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Protracted declines in coral cover and fish abundance following climate-induced coral bleaching on the Great Barrier Reef

M.S. Pratchett[1], A.H. Baird[1], D.M. McCowan, D.J. Coker[1], A.J. Cole[1], S.K. Wilson[1]

1) ARC Centre for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

Abstract. Understanding how corals and coral-dependant organisms respond to major disturbances is critical in predicting long-term changes in the structure and dynamics of coral reef assemblages affected by ongoing climate change. This study documents changes in coral and butterflyfish assemblages at Trunk Reef in the central Great Barrier Reef, Australia, following severe climate-induced coral bleaching in 2001-02. Coral cover declined by 90%, to a low of 3.2% (± 0.8SE) in March 2005. However, coral cover has started to recover, increasing to 6.5% in January 2008 (±1.0 SE). Despite recent increases in the abundance of corals there has been no apparent increase in abundance of butterflyfishes. If anything, overall densities of butterflyfishes declined even further between 2005 and 2008, due to recent declines in the abundance of non-coral feeding butterfly fish. Although there are some signs of coral recovery, it is clear that severe episodes of coral bleaching can have enduring effects on coral reef ecosystems, and that recovery typically takes many years (>5 years). Protracted declines and limited recovery of coral and fish communities indicate that reef ecosystems will gradually deteriorate as bleaching events become more frequent and more severe.

Key words: Bleaching, Butterflyfishes, Coral Reefs, Coral loss, Disturbance, Reef fishes

Introduction

Coral reef ecosystems are subject to frequent and often catastrophic disturbances caused by a variety of different agents, including severe tropical storms, freshwater plumes, temperature extremes, and infestations of the coral eating crown-of-thorns sea star. These acute, but increasingly frequent, disturbances often cause marked reductions in the abundance of reef-building corals (Hughes et al. 2003; Hoegh-Guldberg et al. 2007), which are the major architects and significant contributors to endogenous carbon production on coral reefs. Changes in the physical and biological structure of benthic reef habitats are likely to have further, often detrimental, effects on other reef associated organisms, particularly coral reef fishes (Wilson et al, 2006; Pratchett et al. 2008a).

Among those fishes with the greatest reliance on hard corals are butterflyfishes from the genus Chaetodon (family Chaetodontidae), many of which feed on hard corals (Harmelin-Vivien and Bouchon-Navaro 1983; Halford et al. 2004; Pratchett 2005). Spatial variation in the abundance of butterflyfishes is often strongly correlated with hard coral cover (Cadoret et al. 1999; Pratchett and Berumen 2008), indicating a close association between butterflyfishes and coral prey. Moreover, many butterflyfishes exhibit rapid and dramatic declines in abundance following coral depletion (Williams 1986; Pratchett et al. 2006; Graham 2007).

The strong reliance on corals by coral-feeding butterflyfishes makes them very susceptible to effects of climate-induced coral bleaching (Pratchett et al, 2006). However, provided bleaching is sporadic and does not cause 100% mortality of critical coral species, even highly susceptible fish populations may have the potential to persist and recover. The recovery and resilience of fishes will however, be critically dependant upon recovery of coral habitats (Halford et al. 2004). In the absence of any further disturbances, it may take as little as 5 years for coral cover to return to pre-disturbance levels (Halford et al. 2004), though this will depend on the severity and spatial extent of coral loss, which dictates the ability of surviving corals to recover, reproduce and reseed affected areas (Hughes and Connell 1999; Riegl and Piller 2003; Golbuu et al. 2007). Recovery will be much faster if at least some coral colonies survive the bleaching (Baird and Marshall 2002), because growth of surviving corals leads to more rapid increases in coral cover compared with settlement and subsequent growth of new individuals (Connell et al. 1997).

