Coral bleaching, reef fish community phase shifts and the resilience of coral reefs

DAVID R. BELLWOOD*†, ANDREW S. HOEY*†, JOHN L. ACKERMAN*‡ and MARTIAL DEPCZYNSKI*

*School of Marine Biology, James Cook University, Townsville, Qld 4811, Australia, †Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld 4811, Australia, ‡Fisheries and Marine Sciences Program, Bureau of Rural Sciences, GPO Box 858, Canberra, ACT 2610, Australia

Abstract

The 1998 global coral bleaching event was the largest recorded historical disturbance of coral reefs and resulted in extensive habitat loss. Annual censuses of reef fish community structure over a 12-year period spanning the bleaching event revealed a marked phase shift from a prebleach to postbleach assemblage. Surprisingly, we found that the bleaching event had no detectable effect on the abundance, diversity or species richness of a local cryptobenthic reef fish community. Furthermore, there is no evidence of regeneration even after 5–35 generations of these short-lived species. These results have significant implications for our understanding of the response of coral reef ecosystems to global warming and highlight the importance of selecting appropriate criteria for evaluating reef resilience.

Introduction

Coral reefs are highly dynamic systems characterized by variable and stochastic recruitment and disturbance. Our understanding of these factors has offered much to explain local variation in population numbers and community composition during periods of apparent stability (Caley *et al.*, 1996; Connell *et al.*, 1997). Today, however, coral reefs around the world are facing a scenario of steady declines in coral cover punctuated by periodic large-scale perturbations. Of these, the 1998 mass coral bleaching event was perhaps the most noteworthy (Hoegh-Guldberg, 1999; Hughes *et al.*, 2003; Wilkinson, 2004). The critical question to arise from these changes is: to what extent can coral reefs recover (*sensu* Edwards *et al.*, 2001) or regenerate (*sensu* Hughes *et al.*, 2003) after disturbance (i.e. to what extent do they exhibit resilience; Holling, 1973; Gunderson, 2000)? In particular, can coral reef ecosystems maintain the critical feedbacks, functions and processes in the face of climate change?

Correspondence: David Bellwood, School of Marine Biology, James Cook University, Townsville, Qld 4811, Australia, tel. + 61 (0)7 47814447, fax + 61 (0)7 47251570, e-mail: David.Bellwood@jcu.edu.au

Resilience and the ability to regenerate after disturbance is a central feature of coral reefs. Indeed, it is their capacity to recolonize and maintain populations in the face of disturbance that has underpinned their success in dominating exposed and high-energy locations in the tropics (Connell *et al.*, 1997). Recently, large-scale bleaching has presented coral reefs with a new challenge: rapid large-scale loss of coral cover (Wilkinson, 2004). This widespread disturbance has impacted numerous reefs, many of which were already weakened by human activities, including systematic overfishing, habitat destruction and pollution (Jackson *et al.*, 2001; Hughes *et al.*, 2003; Pandolfi *et al.*, 2003). The response of corals to bleaching has been highly variable, with many species showing limited evidence of short-term recovery (Loya *et al.*, 2001; Baird & Marshall, 2002; Hughes *et al.*, 2003; Donner *et al.*, 2005). Thus, from a coral perspective the evidence, to date, suggests that corals show limited short-term resilience to elevated sea surface temperatures.

In marked contrast, it appears that reef fishes are relatively resilient to disturbance, with reef fish assemblages exhibiting only a limited response to the loss of corals through large-scale crown of thorns starfish outbreaks (Williams, 1986; Hart *et al.*, 1996; Sano, 2000) and coral bleaching (Kokita & Nakazono, 2001; Booth &

Beretta, 2002). In most cases the changes are restricted to changes in a few strongly coral-associated fishes (Williams, 1986; Kokita & Nakazono, 2001; Munday, 2004; Pratchett *et al.*, 2004). The only studies to document long-term impacts on fish communities were related to a gradual decline in reef condition through a combination of bleaching, crown of thorns outbreaks and increased terrestrial runoff (Jones *et al.*, 2004; Munday, 2004). Coral reef fishes would thus appear to be relatively resilient, in ecosystem terms, to short-term perturbations. It would appear that reef fishes are able to maintain ecosystem processes; the implicit assumption being that no change in the community composition is a reasonable indication that ecosystem processes are intact.

