Palau’s coral reefs show differential habitat recovery following the 1998-bleaching event

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REPORT

Palau's coral reefs show differential habitat recovery following the 1998-bleaching event

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Abstract Documenting successional dynamics of coral communities following large-scale bleaching events is necessary to predict coral population responses to global climate change. In 1998, high sea surface temperatures and low cloud cover in the western Pacific Ocean caused high coral mortality on the outer exposed reefs of Palau (Micronesia), while coral mortality in sheltered bays was low. Recovery was examined from 2001 to 2005 at 13 sites stratified by habitat (outer reefs, patch reefs and bays) and depth (3 and 10 m). Two hypotheses were tested: (1) rates of change of coral cover vary in accordance with habitat, and (2) recovery rates depend on recruitment. Coral cover increased most in the sheltered bays, despite a low recruitment rate, suggesting that recovery in bays was primarily a consequence of remnant regrowth. Recruitment densities were consistently high on the wave-exposed reefs, particularly the western slopes, where recovery was attributed to both recruitment and regrowth of remnants. Recovery was initially more rapid at 10 m than 3 m on outer reefs, but in 2004, recovery rates were similar at both depths. Rapid recovery was possible because Palau's coral reefs were buffered by remnant survival and recruitment from the less impacted habitats.

Keywords Bleaching · Recovery · Corals · Recruitment · Habitats

Introduction

Disturbances are an integral part of coral reef systems (Darwin 1842; Connell 1978). For example, wave energy regulates community structure on the west coast of Hawaii, by selecting against less wave-tolerant coral species (Dollar 1982); but more subtly, the energy regime is inversely related to intra-specific genetic diversity, a consequence of differential breakage and clone propagation (Hunter 1993). The dynamics and recovery processes of coral communities are complex because reefs are subjected to a variety of disturbances that vary in intensity, frequency and duration (Pearson 1981; Huston 1985; Done 1987; Hughes 1989; Karlson and Hurd 1993; Tomascik et al. 1996). Recovery from major disturbances ranges anywhere from five to hundreds of years, depending on the type of disturbance, the initial conditions and the type of coral community that was impacted (Pearson 1981; Colgan 1987; Endean et al. 1989; Done et al. 1991; Dollar and

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Tribble 1993). For example, the recovery of a sheltered stand of 2 m *Porites lutea* and *Diploastrea helipora* coral colonies, through recruitment and regrowth, may take hundreds of years to reach former size-frequency structure (Done 1987), while the recovery of shallow *Acropora hyacinthus* and *A. digitifera* populations may reach similar size frequency distributions within 5 years after a disturbance (Tomascik et al. 1996).

While recruitment events and post-settlement survival are essential processes influencing recovery and species composition (van Woesik et al. 1999; Hughes et al. 1999; van Woesik 2002), few disturbances remove all life and the abundance and composition of remnants play a crucial role in recovery (Done 1987). Recovery trajectories may depend on the survival of coral populations on adjacent reefs and the capacity of these refuges to supply recruits. This capacity to absorb disturbances, at the system level, has recently been termed 'reef resilience' (Hughes et al. 2003).

Recovery and resilience

While recovery of a reef can be literally considered as the rate at which a reef re-covers with coral, resilience, on the other hand has two primary definitions in the literature: (1) the return to a single equilibrium point following a disturbance (Pimm 1984), or alternatively (2) the maintenance at potentially multiple equilibrium points (Holling 1973). Coral communities are not easily perceived at single equilibrium points (Knowlton 1992), since each community is an aggregation of populations that vary in accordance with depth and habitat, shaped by physical, chemical and biological processes over time (Chappell 1980; Done 1982). Furthermore, whether the multiple points are in equilibrium is arguable because they are largely dependent on the timeframe under observation, and hence equilibrium is more useful for theoretical constructs (van Woesik 2002). Therefore, our working definition of resilience is simply the capacity of a reef system to absorb a disturbance. Implicit in this definition is the capacity of the system to resist phase shifts, and to regenerate and reorganize to maintain key functions (McClanahan et al. 2002). Yet, the time frame (or rate) and spatial scale, at which regeneration and reorganization takes place is of fundamental importance and the focus of this study.

Coral bleaching

Coral bleaching events in recent years have been a consequence of high sea surface temperatures in direct combination with high irradiance (Glynn 1993, 1996; Shick et al. 1996; Hoegh-Guldberg 1999; Marshall and Baird 2000). Bruno et al. (2001) reported wide-scale coral bleaching and high mortality on the reefs of Palau in 1998 (Fig. 1). Similar coral bleaching and coral mortality was evident in nearby southern Japan (Loya et al. 2001) and other tropical oceans (McClanahan 2002; Sheppard 2003). Loya et al. (2001) showed that some species are tolerant to thermal stresses and were classified as 'winners', while others were not so tolerant, and were called the 'losers'. Many other reports have highlighted the extent of damage caused by the 1998-bleaching event, suggesting that differential survival varied in accordance with species type (Marshall and Baird 2000), colony size (Bena and van Woesik 2004), depth (van Woesik et al. 2004), flow rates (Nakamura and van Woesik 2001) and geographic location (van Woesik 2001; Sheppard 2003).

Few studies have followed a bleaching event through time and (1) traced the recovery processes, (2) assessed whether 'winners' in the short term are also 'winners' in the long-term and (3) examined shifts in community structure over time (but see Glynn et al. 2001). Indeed, what may appear to be a winning strategy in the short term, through survival of small colonies (Loya et al. 2001; Nakamura and van Woesik 2001) or the apparent short-term survival of a 'winning' growth form (Loya et al. 2001), may turn out to be detrimental in the long-term, especially if thermal stress events increase in frequency and intensity, and survival is restricted to small immature colonies (Bena and van Woesik 2004) that do not contribute to future populations.