The purpose of this study was measure rates of recovery in butterflyfish and coral assemblages at Trunk reef, Great Barrier Reef (GBR), Australia, following climate-induced coral bleaching in 2001-

02. Coral depletion was further exacerbated by localised outbreaks of *Acanthaster planci* causing extensive and widespread coral loss throughout the region (Sweatman et al. 2004). Periodic monitoring of butterflyfish and coral assemblages have been undertaken at Trunk Reef since May 2000, testing for long-term changes in abundance of both fish and corals. Until 2005, both coral cover and abundance of most butterflyfishes had exhibited significant declines (Pratchett et al. 2006). It was expected however, that coral cover would have increased significantly from 2005 to 2008, and that coral recovery would initiate commensurate increases in the abundance of coral-dependant butterflyfishes, following Halford et al. (2004).

Material and Methods

This study was conducted at Trunk Reef (18°17'S, 146°53'E), in the central section of the Great Barrier Reef (GBR), Australia. Trunk reef is a large (ca. 125km^2) submerged reef, located ~120km north of Townsville. This reef, like many throughout the GBR, was subject to extensive and wide-spread coral bleaching during the summer (November – March) of 2001-02 (Berkelmans et al. 2004). In order to assess impacts of coral bleaching, local assemblages of both scleractinian corals and butterflyfishes were examined at Trunk Reef in May 2000 (18 months before the bleaching), in March 2002 (towards the end of the bleaching event), in March 2005 (3 years after the bleaching), and most recently, in January 2008 (>5 years post-bleaching). Sampling was conducted on the shallow reef crest (2-3m water depth), at three randomly selected sites along the exposed (south-east) side of Trunk Reef. All sites were non-overlapping and independent, but were very similar in their physical structure, aspect, and exposure to prevailing south-east trade winds.

In 2000, 2002, and 2005, coral cover and composition were assessed using replicate 10-m line-intercept transects. Ten replicate transects were sampled at each site. On each transect, colonies lying directly beneath the transect tape were identified to genus and the intercept length measured to the nearest centimeter. Percentage cover for each taxa was then calculated based on the cumulative intercept length of each taxa on each transect. In 2008 however, coral cover and composition was quantified using photographic records of the benthos taken at 1-m intervals along the length of 50-m transects that were deployed to survey butterflyfishes. Within each photograph we recorded the substrate type or benthic organisms immediately beneath the transect line corresponding with 1-m markings (e.g., 1.0, 2.0 etc).

Densities of butterflyfishes on the reef crest at Trunk reef were quantified using underwater visual census (UVC) along 50-m transects. Adult butterflyfishes observed within 2-m either side of the transect line were counted and recorded to species. All transects were positioned within 10-m of the edge of the reef crest, following the natural contours of the reef. Five replicate transects were conducted at each site. To test for differences in responses of butterflyfishes according to their specific trophic requirements (following Pratchett et al. 2006; Graham 2007), all species were categorised as either i) obligate corallivores (OC), ii) facultative corallivores (FC), or iii) non-coral feeders (NC). Species were assigned to feeding guilds following Pratchett (2005).

Results

Coral cover on the reef crest at Trunk reef declined significantly between May 2000 and March 2005, to a low of 3.2% (± 0.8SE) in March 2005 (Fig. 1, Table 1). Since 2005, there has been a 100% increase in coral cover to 6.5% (±1.0 SE) in January 2008 (Fig. 1). Recent increases in coral cover are mainly due to increased cover of *Acropora* species (Table 1), especially *A. hyacinthus*. In January 2008, mean cover of *Acropora* spp. was 4.8%, accounting for 73% of live coral cover, compared to 14% and 4%, for the next most abundant genera, *Pocillopora* and *Porites*, respectively. Other genera (comprising mainly *Favites*, *Goniastrea*, *Montipora*, and *Stylophora*) together accounted for only 8% of coral recorded in 2008.

