reefs with the best chance of survival in the face of climate change will be the resistant reefs without *Acropora*. They also suggested that *Acropora* and *Montipora* will be replaced by *Porites* and *Platygyra* in the Indo-Pacific. *Porites*, in particular *P. lobata*, *P. lutea*, *P. rus* and *P. cylindrica*, which are the main reef-building *Porites* of the Indo-Pacific, are all leeward species. *Platygyra* is naturally uncommon (Table 1). Consequently, *Porites* and *Platygyra* might not necessarily replace *Acropora* in the near future, because they are not generally constrained by *Acropora*, they simply occupy different habitats (van Woësik & Done 1997) and are constrained by different environmental variables. What we may witness in the near future is an increase in free space (i.e. carbonate covered in turf algae) on reefs through time.

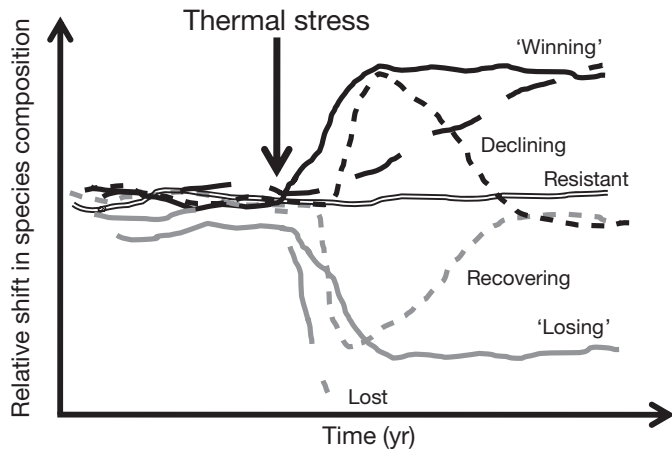


Fig. 5. Winners and losers from 1997 to 2010. The thermal stress event was followed by nearly a decade of average sea surface temperatures. Short-term winners are generally thermally tolerant encrusting and massive corals (*Porites* and faviids) and <5 cm *Acropora* colonies. Ten years after the thermal disturbance, the community was still structurally different from its original composition and consisted of a combination of species that (1) were tolerant to stress, (2) survived as fragments and experienced rapid regrowth, and (3) were regionally persistent colonies that recruited locally

Our study has shown that although there was plenty of open space on the reefs in 1998, the thermally resistant massive *Porites* did not increase in absolute density and cover through time, and soft corals did not take over all the available space (Table 1). Long-term winners and losers differed from short-term winners and losers, although short-term winners were a subset of longer-term winners (Table 1, Fig. 5). *Leptastrea* and *Goniastrea* were short-term winners and locally dominant in 2010. Both of these species fragment easily by partial mortality. *Goniastrea aspera* can remain reproductive even after fragmenting into smaller colonies (Kai & Sakai 2008). After spawning, the eggs that remain in *G. aspera* develop into brooding planulae, which have the capacity for short-distance dispersal (Sakai 1998). These traits may be partially responsible for the success of *G. aspera* on Sesoko Island, compared with the less common *Favites chinensis* colonies (Table 1), which revert back to immaturity upon fragmentation (Kai & Sakai 2008).

Return frequencies of thermal stress

Barshis et al. (2010) showed that there were more heat-tolerant *Porites lobata* genotypes in a highly fluctuating environment than on the physically stable fore-reefs. Such results agree with those of McClanahan & Maina (2003), who examined the coral response in

Kenya to natural temperature variance. Coral colonies in localities with naturally high temperature variance, on a daily basis, fared better under a regional temperature stress than colonies in localities with low daily variance. But are these responses simply a reflection of phenotypic plasticity or adaptations?