Clearly, projected climate change is set to drive temperature and seawater chemistry to levels outside the envelope of modern reef experience (Hoegh-Guldberg 1999; Kleypas et al. 1999). Globally, other disturbances pale in comparison with recent coral bleaching and subsequent mortality events (McClanahan 2002; Hughes et al. 2003; Hoegh-Guldberg 2005; Aronson and Precht 2006). Yet, there is still little information on the successional dynamics of coral communities following large-scale bleaching events, and even less on differential habitat and regional responses, and on what time frame the coral communities recover. Intuitively, we predict that coral reefs that are well managed or at a distance from large human populations have a greater capacity to absorb disturbances than reefs poorly managed or near large human populations. But, there is still little evidence either way (but see McClanahan et al. 2001).

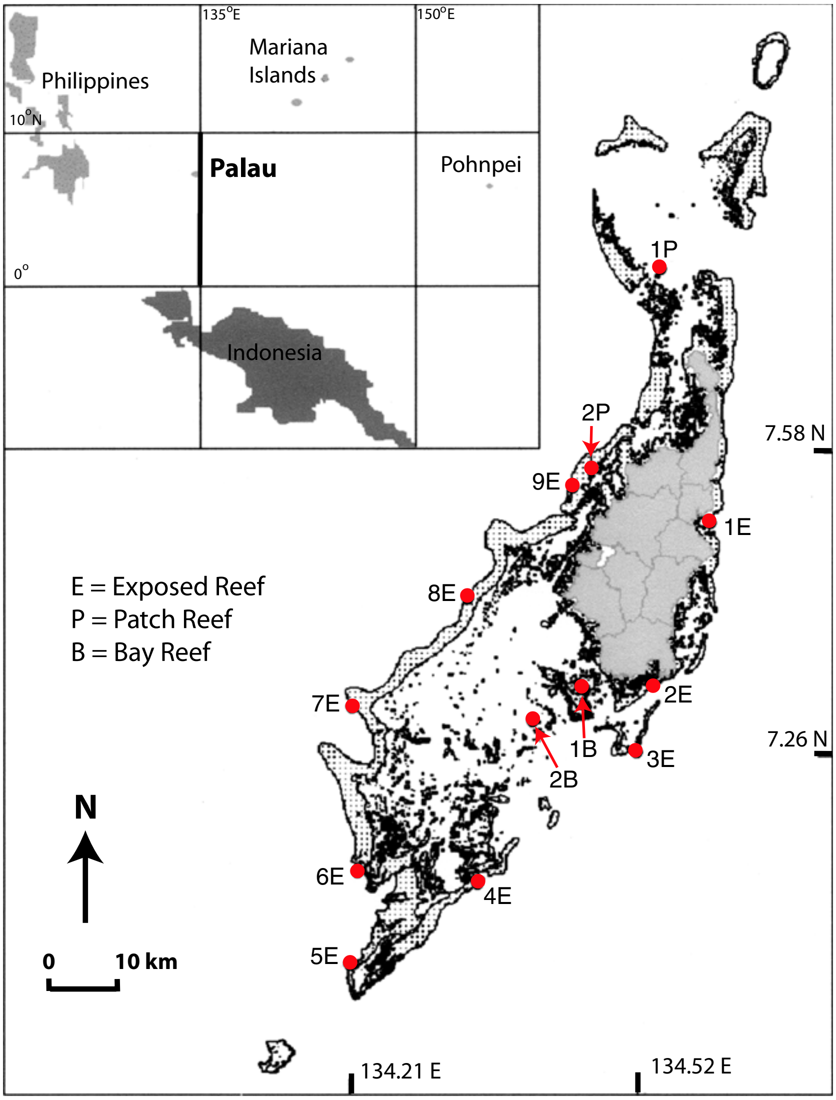


Fig. 1 Thirteen permanent coral reef study sites in Palau, Micronesia

Palau, Micronesia

This study examined recovery rates of coral communities on the Palauan reef complex (7°30′N, 134°30′E), which lies within the western Pacific Ocean (Fig. 1). Palau supports over 500 km^2 of coral reefs, which are well managed (Golbuu et al. 2005), and a human population of 19,907 people. The last 10 years have seen considerable changes in coral cover on Palau's coral reefs (Table 1). Maragos et al. (1994), in an extensive spatial survey in 1992 showed high overall coral cover, except on the Northeastern exposed reef. While Bruno et al. (2001), reported wide-scale coral bleaching and coral mortality on the inner lagoon reefs during the 1998 thermal stress event. A nation-wide spot check survey of the reefs in 2001 showed low, overall coral cover (Table 1). While Micronesia is at a great distance from large human population centers, Donner et al. (2005, their Fig. 2), based on Atmospheric-Ocean general circulation models predicted that Micronesia is particularly vulnerable to climate change over the next 30 years. It is predicted that Micronesia will be subjected to several thermal stress events, experiencing water temperatures considerably higher than historical averages (Donner et al. 2005). Therefore it is critical to examine coral community trajectories following thermal stress events in Micronesia, since this geographic locality may be particularly impacted by global climate change and increased water temperatures in the near future.

In Palau, Penland et al. (2004) reported on reproductive schedules of corals and noted that on sheltered reefs (their Site 1, our Site 1B), the coral communities did not suffer the same high-mortality in 1998 as adjacent patch and outer reefs (see also Table 1). They further stated “the surviving corals may potentially

Table 1 Coral cover at different localities in Palau, recorded by the 1992 rapid ecological assessments (REA) (Maragos et al. 1994), Bruno et al. surveys (Bruno et al. 2001), and the 2001–2003 spot checks (Golbuu et al. 2007)

	1992 REA (range in percentage of coral cover)	1998 Bruno et al. surveys (mean percentage coral cover)	2001–2003 Spot checks (mean percentage coral cover ± SE)
Northern Lagoon			
Barrier—NE slopes	10		13 ± 2
Barrier—W slopes	60–70		15 ± 2
Patch	NA		20 ± 6
West Babeldaob			
Barrier	NA	33	23 ± 2
Channels	50–70		14 ± 2
Patch	50		20 ± 3
Fringing	33–50		33 ± 6
East Babeldaob			
Barrier	50 or more		14 ± 2
Patch	NA		NA
Fringing	10–50		22 ± 3
Southern Lagoon			
Barrier	50	31	17 ± 2
Channels	25–50	37	NA
Channel-Ngerumekaol	52	39	23 ± 5
Patch	NA		35 ± 5
Fringing	NA		39 ± 5

Numbers given are percent coral cover

NA not available

contribute to the recovery of neighboring reefs through recruitment''. Spatial differences in survival may generate refuge sites, which in turn may facilitate recovery through larval supply.