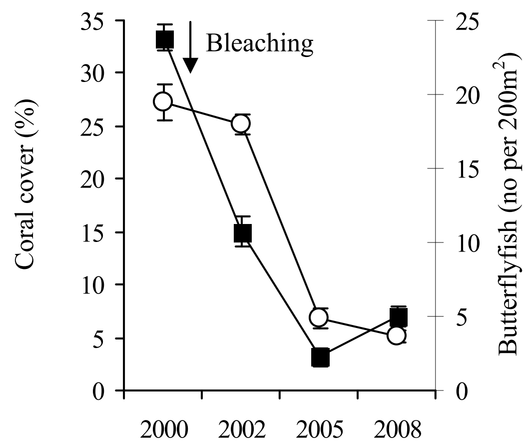

Figure 1. Mean ± SE percentage cover of scleractinian corals (■) and densities of butterflyfishes (O) at Trunk Reef in May 2000 (before bleaching), March 2002 (during bleaching), March 2005, and January 2008 (post-bleaching).

Table 1. Changes (%) in coral cover and butterflyfish abundance at Trunk Reef over two distinct intervals (2000-2005, and 2005-2008) Absolute changes were analysed using nested ANOVAs (between years and among sites within years), with F and p shown for temporal contrasts. Coral cover data was arcsine- square root transformed, while butterflyfish densities were $\log_{10}$ transformed prior to analyses (df = 1, 4). Values in bold are significant even when applying Bonferroni correction for multiple comparisons across coral genera and trophic groups for butterflyfishes (OC – Obligate corallivores, FC – Facultative corallivores, and NC – Non-coral feeders).

	2000-2005		2005-2008	
	Change	F, *p*	Change	F, *p*
Coral Cover	-90.4%	**236.4, 0.00**	104.0%	**8.96, 0.03**
Acropora	-85.8%	**87.9, 0.00**	207.0%	**10.7, 0.02**
Pocillopora	-50.1%	2.89, 0.16	-16.7%	0.02, 0.88
Porites	-96.9%	**27.6, 0.01**	9.6%	0.74, 0.43
Others	-97.8%	**114.9, 0.00**	90.5%	3.08, 0.14
Butterflyfish	-75.0%	**57.7, 0.00**	-24.7%	1.61, 0.27
OC	-90.8%	**172.8, 0.00**	-9.5%	0.20, 0.68
FC	-29.8%	1.18, 0.34	-24.2%	1.07, 0.36
NC	18.8%	0.09, 0.77	-47.5%	**57.4, 0.00**

Despite recent increases in coral cover at Trunk Reef, there has not been any concomitant increase in the abundance of butterflyfishes (Fig. 1). Mean densities of butterflyfishes declined from 19.5 (±1.2SE) fishes per 200m^2 (per transect) in March 2000 down to 3.7 (±0.4SE) fishes per 200m^2 in January 2008. The greatest decline occurred between 2002 and 2005, but there have been further (albeit not significant) declines between 2005 and 2008 (Fig. 1).

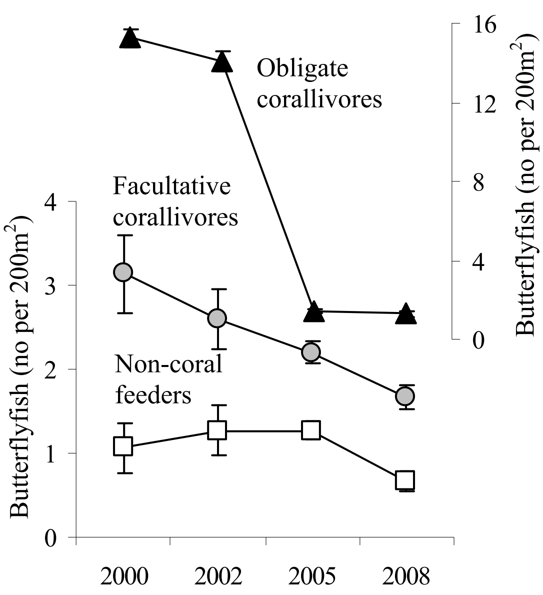

Figure 2. Temporal variation in mean ± SE densities of butterflyfishes within each trophic group (i. obligate corallivores, ii. facultative corallivores, and iii. non-coral feeders) on the reef crest at Trunk Reef

