

Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef

C. Linares^{1,2,*}, M. S. Pratchett², D. J. Coker²

¹Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Spain

²ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

ABSTRACT: Given projected increases in the frequency and/or severity of climatic disturbances, the persistence of corals may be more a function of their capacity for regeneration than resistance to such episodic disturbances. If so, climate change may favour those corals that regenerate fastest following acute disturbance. The tabular coral *Acropora hyacinthus* is fast-growing and typically dominates shallow wave-exposed habitats on the Great Barrier Reef, but it is extremely vulnerable to climate-induced coral bleaching and other disturbances (e.g. cyclones and outbreaks of crown-of-thorns starfish). The present study explores temporal changes in percentage cover and size structure of *A. hyacinthus* on reefs affected by the 2001–2002 bleaching event. Annual surveys conducted at 3 mid-shelf reefs from 2008 to 2010 revealed rapid, but very patchy, recovery of *A. hyacinthus*. Following extensive coral loss, local cover of *A. hyacinthus* increased due to growth of established colonies as well as addition and subsequent growth of new colonies. At one reef, recovery was mostly due to increased abundance of small colonies, assumed to have recruited since the bleaching, whereas recovery at the 2 other study reefs (<5 km away) was the sustained growth of established colonies. These results show that resilience of *A. hyacinthus* populations may be due to either recolonisation or persistence, but that, either way, these corals are well suited to rapid recovery following acute disturbance.

KEY WORDS: Bleaching · Climate change · Coral reefs · Disturbance · Recovery · Resilience

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Coral reefs are increasingly subject to a combination of anthropogenic and natural disturbances, which are further compounded by episodic disturbances (e.g. mass-bleaching of coral) associated with sustained and ongoing climate change (Hughes et al. 2003, Bellwood et al. 2004). Severe climate-induced coral bleaching causes widespread mortality among reef-building corals (Wilkinson 2000) and is predicted to become more frequent and more severe in coming decades (Sheppard 2003, Donner et al. 2005).

However, susceptibility to bleaching—particularly proportional mortality due to bleaching—varies greatly within and among coral genera (Brown & Suharsono 1990, Marshall & Baird 2000, Loya et al. 2001, McClanahan et al. 2004, 2008). Therefore, increased incidence of climate-induced coral bleaching is more likely to cause marked changes in the structure of coral assemblages than to kill all corals within similar time frames (Hughes et al. 2003).

The hierarchy of bleaching susceptibility among different coral genera is well established (Marshall & Baird 2000, Loya et al. 2001, McClanahan et al.

*Email: cristinalinares@ub.edu

2004). *Acropora* is the first and worst affected scleractinian coral, whereas *Porites* is resistant to all but the most severe episodes of coral bleaching (Riegl 1999, Loya et al. 2001, Baird & Marshall 2002). Increasing frequency of coral bleaching and differential mortality between these 2 genera (Loya et al. 2001, McClanahan et al. 2004) have led to predictions of increasing dominance of *Porites* at the cost of *Acropora* (Riegl & Purkis 2009). However, the increasing incidence of climate-induced coral bleaching will not necessarily favour those corals that are resistant to bleaching (Baker et al. 2008). Given projected increases in the frequency and/or severity of coral bleaching episodes (Hoegh-Guldberg 1999, Sheppard 2003, Donner et al. 2005), the long-term persistence of different corals may depend largely upon their capacity for recovery following recurrent bleaching (Hughes et al. 2003, Baker et al. 2008).

While recovery from strong disturbances is likely to be slow, there is evidence that total coral cover can increase very rapidly, mainly due to the recovery of the fast-growing tabular acroporid corals (Halford et al. 2004, Golbuu et al. 2007, Adjeroud et al. 2009). However, past studies in this area have reported such rapid changes only in total coral cover; it is possible that recovery of population structure (e.g. the size structure of coral populations) will take much longer. Since demographic processes such as fecundity, growth and survival are strongly correlated with colony size (Hughes & Jackson 1980), the size structure of coral populations is an important determinant of their ecological dynamics (Bak & Meesters 1998, Meesters et al. 2001). Several studies have explored spatial variation in the size structure of coral populations at various depths and sites (Vermeij & Bak 2003, Adjeroud et al. 2007, Victor et al. 2009), but few have followed the impact of disturbances through time, examining temporal shifts in population structure (van Woessik 2000, Gilmour 2004, McClanahan et al. 2008, Crabbe 2009).