Objectives

It is necessary to document successional dynamics of coral communities following large-scale bleaching events to predict coral population responses to global climate change. Successional dynamics of coral communities following large-scale bleaching events is largely unexplored because mass-coral-bleaching events are relatively recent phenomena. It is critical to understand on what time frame coral communities recover and whether geographic regions, habitats and communities vary in their capacity to absorb these disturbances. Perhaps, even more pertinent is whether reefs subjected to low-human impact, and reefs that are well managed, have a greater capacity to absorb coral bleaching events compared with reefs near large human population centers.

Coral recovery was examined at two depths (3 and 10 m) and in four habitats 3, 4 and 7 years after the 1998-bleaching event. Two hypotheses were tested: (1) rates of change of coral cover vary in accordance with habitat, and (2) recovery rates depend on recruitment. Specifically, this study was interested in habitat-specific-recruitment rates, whether recruitment and recovery rates were linked, how important the initial reef state was to the recovery process, and whether recovery rate depended on the type of habitat and depth.

Materials and methods

Study location and sampling strategy

The Republic of Palau is located in western Micronesia (Fig. 1). The Palau International Coral Reef Center (PICRC) launched a nationwide coral reef monitoring program in 2001. Thirteen permanent study sites were established to examine temporal and spatial changes in the benthic communities. Site selection was based on exposure and habitat type; nine outer reef wave-exposed sites were established, four on the east coast and five on the west coast; two sites were located on patch reefs, and two within sheltered bays. Each site was depth-stratified at 3 and 10 m below low water datum. The first surveys were conducted in late 2001 to early 2002 (presented throughout as 2001); the second survey was conducted in late 2002 to early 2003 (presented as 2002), and the third in late 2004 to early 2005 (presented as 2004).

Field methods

Coral communities were examined using a digital-video analysis technique (Carlton and Done 1995) and the field-sampling strategy followed the protocol and justifications outlined for northwestern Pacific coral assemblages by Houk and van Woesik (2006). At each depth, 5 × 50 m fiberglass-transect lines were haphazardly placed along each depth contour and separated by approximately 2–3 m intervals. An underwater digital video camera (SONY, DCR-PC120, NTSC, with a 0.6× wide lens) in a Sea & Sea VX-PC Underwater Video housing 120, recorded ~50 × 50-cm-wide by 50-m-long belt transects onto DV mini-cassettes by keeping a consistent height of 60–70 cm above the substrate. It took approximately 5 min to record each 50-m line. A global positioning system (GPS) unit was used to mark the location of each site. Coral recruits ≤5 cm were recorded on underwater paper along 0.3 m either side of the first 10 m of each transect. Recruits were measured for maximum diameter and categorized as either *Acropora*, faviids, *Montipora*, pocilloporid, *Porites* or 'other'. During a cloud-free day (22 February 2005) irradiance profiles were compiled for two key habitats (1) at Site 1B (Nikko Bay) and (2) on the outer eastern reef (Site 3E) using a quantum scalar photosynthetically active radiation (PAR) sensor (Biospherical Instrument Inc., Model number, QSP-170).

Data extraction

To obtain coral cover information, images were systematically extracted, at a rate of one image every 6.5–7.0 s, to obtain 40 images per 50-m belt transect. These images were stored in a database for further analysis. Five random crosses were placed on a computer screen; these crosses were used as our sampling unit within each frame, and the benthic component under each cross was systematically recorded. Our only assumption in the data acquisition protocol was that there was only one organism or substrate type under each cross, yielding five data points from each image. The taxa, or geological feature, under each point was recorded on a data sheet using defined categories.

Data processing and statistical analyses

Although the same sites were examined for the different time periods (re-identified with GPS fixes), the haphazard nature of the video-belt transects within those sites meant that the exact transects were not re-surveyed. Therefore, analyses involving repeated measures were not appropriate. Instead, the sampling protocol allowed us to calculate the (first) difference between the dependent variables for the different time periods, upon which statistical analyses were performed. Prior to statistical analysis, the raw data sets were tested for violations of normality and homogeneity of variance assumptions; normality was assessed using the normal probability plot procedure and the Shapiro–Wilks test using the software Statistica®. Homogeneity of variances was tested for using Levene's test. When appropriate, transformations were applied to the datasets using the maximum-likelihood estimate of lambda ($y = x^{\lambda}$) using the Box–Cox power transformation of the dependent variable (Box and Cox 1964). Analysis of variance (ANOVA) was performed on the datasets (reef type, west or east coast, and depth as fixed factors) to test a general null hypothesis that there were no differences in coral cover and recruitment of each taxa over time and among habitats and depths. Tukey-HSD post hoc tests were undertaken to examine significant differences that were identified by the ANOVA tests.

Results

The initial reef condition, 3 years after the 1998-bleaching event, showed highest percentage coral cover on the reefs within the protected bays at both 3 and 10 m, and on the deep (10 m) western wave-exposed slopes (Fig. 2; ANOVA, $p < 0.001$). Notably, the initial recovery rate in the bays was significantly faster than elsewhere (ANOVA, $p < 0.001$: Tukey 3 m, Bay > WE, $p < 0.001$; Bay > EE, $p < 0.001$; Bay > P, $p < 0.001$; 10 m Bay > WE, $p < 0.05$; Bay > EE, $p < 0.001$; Bay > P, $p < 0.001$) (Table 2), primarily a consequence of regrowth of 'other' colonies at 10 m depth, and *Porites* and 'others' at 3 m (Table 3). Recovery rates were significantly higher between 2002 and 2004 compared with the rates between 2001 and 2002 at all habitats, except in bays where recovery was similar for both periods (Table 2); this difference in recovery rates was particularly notable for *Montipora* on western slopes and *Porites* (which was primarily *P. rus*) in bays (Table 3). Recovery was less pronounced on eastern reef slopes compared with western slopes at 10 m (Fig. 2; ANOVA, $p < 0.001$: Tukey 10 m WE > EE, $p < 0.001$), while the shallow exposed slopes recovered at a similar rate to each other. The highest rate of change for *Acropora* corals occurred at 3 m between 2001 and 2002 (Table 4), while *Pocillopora* showed highest rate of change between 2002 and 2004 at both 3 and 10 m (Table 4). The recovery rates of faviids were significantly different between years, with higher rates of recovery in 2004 (Table 4). Although the ANOVA also identified a significant year effect for *Porites*, this was not confirmed by the Tukey post hoc test (Table 4). *Montipora* was the only genera to show significant habitat effects, with most favorable recovery on the western exposed slopes at 10 m (Table 4).