Resilience is often difficult to measure, and the extent to which systems exhibit resilience is often a reflection of the metrics used to evaluate ecosystem 'health' and the status of populations (Gunderson, 2000). Central to this issue is the potential for a cryptic loss of resilience (i.e. changes in the ability of a system to maintain ecosystem processes which are not apparent using existing monitoring metrics; Bellwood *et al.*, 2004). Such cryptic loss of resilience may lay the foundations for some of the 'ecological surprises' that beset ecosystem management and are characterized by phase shifts or ecosystem flips (Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003). Coral reefs are no exception. Although coral reefs are highly dynamic systems with a great capacity for regeneration (Connell *et al.*, 1997), there is increasing evidence of reefs undergoing phase shifts from coral-dominated to other alternate states (Nystrom & Folke, 2001; Aronson *et al.*, 2002; Bellwood *et al.*, 2004; McManus & Polsenberg, 2004). One critical component in identifying these phase or regime shifts is the ability to separate short-term changes from long-term trends. This is often difficult, as relatively few long-term ecological data sets are available for reef systems (although Connell *et al.*, 1997, 2004; Aronson *et al.*, 2002; Halford *et al.*, 2004 provide notable exceptions; cf. Pandolfi, 1999). The present study, therefore, takes advantage of a 12-year census of small benthic reef fishes, using a method that accurately quantifies entire cryptobenthic reef fish assemblages, in one of the world's best protected coral reef ecosystems. Annual censuses from 1993 to 2004 broadly span the 1998 mass coral bleaching event. In this event approximately 75% of the corals in the study location died, with the local extirpation of some abundant habitat forming taxa (Marshall & Baird 2000; D. R. Bellwood, personal observation). This fish assemblage is particularly suited to the detection of changes in response to disturbance. With maximum longevities spanning from several weeks to just over 1 year (Wilson, 2004; Depczynski & Bellwood, 2005,

2007; Hernaman & Munday, 2005), this is a highly dynamic fish community in close association with the benthos. As such, it presents a model for investigating community-level responses to disturbance. This study, therefore, quantifies long-term changes in the community composition of a cryptobenthic reef fish assemblage in response to the 1998 bleaching event and evaluates the resilience of this assemblage to habitat change as a result of global warming.

Material and methods

Censuses have been undertaken annually from 1993 to 2004 on the leeward reef slope of Orpheus Island (18°35′S, 146°28′E), in the central Great Barrier Reef. Each year 2–4 coral bommies of approximately $2\,m^3$ were censused using an enclosed ichthyocide technique (Ackerman & Bellwood, 2000). The number of replicates per year was constrained by permit requirements as the censuses were in a highly protected area within a World Heritage Site. Censuses were undertaken in the same reef slope habitat (but not from the same coral bommies) at approximately the same time of year (in late March to early April; September in 1993–1995). The last 10 years samples were all within the same 3-week period during the Austral cool season, several months after the summer peak recruitment period. The 1998 censuses were immediately after the December 1997–February 1998 bleaching event and included fishes living in or on bleached corals. By 1999 most bleached *Acropora* spp. and almost all *Montipora* spp. corals had died (Marshall & Baird, 2000; Baird & Marshall, 2002), although their skeletons remained intact. In each census a small coral bommie was enclosed in a 2 mm mesh net of $3.5\,m^2$ basal area before adding an ichthyocide (rotenone or high-dose clove oil). Coral bommies were selected to be as similar as possible each year with 'typical' fish assemblages and coral cover (evaluated in Ackerman & Bellwood, 2000). Each bommie is a large isolated piece of consolidated reef matrix with a number of relatively small coral colonies growing on it; in postbleach years these corals were in place but dead. The ichthyocides are nonselective and provide a relatively complete census of all species within the netted area (methodological details are provided in Ackerman & Bellwood, 2000, 2002). Fishes in the netted area were collected during an intensive search by 5–9 divers (approximately one diver-hour per m^2). All specimens were placed in an ice-seawater slurry and transferred to the laboratory for identification and fixation. Larger mobile reef fishes are not sampled using this methodology and are not included in the analyses. In all years, the overwhelming majority of specimens were of adult size (cf. Ackerman & Bellwood, 2000; Ackerman *et al.*,