In the present study, we examined the temporal changes in percentage cover and size structure of *Acropora hyacinthus* over a 2 yr period (from January 2008 to January 2010) on the Great Barrier Reef (GBR) off the coast of northeast Australia. Between November 2001 and March 2002, the GBR was affected by the most severe episode of coral bleaching ever recorded for this region (Berkelmans et al. 2004). The purpose of the study was to understand the underlying processes which foster coral resilience by investigating the dynamics and recovery of *A. hyacinthus* populations following this bleaching event.

MATERIALS AND METHODS

Study species and study sites

Acropora hyacinthus is a fast-growing (approx. 10 cm in diameter yr^{-1}) and relatively short-lived species (Stimson 1985), which often dominates the reef crest and shallow reef slope on coral reefs throughout the Indo-Pacific (Veron & Wallace 1984). However, *A. hyacinthus* is highly susceptible to coral bleaching (e.g. McClanahan et al. 2004) as well as to hydrodynamic disturbance (Madin & Connolly 2006) and outbreaks of *Acanthaster planci* (Pratchett et al. 2009). *A. hyacinthus* also tends to dominate shallow, exposed reef habitats in the western Pacific, and exerts a major influence on community structure and dynamics there. High mortality and the rapid recovery of tabular corals due to high recruitment (Wallace 1985, Wakeford et al. 2008) and fast growth create a complex mosaic of shaded and unshaded habitats (Sheppard 1981), making it possible for organisms with different life histories and physiological requirements to adapt to different stages of recovery (Baird & Hughes 2000).

The present study was conducted at 3 reefs in the central section of the GBR: Bramble ($18^{\circ}24'25''\text{S}$, $146^{\circ}42'24''\text{E}$), Rib ($18^{\circ}28'50''\text{S}$, $146^{\circ}52'13''\text{E}$) and Trunk ($18^{\circ}20'49''\text{S}$, $146^{\circ}49'46''\text{E}$) Reefs. Shallow-water habitats (<10 m depth) at each of these reefs were subjected to significant levels of bleaching in January and February 2002 (Berkelmans et al. 2004). At the 3 study reefs, the estimated bleached coral cover exceeded 60%, and the maximum temperature recorded during this period ranged from 30.9 to 31.8°C for Bramble and from 31.8 to 32.7°C for both Trunk and Rib Reefs (Berkelmans et al. 2004; <http://e-atlas.org.au/content/coral-mass-bleaching-extent-2002>). Given the extreme vulnerability of *Acropora hyacinthus* to bleaching, it is likely that most colonies died as a consequence of this bleaching event. At Trunk Reef, a previous survey had shown that the coral cover decreased from 35 to 3% between 2000 and 2005, although, due mainly to increased cover of *A. hyacinthus*, a slight increase in coral cover (6.5%) was detected in 2008 (Pratchett et al. 2008a). To assess spatial variation in recovery of *A. hyacinthus*, we quantified the percentage of coral cover and size structure at the 3 subject reefs, which are from 2 to 5 km distant from one another.

Field sampling

To examine the recovery of *Acropora hyacinthus*, total cover and size structure were measured on the

reef crest at 3 sites per reef. Data were collected in January of 2008, 2009 and 2010. Percentage cover of *A. hyacinthus* was measured using 50 m point-intercept transects, following Dodge et al. (1982). Sampling was conducted within well defined reef crest habitat (from 2 to 5 m depth), with replicate transects positioned between 5 and 10 m from the reef edge and aligned parallel with the reef crest. The starting position of the first transect per site was relocated each year using GPS coordinates, and further transects were then deployed sequentially from randomly selected starting points. The distance between transects ranged from 1 to 20 m. A total of 100 points, spaced at 0.5 m intervals along each transect, were surveyed. Along each transect, the number of points (out of 100) that overlaid living tissue of *A. hyacinthus* was recorded. Differences in percent coral cover among reefs and between years were analyzed using 2-factorial univariate PERMANOVA, based on Euclidean distances, as the data were not distributed normally, even with transformations. Although the variables were univariate, we used PERMANOVA because the null distribution of the test statistic in PERMANOVA is produced by permutation, which avoids the usual normality assumptions of ANOVA (Anderson 2001). These analyses were performed using the Primer v.6 statistical package in conjunction with the Windows PERMANOVA+ module (Anderson et al. 2008).