While recruitment densities were consistently high on the exposed and patch reefs, particularly at 10 m on the western coast in 2001 and 2002 (2001 ANOVA,

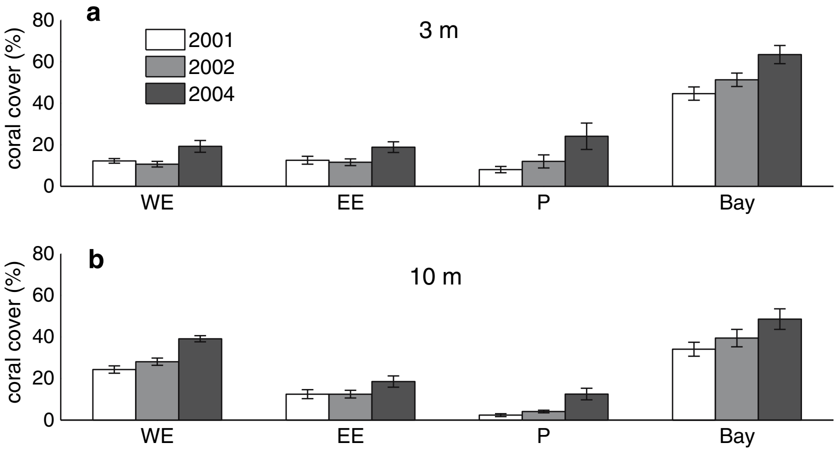


Fig. 2 Mean coral cover (±standard errors) on Palauan reefs presented in accordance with habitats from 2001 to early 2005, at 3 m (**a**) and 10 m (**b**)

Table 2 Rate of change in the coral cover on the reefs of Palau at 3 and 10 m in four habitats: west exposed (WE), east exposed (EE), patch (P) and Bay (B), showing mean ± SE/year

Habitats	3 m (2002–2001)	10 m (2002–2001)	3 m (2004–2002)/2	10 m (2004–2002)/2
WE	–1.6 ± 1.2	3.8 ± 1.8	4.3 ± 1.0	5.5 ± 0.9
EE	–0.9 ± 1.6	–0.0 ± 1.6	3.6 ± 1.1	3.0 ± 1.2
P	3.9 ± 2.4	1.7 ± 0.9	6.0 ± 2.5	4.2 ± 1.5
B	6.6 ± 1.5	5.4 ± 3.6	6.1 ± 1.9	4.6 ± 1.3

Numbers given are percent coral cover

Table 3 Rate of change in the cover of four different coral genera (*Acropora*, *Montipora, Pocillopora* and *Porites*) and one family (family Faviidae) on the reefs of Palau at 3 and 10 m in four habitats: west exposed (WE), east exposed (EE), patch (P) and Bay (B), showing mean ± SE/year

	Habitats	3 m (2002–2001)	10 m (2002–2001)	3 m (2004–2002)/2	10 m (2004–2002)/2
Acropora	WE	0.3 ± 0.2	0.3 ± 0.2	0.3 ± 0.1	1.0 ± 0.3
	EE	0.9 ± 0.4	0.6 ± 0.7	–0.1 ± 0.2	0.5 ± 0.9
	P	2.2 ± 1.7	–0.3 ± 0.6	–2.2 ± 1.4	0.3 ± 0.4
	B	0.1 ± 0.1	–0.0 ± 0.0	–0.1 ± 0.1	0.3 ± 0.3
Faviid	WE	–0.2 ± 0.6	1.5 ± 0.8	0.2 ± 0.3	0.2 ± 0.3
	EE	0.4 ± 0.5	–0.1 ± 0.3	0.9 ± 0.6	1.4 ± 0.4
	P	0.4 ± 0.4	0.1 ± 0.2	3.3 ± 1.3	0.4 ± 0.2
	B	0.6 ± 0.8	–3.8 ± 1.1	0.3 ± 0.3	3.1 ± 0.9
Montipora	WE	0.6 ± 0.5	0.8 ± 0.8	3.6 ± 1.0	8.0 ± 1.1
	EE	–0.1 ± 0.8	0.9 ± 0.3	1.0 ± 0.4	2.2 ± 0.7
	P	–0.2 ± 0.3	–0.1 ± 0.1	1.1 ± 0.5	3.7 ± 0.9
	B	0.0 ± 0.0	–0.1 ± 0.1	2.6 ± 1.0	1.1 ± 0.4
Pocillopora	WE	–0.1 ± 0.2	0.1 ± 0.2	1.1 ± 0.2	0.3 ± 0.1
	EE	0.2 ± 0.2	–0.0 ± 0.1	0.4 ± 0.1	0.3 ± 0.1
	P	0.0 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	–0.0 ± 0.0
	B	0.1 ± 0.1	0.0 ± 0.0	–0.0 ± 0.1	0.0 ± 0.0
Porites	WE	0.2 ± 0.4	2.7 ± 1.5	0.6 ± 0.3	0.9 ± 1.1
	EE	–0.3 ± 1.2	0.8 ± 0.9	0.6 ± 0.5	–0.4 ± 0.7
	P	2.0 ± 1.4	0.8 ± 0.3	0.9 ± 0.6	0.9 ± 0.6
	B	1.5 ± 2.1	-4.6 ± 2.9	5.2 ± 2.9	3.6 ± 1.6
Others	WE	–2.8 ± 1.1	1.5 ± 0.4	0.1 ± 0.1	0.0 ± 0.3
	EE	0.7 ± 0.7	0.7 ± 0.6	0.8 ± 0.5	0.1 ± 0.4
	P	1.6 ± 1.0	0.3 ± 0.6	0.2 ± 0.7	1.8 ± 1.0
	B	0.9 ± 1.9	5.3 ± 3.5	0.6 ± 0.6	1.7 ± 1.9