The group of butterflyfishes that exhibited the most rapid and dramatic declines in abundance following extensive coral depletion were the obligate coral feeders (comprising *Chaetodon aureofasciatus, C. baronessa, C. lunulatus, C. plebeius, C. rainfordi,* and *C. trifascialis*). Between 2002 and 2005, the proportional decline in abundance of these species corresponded very closely to the decline in total coral cover (Table 1). Densities of obligate corallivores have remained at or below 1.4 (±0.8SE) fishes per 200m^2 since 2005 with no evidence of recovery (Table 1).

Facultative corallivores (e.g., *C. citrinellus* and *C. melannotus*) and non-coral feeding butterflyfishes (e.g,, *C. auriga* and *C. vagabundus*) did not exhibit any significant variation in abundance to 2005 (Table 1), though there was an apparent downward trend in mean densities of facultative corallivores throughout this study (Fig. 2). For non-coral feeders, there was no apparent change in abundance between 2000 and 2005, but there have been significant recent declines in abundance (Table 1), from 1.3 (±0.1SE) fishes per transect in 2005 down to 0.7 (±0.1SE) in 2008 (Fig. 2).

Discussion

Climate-induced coral bleaching represents one of the most significant and increasingly prevalent disturbances to coral reef ecosystems, which not only causes extensive coral mortality, but also reduces the abundance of many other coral reef organisms that are reliant on corals for food, shelter or recruitment (Wilson et al, 2006; Pratchett et al, 2008a). At Trunk Reef, extensive coral depletion was accompanied by a 5-fold reduction in the abundance of butterflyfishes. Declines in abundance of butterflyfishes were most rapid and most severe for obligate corallivores, which is to be expected given their obligate dependence on coral for food. Corallivorous fishes have the most apparent and direct reliance on live corals and are consistently among the worst affected fishes following extensive coral loss (Wilson et al. 2006).

The extent to which corallivorous fishes feed on corals (versus other non-coral prey) is highly variable (e.g., Hobson, 1974; Pratchett, 2005) and obligate coral-feeders are much more affected by coral loss than facultative coral-feeders (Bouchon-Navaro et al. 1985; Williams 1986; Pratchett et al. 2006; Graham 2007). Accordingly, facultative corallivores were relatively unaffected by initial declines in abundance of corals at Trunk Reef. These fishes presumably persisted on increased intake of non-coral prey, but there has been a persistent decline in abundance of these fishes throughout the study, suggesting that corals may represent an important and necessary component of their diet. Alternatively, protracted declines in the abundance of these fishes may be attributable to the loss of habitat structure or habitat diversity associated with extensive coral loss (Graham et al. 2006; Pratchett et al. 2008a), and this may also be the reason why non-coral feeding butterflyfishes have ultimately declined in abundance >5 years after the initial coral loss. It is also possible that coral depletion has reduced settlement success by butterflyfishes (Jones et al. 2004), which might explain protracted declines in population size. However, butterflyfishes with low coral content in their diet as adults tend not to recruit to live corals (Pratchett et al. 2008b), but overall declines in habitat complexity may have reduced post-settlement survivorship of all species (Graham et al. 2007).

Topographic complexity of coral reef habitats has an important influence on biotic interactions, such as predation and competition, and has a major influence on the local abundance of coral-reef fishes, especially during early life stages (Almany 2004; Hixon and Jones 2005). Climate-induced coral bleaching kills corals, but leaves the underlying skeleton completely intact (Hoegh-Guldberg 1999). Exposed coral skeletons are then subject to a whole suite of bio-eroding organisms that undermine the structural integrity of these carbonate structures (Hutchings 1986). Reef habitats with reduced topographic complexity typically support lower fish abundance, fewer species, and increased evenness (Gratwicke and Speight 2005; Graham et al. 2006).