To explore changes in the size structure of *Acropora hyacinthus*, the maximum diameter (L) of at least 100 colonies was measured at each reef in each of the 3 sampling months. Adult colonies were measured along replicate 50 m transects, while juvenile colonies (<5 cm diameter) were counted along 10 × 1 m transects. A total of 2696 colonies of *A. hyacinthus* were measured during the study. In 2010, for a subset of colonies ($n = 1220$), the perpendicular diameter (l) was also measured to provide improved estimates of colony area. For these colonies, because L and l were significantly correlated (Fig. 1; $r = 0.869$, $p < 0.001$, $n = 1220$), the resulting function ($l = 2.28 + 0.67L$) was used to estimate l for all remaining colonies. The area of each colony was then calculated on the assumption that the colony was an ellipse ($A = L/2 \times l/2 \times \pi$). Size-frequency distributions were constructed for *A. hyacinthus* populations at each reef in each year using log transformations of area estimates to normalize size-frequency distributions and to increase resolution among smaller size classes (Bak & Meesters 1998, Vermeij & Bak 2003). Kolmogorov-Smirnov tests were used to examine differences in size-frequency distributions. We also esti-

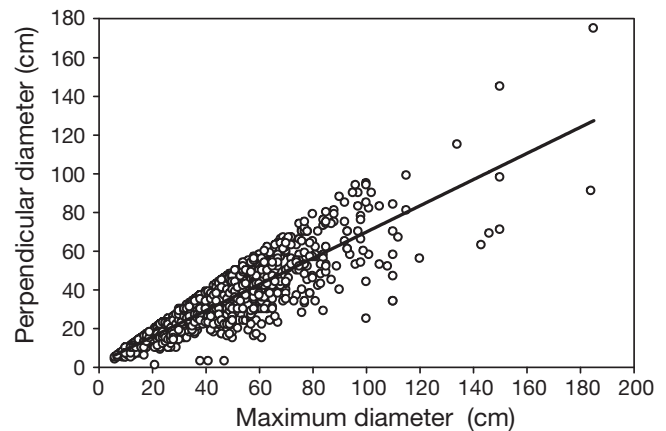


Fig. 1. *Acropora hyacinthus*. Relationship between the maximum and perpendicular diameters of colonies, pooling together all measurements at all 3 study reefs in 2010 ($n = 1220$)

ated the skewness and kurtosis coefficient from log-transformed distributions.

In order to assess the relative contribution of new recruits versus growth of established colonies (i.e. recolonisation versus persistence) in local recovery of *Acropora hyacinthus* populations, we estimated the number of colonies that survived the 2001–2002 bleaching event, using growth rates of *A. hyacinthus* for each reef to calculate maximum size of colonies that recruited since 2008. It is possible that small colonies represent remnants of once larger and older colonies, but ongoing disturbance recorded between 2002 and 2008 was limited (Pratchett et al. 2008a).

RESULTS

Acropora hyacinthus cover increased at all 3 study reefs over the study period. From 2008 to 2010, average cover of *A. hyacinthus* increased from (mean \pm SE) 15.54 ± 7.87 to 22.66 ± 7.60 % at Bramble Reef; from 9.42 ± 3.70 to 16.40 ± 5.18 % at Rib Reef, and from 2.13 ± 1.34 to 4.66 ± 2.10 % at Trunk Reef (Fig. 2). However, percentage cover of *A. hyacinthus* was more variable among sites than between years or among reefs (Table 1, Fig. 2). In fact, the only significant differences in cover of *A. hyacinthus* were from site to site on the same reef (Table 1).