Numbers given are percent coral cover

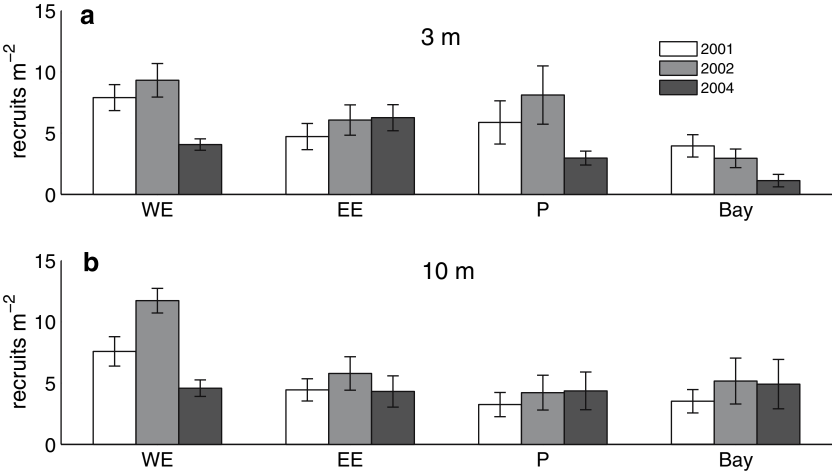
Table 4 Three-way analysis of variance (ANOVA) assessing the impact of habitat, depth and time on the rate of change in coral cover of different coral genera

Source of variation	*Acropora*		Faviid		*Montipora*		*Pocillopora*		*Porites*	
	F (*df*)	P level	F (*df*)	P level	F (*df*)	P level	F (*df*)	P level	F (*df*)	P level
Habitat	0.651 (3)	0.583	0.651 (3)	0.143	8.600 (3)	***	2.570 (3)	0.055	1.463 (3)	0.225
Depth	559.13 (1)	***	1.140 (1)	***	6.900 (1)	**	1.440 (1)	0.232	1.283 (1)	0.258
Year	847.49 (1)	***	847.487 (1)	***	40.300 (1)	***	7.970 (1)	**	7.349 (1)	**
Habitat × depth	1.438 (3)	0.232	2.310 (3)	0.077	2.900 (3)	*	0.650 (3)	0.582	1.527 (3)	0.208
Habitat × year	0.651 (3)	0.583	0.651 (3)	0.583	6.200 (3)	***	4.970 (3)	**	5.535 (3)	**
Depth × year	405.03 (1)	***	405.034 (1)	***	3.400 (1)	0.067	1.440 (1)	0.231	00 (1)	0.992
Habitat × depth × year	1.438 (3)	0.232	1.438 (3)	***	2.000 (3)	0.121	2.580 (3)	0.054	0.879 (3)	0.453
Error	(244)		(244)		(244)		(244)		(244)	
Tukey HSD	Mean ± SE		Mean ± SE		Mean ± SE		Mean ± SE		Mean ± SE	
Depth	3 m (4.955 ± 0.063) > 10 m (3.050 ± 0.188), ***				3 m (1.145 ± 0.029) < 10 m (1.157 ± 0.030), ***					
Year	Year 1 (5.201 ± 0.076) > Year 2 (2.804 ± 0.159), ***		Year 1 (3.037 ± 0.032) < Year 2 (3.232 ± 0.038), ***		Year 1 (1.139 ± 0.002) < Year 2 (1.163 ± 0.003), ***		Year 1 (1.608 ± 0.017) < Year 2 (1.746 ± 0.027), ***		Year 1 (11.488 ± 0.185) = Year 2 (12.046 ± 0.260), Tukey ns	
Habitat					West exposed (1.160 ± 0.003) > east exposed (1.145 ± 0.003), *** west exposed (1.160 ± 0.003) > patch (1.143 ± 0.001), *** west exposed (1.160 ± 0.003) > bay (1.147 ± 0.002), *					

The Tukey HSD are given in mean ± SE. Year 1 is the difference between coral cover in 2002 and 2001 and Year 2 is the difference in coral cover between 2004 and 2002 divided by 2

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Fig. 3 Coral recruits m^{-2} (mean ± standard errors) on Palauan reefs presented in accordance with habitats from 2001 to early 2005, at 3 m (**a**) and 10 m (**b**)



$p < 0.05$ Tukey NS; 2002 ANOVA, $p < 0.001$ Tukey WE > EE, $p < 0.05$; WE > P, $p < 0.05$; WE > B, $p < 0.05$; 2004 ANOVA NS) (Fig. 3); significantly lower recruitment was recorded in the shallow bay reefs at 3 m, but only in 2004 (ANOVA, $p < 0.05$; Tukey Bay < EE, $p < 0.05$) (Fig. 3); *Acropora* recruitment was highest on the eastern coast, and *Pocillopora* recruited more frequently onto patch reefs than the Bay or West Exposed sites (Table 5). There were significantly more faviids, *Montipora* and *Porites* recruits in 2002 than there were in 2004 (Table 5). Recruitment densities in a given year was not related to coral cover in the same year nor to coral cover in prior years, but recruitment densities were significantly correlated with recruitment densities in subsequent years (Table 6), suggesting that recruitment densities were temporally consistent within habitats.

The underwater irradiance measurements (Fig. 4) showed that the waters of Nikko Bay had a markedly higher attenuation coefficient for scalar irradiance ($K_{\mathrm{o\ PAR}} = 0.129$) compared with that at the Outer Eastern Reef ($K_{\mathrm{o\ PAR}} = 0.085$).