This study focused on specific study locations along the exposed reef crest at Trunk reef as baseline data on coral and butterflyfish assemblages were recorded prior to the bleaching in 2000 (Pratchett et al. 2004, 2006). However, the extent of coral depletion and declines in abundance of butterflyfishes (especially corallivorous species) reported for Trunk Reef are similar across the full range of locations (reef crest and reef slope habitat at three different reefs; Trunk Reef, Bramble Reef and Rib Reef) surveyed since 2002. Interestingly however, coral recovery has been highly variable within and among reefs. At Bramble reef, for example, there are two sites where coral cover has increased to 90% within the 5 years since the bleaching (Fig. 3). Even so, there has been no apparent recovery of butterflyfishes at any of these sites. These findings contradict previous studies that suggested recovery of fishes would closely follow coral recovery (Halford et al. 2004). Recovery of fish populations at these sites appears to be currently limited by a lack of new recruits. Recruitment rates by butterflyfishes are generally low (Pratchett et al. 2008b) and may have been further constrained by limited coral cover at potential settlement sites, as well as widespread depression of breeding populations.

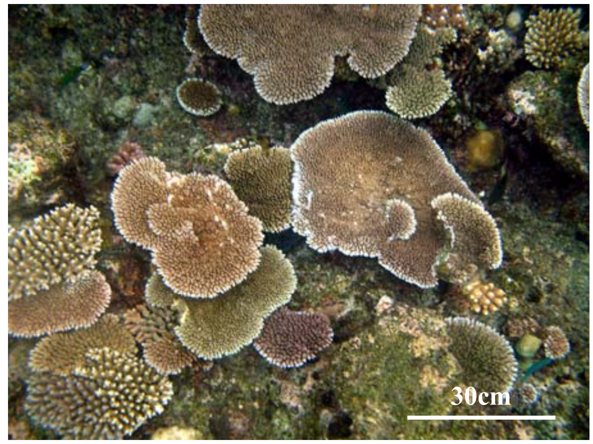

Figure 3. Extensive cover of *Acropora* (mostly, *A. hyacinthus*) at Bramble Reef in January 2008.

The rapid recovery and increasing dominance of *Acropora* spp. in the aftermath of extensive coral bleaching suggests that climate forcing of coral communities may initially favor coral species with rapid recovery potential, rather than slow-growing corals that might otherwise have greater resistance to bleaching, as suggested previously (Hughes et al. 2003; McClanahan et al, 2007). Fortunately, faster growing corals (especially *Acropora*) contribute most to topographic complexity of reef habitats (Sheppard et al. 2002) and are also the major corals used by corallivorous and coral-dwelling fishes (Munday et al. 1997; Pratchett 2005). However, persistence of *Acropora* populations will depend on sufficient time between successive bleaching events to allow for recovery. Recovery was mostly very limited (but occasionally spectacular) in the 5 years since extensive bleaching in the central GBR. Donner et al. (2005) project that bleaching is likely to occur at least every 2 years on most coral reefs around the world by 2040, meaning that there would be insufficient time for recovery of *Acropora* spp., let alone other slower growing species (e.g., *Porites*). Sustained and ongoing climate change will undoubtedly change the community structure of coral assemblages (Hughes et al. 2003; McClanahan et al. 2007), yet specific effects will depend on the severity, extent and recurrence of future bleaching events.

In conclusion, this study shows that coral communities are starting to recover at Trunk Reef. However, recovery has been very slow and follows highly protracted declines in coral cover. Moreover, coral depletion led to extensive and long-term declines in the abundance of butterflyfishes, and these fishes are yet to respond to increased availability of corals, which are critical in providing both food and habitat (Pratchett et al. 2006). These systems are likely to recover in the absence of any further disturbances. However, it is clear that projected increases in the frequency and severity of coral-bleaching events are likely to cause extensive ongoing degradation and biodiversity loss on coral reefs throughout the world (Hoegh-Guldberg et al. 2007).

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