The mean diameter of *Acropora hyacinthus* colonies showed marked differences among reefs, ranging (in 2008) from 20.57 ± 0.44 cm at Trunk Reef to 34.57 ± 0.78 cm at Bramble Reef (Table 2). All reefs showed an increase in average colony diameter throughout the study (Table 2). As with coral cover,

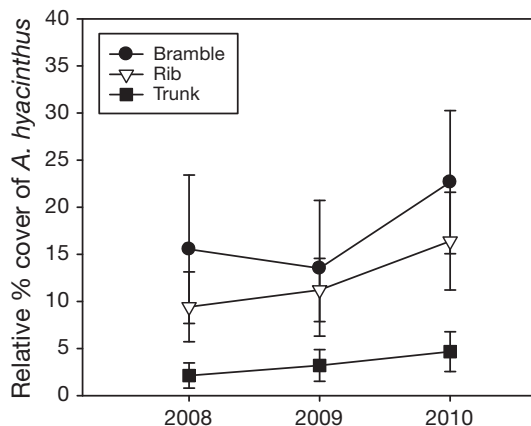


Fig. 2. *Acropora hyacinthus*. Changes in relative percent cover (mean \pm SE) of *A. hyacinthus* in relation to total coral cover at the 3 study reefs

Table 1. *Acropora hyacinthus*. Three-factor PERMANOVA for *A. hyacinthus* cover, with Year (3 levels), Reef (3 levels) and Site nested in Reef (3 levels) as fixed and random factors, respectively

Source	df	Mean square	Pseudo-F	p
Year	2	133.81	6.555	0.056
Reef	2	1622.8	2.087	0.169
Site	6	794.34	24.116	0.001
Year \times Reef	4	20.303	0.483	0.774
Year \times Site (reef)	11	42.026	1.275	0.211
Residual	98	32.938		
Total	123			

the largest individual colonies (ranging in diameter from 34.57 ± 0.78 to 48.87 ± 1.19 cm) were observed at Bramble Reef, while the smaller colonies were found at Trunk (from 20.57 ± 0.44 to 38.71 ± 0.88 cm diameter). The largest colonies recorded in this study were found at Bramble (185 cm diameter) and Rib (184 cm diameter; Table 2).

The size-frequency distributions also showed significant differences among the 3 reefs studied (K-S tests, $p < 0.05$; Fig. 3). Size-frequency distributions at the start of the study were negatively skewed for Bramble and Rib Reef ($g_1 = -0.43$ and -0.19 , respectively) and positively skewed for Trunk Reef ($g_1 = 0.02$; Fig. 3, Table 2), indicating a higher predominance of large colonies at Bramble and Rib. At the end of the study, the 3 reefs showed similar size-frequency distributions with negative skewness coefficients (g_1 at Bramble, -0.72 ; at Rib, -0.67 ; at Trunk, -0.36 ; Fig. 3, Table 2). All size-frequency distributions obtained among reefs and between years were leptokurtic ($g_2 > 0$) except for the distri-

Table 2. *Acropora hyacinthus*. Descriptive statistics and log-transformed size-frequency distribution of colony diameters in the 3 study reefs. g_1 : skewness; g_2 : kurtosis. N = number of colonies

Reef	N	Diameter (cm)				g_1	g_2
		Mean	SE	Min	Max		
2008							
Bramble	202	34.57	0.78	11	65	-0.44	0.01
Rib	130	30.55	0.91	11	63	-0.19	-0.34
Trunk	230	20.57	0.44	8	49	0.02	0.15
2009							
Bramble	242	41.94	0.92	9	87	-0.51	0.32
Rib	310	32.71	0.67	10	107	-0.29	0.58
Trunk	362	29.98	0.58	6	75	-0.71	0.23
2010							
Bramble	500	48.87	1.19	6	185	-0.37	0.26
Rib	349	41.93	1.09	7	184	-0.68	0.38
Trunk	371	38.71	0.88	7	100	-0.72	0.45

bution found at Rib Reef in 2008 ($g_2 = -0.33$; Fig. 3, Table 2).

Based on changes in the diameter of *Acropora hyacinthus* from year to year, average annual growth was estimated to be 6.42 ± 3.08 cm yr⁻¹. However, estimates of colony growth were highly variable from reef to reef, ranging from 4.06 ± 3.32 cm yr⁻¹ at Rib Reef to 8.65 ± 0.26 cm yr⁻¹ at Trunk Reef (Fig. 4a). The highest variability in annual change was recorded from 2008 to 2009, while similar diameter changes were obtained between 2009 and 2010 across the 3 reefs. Trunk Reef showed the largest increases for both annual transitions (from 8.39 ± 1.54 cm to 8.91 ± 0.30 cm; Fig. 4a). Based on the observed size structure and estimates of annual growth, the percentage of colonies that survived the 2001–2002 bleaching event ranged from 2 to 62%, with the lowest values obtained at Trunk Reef (t -test, $p < 0.01$; Fig. 4b).