2004). A total of 35, 3.5 m^2 ichthyocide stations were examined, yielding a total of 3682 individuals in 145 species.

Changes to the cryptobenthic reef fish community over the 12 years were evaluated using four different metrics: species richness, species diversity (Shannon–Weiner diversity index, H'), total abundance and community composition. The first three are commonly utilized methods for evaluating changes in reef assemblages following disturbance (e.g. Sano, 2000; Halford et al., 2004; Jones et al., 2004). Total abundance, species richness and species diversity were compared among years using three one–way ANOVA's. Total abundance was log$_{10}$ transformed to meet the assumptions of normality and homoscedasticity. Following a significant result, nonsignificant groupings were identified using Tukey's HSD tests. Long-term trends within the data were examined using least-squares regression of the untransformed annual means. All analyses were undertaken using SPSS (v. 12.0).

Changes in community composition were investigated using a principal components analysis (PCA) of the mean number of individuals per sample (i.e. per 3.5 m^2); mean values are based on the 2–4 samples per year. We examined only those species with more than 10 individuals over the 12-year period (i.e. we examined the 36 most abundant species; mean abundance = 92.4 ± 42.2 SE individuals). In three cases, closely related species were grouped as spp. as species separation was uncertain. The analyses were based on the covariance matrix of log$_{10}(x + 1)$ transformed data. An ordination technique (PCA) was selected as it made no a priori assumptions about group membership (e.g. pre- or post-1998). A Ward's method cluster analysis was performed on the squared Euclidian distances of the log abundance data to provide an objective description of yearly groupings. A multivariate analysis of variance (MANOVA) was performed on the abundance data to examine the significance of the major groupings identified by the Ward's cluster analysis. Data were log$_{10}$ transformed before analyses to help fit multivariate normality and homoscedasticity. To confirm statistical differences between the two major groups, an analysis of similarities (ANOSIM) was undertaken using Primer 5.22 (Clarke & Warwick, 1994), using a one-way design with the maximum number of permutations (792).

Results

The community composition exhibited a major shift during the 12-year study period (Fig. 1). The PCA revealed two distinct clusters, the first contains prebleached (1993–1997), bleaching (1998) and immediate
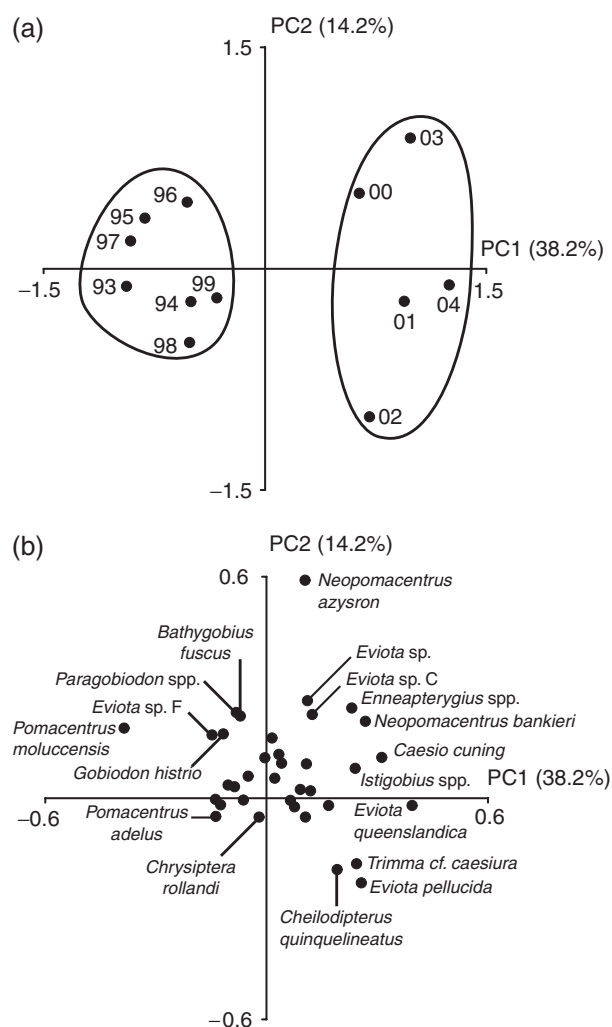