Discussion

Palau's reefs in context

The initial survey, 3 years after the 1998-bleaching event, showed the highest percentage coral cover on the reefs within the protected bays and deep exposed slopes. In addition, coral community composition differed considerably in the bays compared other habitats. The bays supported coral colonies mainly within the families Faviidae (*Goniastrea, Favia, Favites* and *Echinopora lamellosa*), and Poritidae (particularly *P. rus*), together with *Lobophyllia, Merulina, Pachyseris, Plerogyra, Anacropora* and *Acropora* colonies. Other habitats supported mainly faviids and poritids (particularly massive *Porites* spp., and *P. latistella*). Collectively, these results suggest that (1) the corals in the bays and deep slopes were less affected by the 1998-bleaching event, compared with patch and outer shallow reefs, or (2) that these reefs had already partially recovered within the 3-year interim period, or (3) that (1) and (2) occurred. The coral communities in the bays differed from other habitats; therefore, it may be argued that the bays supported more thermally tolerant coral species. Personal observations and extensive qualitative surveys in 1998 prior to the bleaching, and extensive spot checks in 2001 (Table 1) showed that the protected reefs within the bays continued to support stands of *Acropora* colonies (YG and SV, personal observations), the most thermally vulnerable corals during the bleaching event (Loya et al. 2001). Other habitats supported very few or no *Acropora* colonies, a consequence of high-mortality in 1998 (Bruno et al. 2001); therefore, it is suggested that the bays suffered less in the 1998-thermal stress event for reasons proposed below.

Coral bleaching is a consequence of high-irradiance and high water temperatures (Iglesias-Prieto et al. 1992; Jones et al. 1998; Warner et al. 1999, 2002; Mumby et al. 2001). Recently, it has been shown that the interrelatedness of temperature and light has reciprocal effects, whereby the increase in temperature under high light conditions will be perceived by the symbionts as an increase in light stress, and vice versa (Iglesias-Prieto et al. 2004; Takahashi et al. 2004; Nakamura et al. 2005). Figure 4 shows the considerably reduced scalar irradiance in Nikko Bay, compared with that at the Outer Eastern Reef site where the attenuation is more characteristic of a clear oceanic water type (Kirk 1994). This is likely due to the influence of

Table 5 Three-way analysis of variance (ANOVA) assessing the impact of habitat, depth and time on the rate of change in recruitment of different coral genera

Source of variation	*Acropora*		Faviid		*Montipora*		*Pocillopora*		*Porites*	
	F (*df*)	*P* level	*F* (*df*)	*P* level	*F* (*df*)	*P* level	*F* (*df*)	*P* level	*F* (*df*)	*P* level
Habitat	3.959 (3)	**	2.457 (3)	0.065	0.057 (3)	0.982	4.931 (3)	**	1.059 (3)	0.368
Depth	0.520 (1)	0.472	2.223 (1)	0.138	0.047 (1)	0.829	0.018 (1)	0.892	0.083 (1)	0.774
Year	3.206 (1)	0.075	3.922 (1)	*	5.866 (1)	*	0.000 (1)	1.000	23.185 (1)	***
Habitat × depth	0.239 (3)	0.869	0.789 (3)	0.502	0.129 (3)	0.943	0.185 (3)	0.906	0.636 (3)	0.593
Habitat × year	0.138 (3)	0.937	10.257 (3)	***	4.360 (3)	**	0.000 (3)	1.000	8.106 (3)	***
Depth × year	0.246 (1)	0.620	0.424 (1)	0.516	6.407 (1)	0.012	0.000 (1)	1.000	8.387 (1)	**
Habitat × depth × year	0.217 (3)	0.885	2.817 (3)	*	1.690 (3)	0.171	0.000 (3)	1.000	3.223 (3)	*
Error	(168)		(163)		(172)		(164)		(162)	
Tukey HSD	(Mean ± SE)		(Mean ± SE)		(Mean ± SE)		(Mean ± SE)		(Mean ± SE)	
Depth										
Year			Year 1 (7.889 ± 0.181) > Year 2 (6.980 ± 0.232), ***		Year 1 (27.841 ± 0.641) > Year 2 (25.556 ± 0.531), **				Year 1 (17.315 ± 0.388) > Year 2 (14.360 ± 0.334), ***	
Habitat	West exposed (2.843 ± 0.084) < east exposed (3.191 ± 0.078), **						Patch (2.970 ± 0.236) > Bay (2.034 ± 0.176), ** Patch (2.970 ± 0.236) > west exposed (2.102 ± 0.117), **			

The Tukey HSD are given in mean ± SE. Year 1 is the difference between coral recruitment in 2002 and 2001, and Year 2 is the difference between coral recruitment in 2004 and 2002

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

terrestrial input in Nikko Bay throughout the year, although no direct measurements of this were made in the present study. At the bay sites, the rock islands also provide some shading at certain times of day, whilst underwater, the slope and azimuth of the seabed further attenuate the irradiance on the benthic community. In combination, these factors result in a lower irradiance and dose on corals at Nikko Bay compared with the offshore sites, which could have led to reduced bleaching-related mortality during 1998 (Mumby et al. 2001).

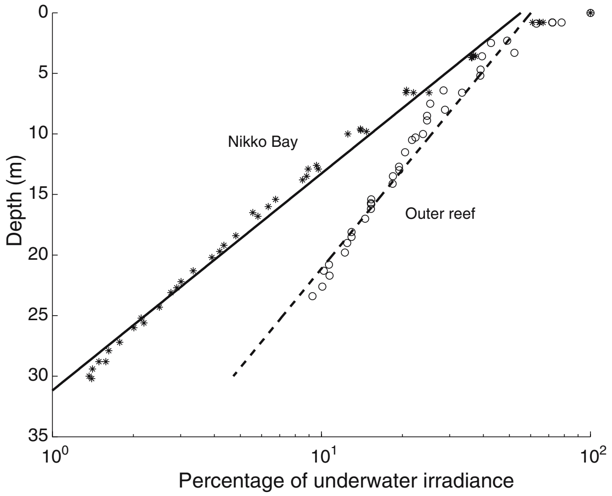


Fig. 4 Attenuation of scalar irradiance at two habitats, Nikko Bay *Site 1B* and (*2*) Outer Eastern Reef *Site 3E*, Palau, using a Photosynthetic Active Radiation sensor, Biospherical Instrument Inc., Model number, QSP–170; data were taken on 22 February 2005 during cloud free conditions. Regressions of the form $\mathrm{Eo}(Z) = \mathrm{Eo}(0)\mathrm{e}^{-\mathrm{Ko}Z}$ were fitted to the data at each site, where Ko is the vertical attenuation coefficient for scalar irradiance, and Eo(Z) and Eo(0) are the scalar irradiance at Z meters depth and just below the surface respectively. Ko for Nikko Bay was 0.129 and for the Outer Eastern Reef Site 0.085