DISCUSSION

Climate-induced bleaching events have had a significant impact on coral reefs both globally and locally, leading to declines in live coral cover and changes in benthic composition (Marshall & Baird 2000, Riegl & Purkis 2009). The 2001–2002 bleaching event affected many shallow reefs on the GBR (Berkelmans et al. 2004) e.g. Trunk Reef experienced a 10-fold decrease in coral cover (from 30 to 3% between 2000 and 2005), with minimal evidence of recovery >6 yr after the disturbance (Pratchett et al. 2008a). However, the high variability of coral cover and percentage of living colonies observed in the

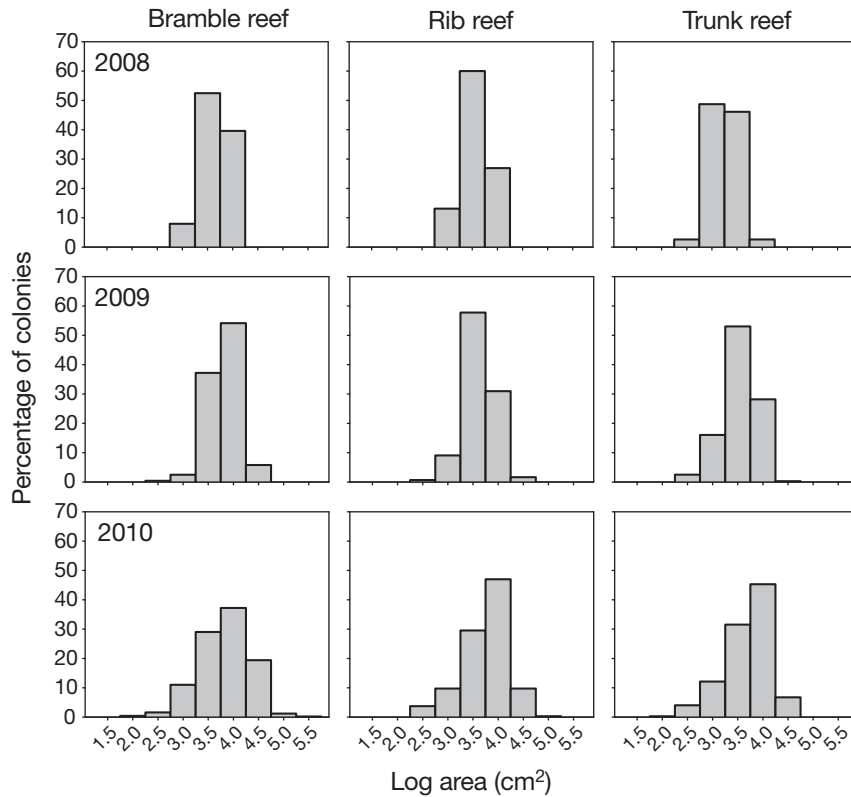


Fig. 3. *Acropora hyacinthus*. Size-frequency distributions for log-transformed estimates of colony surface area at the 3 study reefs

present study among reefs at the beginning of 2008 suggested that the impact of the 2001–2002 bleaching event on GBR reefs was highly uneven and patchy. In particular, the large differences in percentage cover of *Acropora hyacinthus* in 2008 (ranging from 2 to 23%) suggested that Trunk Reef was impacted more severely than the neighbouring Bramble and Rib Reefs. Moreover, the lowest percentages of living colonies after the bleaching event were obtained at Trunk Reef. Major differences in the prevalence of bleaching have been reported over small spatial scales (10s of km) along the GBR during 1998 and 2002, indicating that some reefs, although relatively close to one another, experience different levels of stress or are more resistant to it (Berkelmans et al. 2004).