Fig. 1 A shift in the structure of reef fish communities on the Great Barrier Reef in response to the 1998 global coral bleaching episode. (a) A principal component analysis (PCA) reveals two clusters. One encompasses the prebleaching (1993–1997), bleaching (1998) and immediately postbleaching (1999) years; the other encompasses the postbleaching years (2000–2004). (b) Species loadings on the above PCA showing the species that contributed to the observed shift in community structure.

postbleach (1999) samples. The second cluster encompasses the long-term postbleach communities (2000–2004). The first two axes of the PCA explained 52% of the variation among species, a relatively high value given that 36 species were included in the analyses, with PC1 (explaining 38% of the variation) clearly separating the two distinct groups of years. The Ward's cluster analysis strongly supported this division into two clusters (Fig. 2). PC1 is most clearly characterized by a shift from coral associated species (with low scores), such as Pomacentrus moluccensis and Gobiodon histrio (which decreased in abundance by 83% and 67%, respectively) to less habitat specific forms such as Eviota
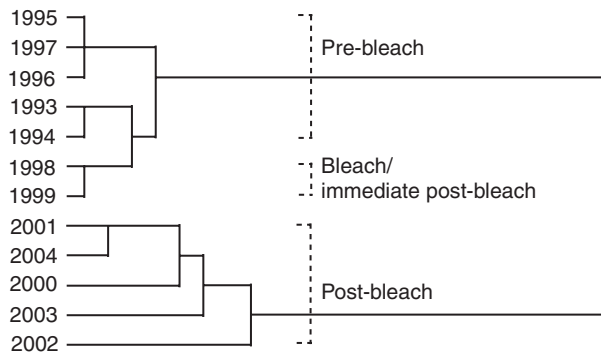
Fig. 2 A Ward's hierarchical cluster analysis reveals two distinct groups in the community composition of cryptobenthic fishes. One encompasses the 5 years prebleaching (1993–1997), and the 2 years immediately postbleaching (1998–1999) years, the other encompasses the 5 years postbleaching (2000–2004).

queenslandica and *Neopomacentrus bankieri* (increasing by 240% and 138%, respectively) (cf. Allen, 1991; Depczynski & Bellwood, 2005). However, a broad range of non-coral associated species also appear to be involved. PC2 (explaining 14% of the variation) is largely driven by variation in the composition of the postbleach assemblages, particularly in the relative abundance of the schooling planktivore *Neopomacentrus azysron*. The MANOVA revealed complete separation of the two groups of years ($F_{10,1} = 802.7$; $P = 0.027$). The ANOSIM, likewise, rejected the null hypothesis of no difference between the two groups (prebleach and postbleach) with a significance level of 0.3% (i.e. <0.01). The sample statistic (global R) was 0.716.