Recruitment

The present study shows that while the coral populations recovered rapidly on the reefs of Palau, recovery trajectories changed over time and were habitat and depth-dependent. Recruitment was significantly lower in the shallow bay reefs at 3 m, but only in 2004. Recruitment was high on the western slopes in 2002, particularly at 10 m. The western slopes also supported high initial coral cover at 10 m, which would suggest that both remnant regrowth and recruitment facilitated recovery. Yet, recruitment was highly variable over time, and there was no statistical relationship between abundance of recruits and coral cover, neither within a year nor in the re-survey (Table 6). While recruitment was essential in the recovery processes of the outer reefs, recruitment in bays at 3 m was relatively low. Therefore, recovery within the bays at 3 m was mostly a consequence of growth of remnant (surviving) coral colonies, while recovery on the exposed slopes was mostly likely a consequence of both remnant regrowth and sexual recruitment events at 10 m, and more a consequence of recruitment at 3 m.

Community shifts

Seven years after the bleaching event, some reefs supported >30% coral cover, and some habitats supported >40% coral cover. Particularly dominant in shallow reefs were the corymbose and plate-like acroporids, *A. digitifera* and *A. hyacinthus* (Fig. 5a). Conspicuously absent from the patch and outer reefs were the large massive colonies. Many studies have shown the effects of disturbances on size-frequency distributions, whereby large massive colonies, if impacted, will take decades to recover to similar size-frequency distributions (Endean 1973; Done 1987; Endean et al. 1989).

The recovery on some of Palau's reefs was similar to, albeit less rapid than, recovery on a lava flow reported by Tomascik et al. (1996). Tomascik et al. (1996) showed remarkable coral community development on a bare andesitic lava substrate following a major volcanic eruption in the Banda Sea, Indonesia. In 5 years, coral coverage averaged over 60%, supporting 124 coral species, which was dominated by *Acropora* plates (note, the Banda Islands lava site

Table 6 Coefficients of determination (r^2) and significance value (p) of Pearson's moment-product correlations of recruitment densities and percentage coral cover for all habitats on reefs of Palau (tabulated by year)

	2001 Recruits		2002 Recruits		2004 Recruits	
	r^2	p	r^2	p	r^2	p
2001 Recruits						
2002 Recruits	0.13	<0.001				
2004 Recruits	0.03	0.13	0.045	<0.05		
2001 Coral cover (%)	0.001	0.95	0.007	0.44	0.001	0.67
2002 Coral cover (%)	0.001	0.94	0.030	0.08	0.002	0.54
2004 Coral Cover (%)	0.0016	0.71	0.030	0.10	0.003	0.53

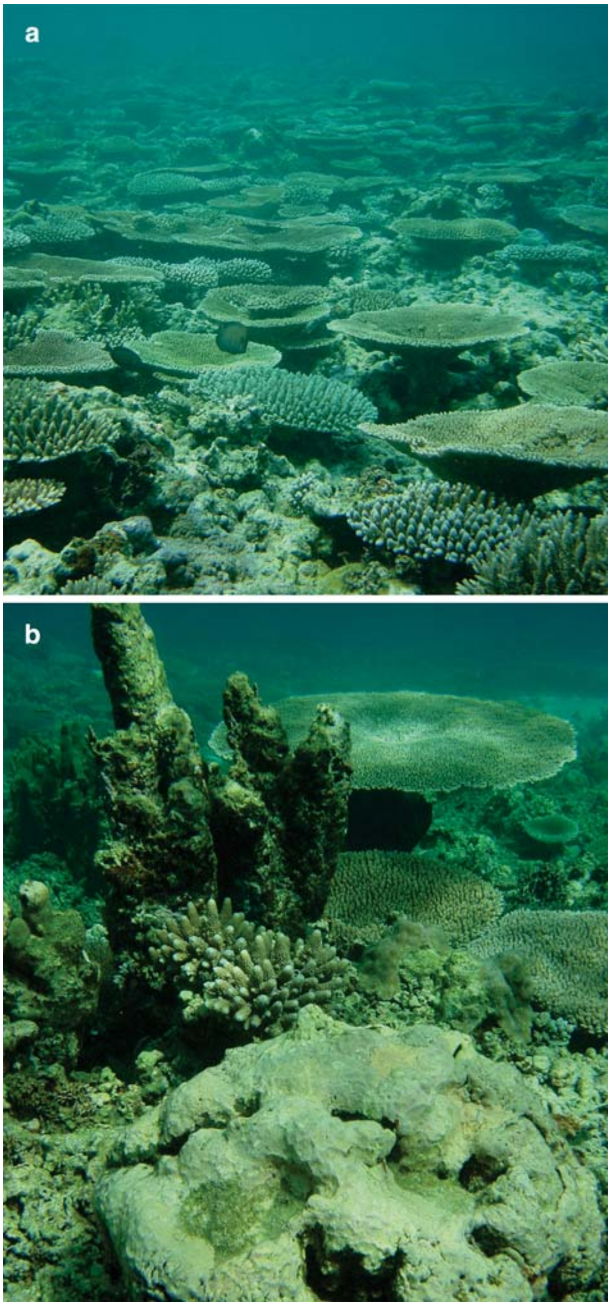


Fig. 5 **a** *Acropora* dominance on northern patch reefs (*Site 1P*), June 2005. **b** Large-dead colonies of *Psammocora digitata* (*background left*) and *Goniastrea edwardsi* (*foreground*); an almost forgotten past is overshadowed by a contemporary dominance of acroporids

closely resembled this study's Site 1P, Fig. 5a). However, in both studies large massive colonies were conspicuously absent and these may take several decades to recover to similar size-frequency distributions (Done 1987).