Aside from temporal changes in coral cover, the present study also explored temporal trends in the size-frequency distribution of *Acropora hyacinthus*, providing significant insights into population dynamics for this dominant and ecologically important coral species. Increasing numbers of small colonies of *A. hyacinthus* from 2008 to 2010 confirmed the capacity of this species to regenerate and recolonise at the 3 study reefs. The density of *A. hyacinthus* colonies at several sites was much higher 5 yr post-disturbance than it had been pre-disturbance, suggesting that,

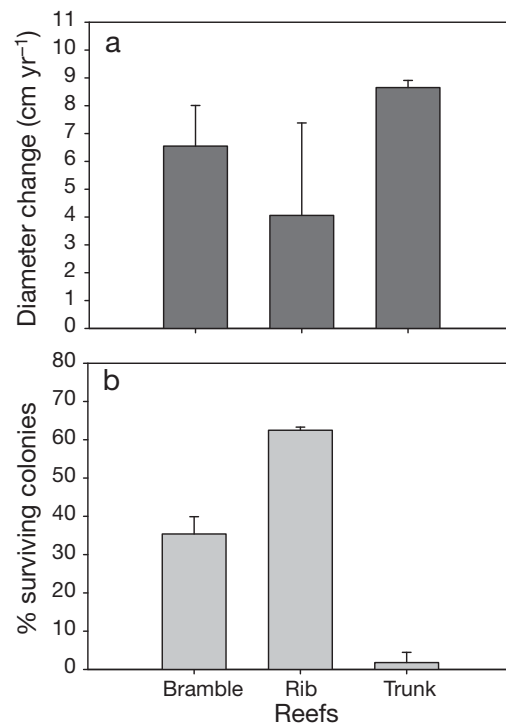


Fig. 4. *Acropora hyacinthus*. (a) Change in mean diameter (\pm SE) of colonies and (b) percentage of colonies that survived the 2001–2002 mass bleaching event, based on growth rates measured (Fig. 4a), at the 3 study reefs over the study period from 2008–2010

once started, recovery of this species can be very rapid (Halford et al. 2004). Changes in the mean size of colonies also revealed significant colony growth across all size classes, which further contributed to increasing cover between 2008 and 2010. Populations at all 3 reefs exhibited a healthy demographic flux, with an increase in colony size comparable to that of recovering populations in other locations. For instance, the average sizes of *A. hyacinthus* colonies measured in 2008 (Table 2) were similar to those obtained 5 yr after a volcanic eruption in Indonesia (38 cm; Tomascik et al. 1996) and 7 yr after the 1998 bleaching event on Palau's reefs (from 13 to 22 cm; Victor et al. 2009). Interestingly, skewness coefficients provided more valuable information than analysis of kurtosis for understanding temporal changes in the size structure of populations. Our results showed a temporal trend to more negative skewness coefficients, indicating a higher predominance of larger colonies over time. In contrast, the kurtosis coefficient did not provide clear information about temporal changes in population size structure.

Despite the high vulnerability of *Acropora hyacinthus* to disturbance, high growth rates enable this species to rapidly recolonise reefs following such disturbance. The relatively high growth rates of this species contributed greatly to increases in total coral cover, as well as providing 3-dimensional structure that is critical for many reef-associated fishes and other organisms (Pratchett et al. 2008b). Estimates of growth rates across the 3 recovering reefs were variable, but within the range of values reported in other studies. Stimson (1985) reported growth rates between (mean \pm SD) 9.45 ± 5.59 and 10.45 ± 8.79 cm yr⁻¹ obtained from tagged colonies over a 2 yr period in the Marshall Islands. The highest growth rates recorded in any study (15 cm yr⁻¹) were estimated 5 yr after a volcanic eruption in Indonesia (Tomascik et al. 1996). However, relatively low growth rates have also been reported in the GBR (e.g. <3 cm yr⁻¹ by Wakeford et al. 2008), emphasising the high variability in coral growth rates within and among reefs.