There is mounting evidence for adaptation under rapid environmental change (Endler 1986, Thompson 1998, Glynn et al. 2001, Berkelmans & van Oppen 2006, Carroll et al. 2007, Maynard et al. 2008). Although studies have shown that reproduction is compromised after bleaching (Szmant & Gassman 1990, Baird & Marshall 2002), thermal stress events will continue to select for more thermally tolerant genotypes, as long as the corals remain sexually active. Sexual recombination alone, however, does not always increase population variability, as the more variable offspring generated by sexual recombination are not always favorable in the new environmental circumstances. Shorter periods between selection events might cause strong and persistent selective forcing. Therefore, ironically, the coral populations most evolutionarily responsive to climate change in the near future might occur in localities of high-frequency return periods. Long periods between thermal stress events (i.e. low-frequency return periods) will allow sexual recombination, but will also return the population to Hardy-Weinberg equilibrium, reducing overall fitness.

On a global scale, some regions have historically experienced either high (~5 yr) or low (~50 yr) return periods of thermal anomalies (Thompson & van Woesik 2009). The same localities that experienced high-return periods over the past several centuries have also recently, in the past 15 yr, experienced the greatest intensities of thermal stress. Sesoko Island and the surrounding region have historically experienced low-frequency return periods of anomalous temperatures (Thompson & van Woesik 2009) (Fig. 1). In the present study, the reef communities had 9 yr to recover. However, if subjected to more frequent thermal stresses, then, along with the differential survival of more thermally resistant corals (causing a further shift in species composition), there may be a shift in the size-frequency distribution of *Acropora* towards smaller colonies. Again, within species of *Acropora*, small colonies are more tolerant to anomalous temperatures than large colonies (Loya et al. 2001, Nakamura & van Woesik 2001, Bena & van Woesik 2004), but the small colonies are sexually immature (Hall & Hughes 1996). Therefore, if bleaching events do become more frequent, the shift toward small *Acropora* colonies will slow recruitment and recovery and will reduce population fitness. Certainly, in a rapidly changing climate, directional selection may be rapid (Thompson 1998, Schoener 2011), and adaptation of corals to climate

change is most likely to take place in localities with high-frequency return periods of anomalous temperatures (Thompson & van Woësik 2009).

Projected changes

The present study suggests that as the oceans warm even further, the coral assemblages will change. Reefs may soon essentially only support heat-tolerant coral species. The narrowing of genetic diversity within communities is likely to impact other dependent species such as fishes and crustaceans, especially if important reef-building branched corals, such as *Acropora*, *Stylophora*, *Pocillopora* and *Porites cylindrica*, become rare on account of their inherent sensitivity to thermal stress. Bleaching may also become punctuated over the next several decades. In the short term, the remnant yet hardy populations may show some resistance to the higher water temperatures, and bleaching may be reduced for a decade or more if *Acropora* and pocilloporids are removed from local reefs. However, reduced bleaching may give false hope because once the inevitable temperature threshold of the remnant communities is surpassed, widespread coral mortality will follow. Given that even the hardiest coral genera have their limits, global temperature increases will eventually lead to an exponential rate of local, regional and global reduction of coral species. To what extent this reduction of coral species will occur will depend on how rapidly and by how much the ocean temperatures increase, which depends on the fossil-fuel-emission pathway that humans choose.

Acknowledgements. We thank the Tropical Biosphere Research Center (TBRC), University of the Ryukyus, for providing a visiting professor fellowship to R.v.W. in the summer of 2010; the Japan Society for the Promotion of Science for providing a Fellowship to Y.L. in the summer of 2007; JSPS KAKENHI (C & A) nos. 21570021 & 21247006 for supporting K.S. We also thank the TBRC Director, Prof. H. Oku, for providing the opportunity and facilities to carry out the research. The assistance of the staff is greatly appreciated, especially that of S. Nakamura, Y. Nakano, A. Takemura, S. Harii and C. Uchima. We also extend thanks to T. Done and L. Devantier for sharing the Great Barrier Reef data. Our special thanks extend to S. van Woësik for editorial comments.

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