Done (1999) proposed various coral-community responses to global climate change; one suggestion was that there may be strategy shifts to more ephemeral coral species. There were not necessarily more ephemeral coral species on the reefs of Palau in 2005 compared with the past, but rather, judging by the abundant, dead massive colonies (e.g., Fig. 5b) there were less large, massive colonies than previously. This transition is more along the lines of what Loya et al. (2001) reported on Okinawan reefs that were subjected to the 1998-bleaching event. Differential species survival leads to marked changes in species composition and community structure, which Loya et al. (2001) termed the 'winners and the losers' to describe such differential selective pressures and consequent outcomes. An interesting twist however, is that while *Acropora* and pocilloporids were clearly the 'losers' in the thermal stress event of 1998 (Bruno et al. 2001; Loya et al. 2001), these weedy species were common on many of the shallow reefs of Palau in 2005. This contrasts with a reduced dominance on the heavily human populated island of Okinawa where *Acropora* species and pocilloporids had not returned to the shallow reefs of many localities, at least in 2004, near high human population centers (van Woesik et al. 2004). Whether these shifts in species composition are permanent in Okinawa, or if (and under what time frame) they return to their previous composition is still unknown.

Disturbance frequency and population adjustment

Recovery often implicitly assumes benign environmental conditions until the communities reach some stability point. Since 1998, there have been no thermal stresses in Palau. Clearly these benign conditions for 7 years, following an extreme thermal stress event, allowed rapid coral cover recovery. However, recovery rates were habitat and depth-dependent. Global climate change predictions foresee increases in the frequency and intensity of thermal stress events (Hoegh-Guldberg 1999), with projections estimating thermal stress conditions every 2–3 years (Donner et al. 2005), not unlike the conditions experienced recently in southern Japan. For example, two thermal stress events of similar intensity and duration were reported in southern Japan in 1998 and again in 2001 (van Woesik et al. 2004). Of 12 coral populations surveyed in detail, 4 populations showed an increase in tolerance in 2001 (*Pocillopora verrucosa, P. cylindrica, Favia pallida* and *Favia favus*), one species appeared less resistant (*Pavona varians*), and the other 7 species showed no significant difference in response between 1998 and 2001 (including *P. lutea*, *Pocillopora damicornis*, *A. gemmifera*, *A. digitifera*, *Pavona minuta*, *Pachyseris speciosa* and *Pachyseris gemmae*).

The 3-year interval between thermal-stress events in Okinawa contrasts markedly with Glynn et al.'s (2001) study in the eastern Pacific that recorded bleaching events in 1982–1983 and in 1997–1998 (a 14 year recovery period), which were both related to El-Niño Southern Oscillations. Glynn et al. (2001) reported high-mortality of *Pavona* spp. after both events, whereas Hueerkamp et al. (2001), in the same locality in 1997–1998, differentiated the species within the genus *Pavona* and reported *Pavona gigantea* as very temperature tolerant and *Pavona clavus* as susceptible. Most interesting, Glynn et al. (2001) found more *Pocillopora* colonies that were temperature-tolerant in 1997–1998 compared with 1982–1983. This change in resistance, under similar thermal stress conditions, suggests selection of more heat tolerant colonies in 1982–1983, and propagation of those colonies on contemporary reefs (Glynn et al. 2001). Similarly, Guzman and Cortes (2001) stated that populations of massive and branched corals in 1997–1998 were more tolerant to elevated thermal stress than populations in 1982–1983 in Costa Rica (also in the eastern Pacific Ocean), where both events recorded similar warming trends and temperature maxima. Guzman and Cortes (2001) suggested the coral populations had adapted to these warmer conditions. However, both Guzman and Cortes (2001) and Glynn et al. (2001) both assume that both bleaching events, for 1982–1983 and 1997–1998 events, had similar light fields. Yet, there were no measurements of irradiance in either study. It is equally possible that while the temperature stresses were similar in 1982–1983 and 1997–1998, cloud cover, for example, and hence the light fields, may have differed; therefore the environmental factors responsible for bleaching in these two periods may have been quite different. Different environmental conditions would thereby confound the conclusions that the corals showed an improved tolerance, when noted responses may simply have been the result of the relaxation of light stresses in 1997–1998.

Climate change

Coral bleaching is a global phenomenon that appears linked to global climate change and increasing ocean temperatures (Glynn 1991, 1993; Brown 1997; Hoegh-Guldberg 1999). Projected climate change may drive temperature and seawater chemistry to levels outside the envelope of modern reef experience, but it is not known which corals will adjust to the contemporary *rates* of climate change.

Loya et al. (2001), Nakamura and van Woesik (2001) and Bena and van Woesik (2004) have shown that small coral colonies are more tolerant to anomalous thermal stresses than large colonies. There is, thus, a suggestion of an increasing trend toward smaller colonies if bleaching events become more frequent. Small colonies may not be reproductively competent if they are remnants of once-larger colonies, and certainly not when they are new recruits, and thus immature. Therefore, a 'winning' strategy, whereby coral populations may endure global climate change, may not be time invariant. What may appear to be a 'winning' strategy in the short-term, through survival of small colonies or the apparent short-term survival of a 'winning' growth form, may turn out to be detrimental in the long term, especially if thermal stress events increase in frequency and the time period for colony growth is reduced.

This study showed that the coral communities on the Palauan reefs recovered rapidly from the 1998-bleaching event, but recovery depended on habitat and depth and differed among coral populations. Coral cover recovery rates were not always closely related to recruitment rates but were highly dependent on the extent of remnant coral survival. Therefore, coral population survival is as much about resistance as it is about recruitment. Faviids and *Porites* spp. were more tolerant than *Acropora*, but *Acropora* recruited in from refuge habitats. Faviids and *Porites* were small throughout the study, and increases in size–frequency distributions, of these slow growing corals, will take decades (Done 1987). This study shows that community recovery rates are dependent on remnant survival and recruitment pulses, but selective pressures are dependent on a complexity of circumstances including thermal-stress return period, habitat type, depth, water-flow rates, seasonal irradiance and temperature extremes, adjacent refuges, and coral species composition. We need to further understand selective pressures through climate change events because we may see further shifts in the coral communities unprecedented since the Triassic (245 million years ago), when contemporary scleractinian corals first evolved.

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