Recovery of degraded reefs depends on the degree of partial- versus whole-colony mortality resulting from acute disturbance, which influences the relative importance of colony growth versus recruitment and subsequent growth of new colonies. Under conditions of low mortality rate, large colonies surviving as remnants or fragments can regenerate relatively quickly. In contrast, if a given disturbance has caused high mortality, as occurred during the 2001–2002

bleaching event, recovery will largely depend on the sexual recruitment of larvae (Smith & Hughes 1999, Baker et al. 2008), a process that is expected to be considerably slower (Baird & Marshall 2002). The large decrease in coral cover observed between 2002 and 2008 (Pratchett et al. 2008a), the low percentage of surviving colonies after the bleaching event and the constant growth of the colonies supports the idea that regeneration of acroporid colonies at the Trunk Reef study sites has been through sexual recruitment. In contrast, at Bramble and Rib Reefs, a higher coral cover and higher percentage of living colonies was observed. In this case, the proportion of living corals explains the total cover observed at these reefs. These results highlighted the fact that resilience of coral populations may be explained by either persistence or recolonisation, and that individual contributions to population resilience may vary greatly among sites and reefs.

Although disturbances and resultant stress are known to reduce coral fecundity (Szmant & Gassman 1990, Hoegh-Guldberg 1999), it is possible that surviving corals may provide sufficient larval supply to replenish coral losses after such major stress events (Riegl 2002, Baker et al. 2008). Due to the disproportionate contribution of a few large colonies to the reproductive output of a population, the survival of these colonies—as has been inferred from this study—has important consequences for population recovery (Hall & Hughes 1996, Sakai 1998).

The rapid recovery of *Acropora hyacinthus* populations may have significant consequences for associated coral reef communities and ecosystem processes. The high growth rate of this species permits the maintenance of high structural complexity, which has positive consequences for associated fish communities. On Indo-Pacific reefs, major changes in fish community composition have resulted from the long-term loss of structure following coral bleaching events (Jones et al. 2004, Graham et al. 2007, Pratchett et al. 2008b). On the other hand, *A. hyacinthus* is an important competitor that can overgrow neighbouring corals and forestall the recruitment of other species (Baird & Hughes 2000). Nevertheless, a lower recovery capacity of *Acropora* has also been observed in some reefs, mainly attributable to environmental conditions or time between disturbances (van Woosik 2000, Berumen & Pratchett 2006). Direct observation as well as modelling have shown monopolization of *A. hyacinthus* over long intervals without disturbance and limited recovery with ongoing disturbance (Berumen & Pratchett 2006, Wakeford et al. 2008).

The frequency and intensity of climate-induced coral bleaching is likely to increase over the next 50 yr, resulting in widespread degradation of coral communities (Hoegh-Guldberg et al. 2007). The capacity of reefs to recover from these impacts will depend not only on the time between bleaching events but also on the existence of remaining colonies to recolonise the reefs. Recovery of coral cover on the 3 reefs (from 2 to 5 km apart) studied in the central GBR was due to both recolonisation and colony persistence, depending on which reef one looks at. Nonetheless, *Acropora hyacinthus* populations require at least 5 yr between disturbances to ensure complete recovery, and much longer at some sites. Given a business-as-usual scenario of CO₂ emissions, mass bleaching is predicted to become a biannual event on the GBR by 2030 (Hoegh-Guldberg 1999, Lesser 2007). It is clear therefore that even the most resilient of coral species will be adversely affected unless immediate action be taken to reduce greenhouse gas emissions and minimise future increases in ocean temperatures.

Acknowledgements. This work was supported by the ARC Centre of Excellence for Coral Reef Studies and by the Australian government's Marine and Tropical Science Research Facility. C.L. was funded by a Juan de la Cierva postdoctoral fellowship from the Ministerio de Ciencia e Innovación of Spain. Research assistance was provided by D. McCowan, A. Cole, M. Trapon, D. Stewy and the crew of the 'Kalinda'.

LITERATURE CITED

- Adjeroud M, Pratchett MS, Kospartov MC, Lejeune C, Penin L (2007) Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. *Hydrobiologia* 589:117–126
- Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y and others (2009) Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28:775–780
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understory assemblages. *J Exp Mar Biol Ecol* 251:117–132
- Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar Ecol Prog Ser* 237:133–141
- Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. *Mar Ecol Prog Ser* 162:301–306
- Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar Coast Shelf Sci* 80:435–471
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429:827–832
- Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs* 23:74–83
- Berumen ML, Pratchett MS (2006) Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* 25:647–653
- Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163–170
- Crabbe MJC (2009) Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. *Mar Environ Res* 67: 189–198
- Dodge R, Logan A, Antonius A (1982) Quantitative reef assessment studies in Bermuda: a comparison of methods and preliminary results. *Bull Mar Sci* 32:745–760
- Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob Change Biol* 11:2251–2265
- Gilmour JP (2004) Size-structures of populations of the mushroom coral *Fungia fungites*: the role of disturbance. *Coral Reefs* 23:493–504
- Golbuu Y, Victor S, Penland L, Idip D and others (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. *Coral Reefs* 26:319–332
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson JAN, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv Biol* 21:1291–1300
- Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85:1892–1905
- Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* 77:950–963
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, and others (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209:713–715
- Hughes TP, Baird AH, Bellwood DR, Card M, and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Lesser MP (2007) Coral reef bleaching and global climate change: Can corals survive the next century? *Proc Natl Acad Sci USA* 104:5259–5260
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122–131

- Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* 444:477–480
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155–163
- McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Mar Pollut Bull* 48:327–335
- McClanahan TR, Ateweberhan M, Omukoto J (2008) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Mar Biol* 153: 755–768
- Meesters EH, Hilterman M, Kardinaal E, Keetman M, de Vries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Mar Ecol Prog Ser* 209:43–54
- Pratchett MS, Baird AH, McCowan DM, Coker DJ, Cole AJ, Wilson SK (2008a) Protracted declines in coral cover and fish abundance following climate-induced coral bleaching on the Great Barrier Reef. *Proc 11th Int Coral Reef Symp, Fort Lauderdale* 2:1315–1319
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ and others (2008b) Effects of climate-induced coral bleaching on coral-reef fishes: ecological and economic consequences. In: Pratchett MS, Munday PL, Wilson SK, Graham NAJ and others (eds) *Oceanography and marine biology: an annual review*, Vol 46. CRC Press, Boca Raton, FL, p 251–296
- Pratchett MS, Shenk TJ, Baine M, Syms C, Baird AH (2009) Selective coral mortality associated with outbreaks of *Acanthaster planci* L. in Bootless Bay, Papua New Guinea. *Mar Environ Res* 67:230–236
- Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): fauna and community structure in response to recurring mass mortality. *Coral Reefs* 18:63–73
- Riegl B (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). *Mar Biol* 140: 29–40
- Riegl BM, Purkis SJ (2009) Model of coral population response to accelerated bleaching and mass mortality in a changing climate. *Ecol Modell* 220:192–208
- Sakai K (1998) Effect of colony size, polyp size, and budding mode on egg production in a colonial coral. *Biol Bull* 195: 319–325
- Sheppard CRC (1981) Illumination and the coral community beneath tabular *Acropora* species. *Mar Biol* 64:53–58
- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* 425:294–297
- Smith L, Hughes TP (1999) An experimental assessment of survival, reattachment and fecundity of coral fragments. *J Exp Mar Biol Ecol* 235:147–164
- Stimson J (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory corals. *Ecology* 66: 40–53
- Szmant AM, Gassman NJ (1990) The effects of prolonged 'bleaching' on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8:217–224
- Tomascik T, van Woesik R, Mah AJ (1996) Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. *Coral Reefs* 15:169–175
- van Woesik R (2000) Modelling processes that generate and maintain coral community diversity. *Biol Conserv* 9: 1219–1233
- Vermeij MJA, Bak RPM (2003) Species-specific population structure of closely related coral morphospecies along a depth gradient (5–60 m) over a Caribbean reef slope. *Bull Mar Sci* 73:725–744
- Veron JEN, Wallace CC (1984) Scleractinia of Eastern Australia, Part 5: Acroporidae. Australian Institute of Marine Science Monograph Series, Angus and Robertson, Sydney
- Victor S, Golbuu Y, Yukihiro H, van Woesik R (2009) Acropora size-frequency distributions reflect spatially variable conditions on coral reefs of Palau. *Bull Mar Sci* 85: 149–157
- Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* 27:1–13
- Wallace CC (1985) Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. *Mar Ecol Prog Ser* 21:289–298
- Wilkinson C (2000) Status of coral reefs of the world: 2000. Australian Institute of Marine Science, Townsville

Editorial responsibility: Charles Birkeland, Honolulu, Hawaii, USA

*Submitted: April 8, 2011; Accepted: June 23, 2011
Proofs received from author(s): September 18, 2011*