In marked contrast to the clear shift in community composition, analyses of the three traditional variables for monitoring reef fishes (total abundance, species richness, and diversity) exhibited limited variation over the study period and no evidence of a change in relation to the 1998 bleaching event (Fig. 3). Although all three metrics exhibit a statistically significant difference among years (abundance $F_{11,23} = 2.74$, $P = 0.02$; species richness $F_{11,23} = 6.36$, $P < 0.001$; diversity $F_{11,23} = 4.57$, $P < 0.01$), and all contain 2–4 distinct groups based on Tukey's HSD tests, none of the groups lie on either side of the 1998 bleaching event. Indeed, all groups include at least 2 years on either side of the 1998 event. In terms of long-term trends only abundance had a significant trend, marked by increasing abundance over the study period ($r^2 = 0.67$, $P = 0.001$). The other two parameters exhibited no significant trend (species richness $r^2 = 4.9 \times 10^{-7}$, $P = 0.998$; diversity $r^2 = 0.33$, $P = 0.052$). Changes in the abundance of individual species after the 1998 bleaching event reveal a marked difference between increases in generalist omnivorous species, and the planktivore *N. bankieri*, and decreases in coral-dependent species (Fig. 4).
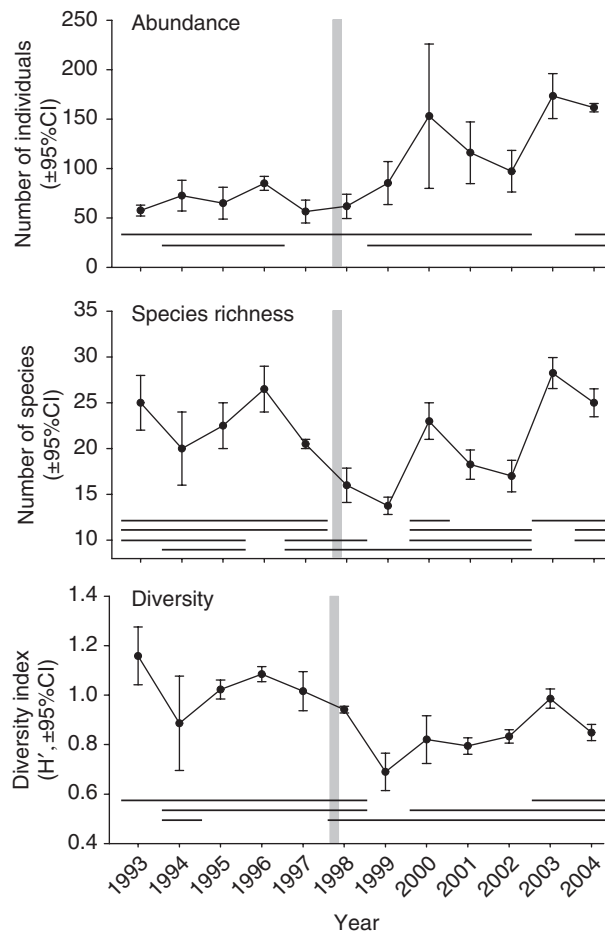

Fig. 3 Conventional measures of the status of coral reef fish assemblages. Abundance, richness and diversity are expressed in terms of the mean number or diversity of fishes within replicate fish censuses. The vertical shaded bar indicates the timing and duration of the global coral bleaching event which killed approximately 75% of the corals in the study area. The horizontal lines indicate years that were not significantly different in Tukey's HSD tests.

Discussion

There have been several reports of resilience or a limited response of reef fishes to large-scale coral loss through storms (Halford *et al.*, 2004), crown of thorns starfish outbreaks (Williams, 1986; Hart *et al.*, 1996; Sano, 2001) and bleaching (Kokita & Nakazono, 2001; Booth & Beretta, 2002). Our results also show a limited response to coral bleaching using traditional metrics. However, changes in community composition reveal an unexpected vulnerability of reef fish communities to coral bleaching. These results present a fundamentally different perspective, which highlights the need for caution when selecting metrics to evaluate the resilience of coral reef ecosystems.
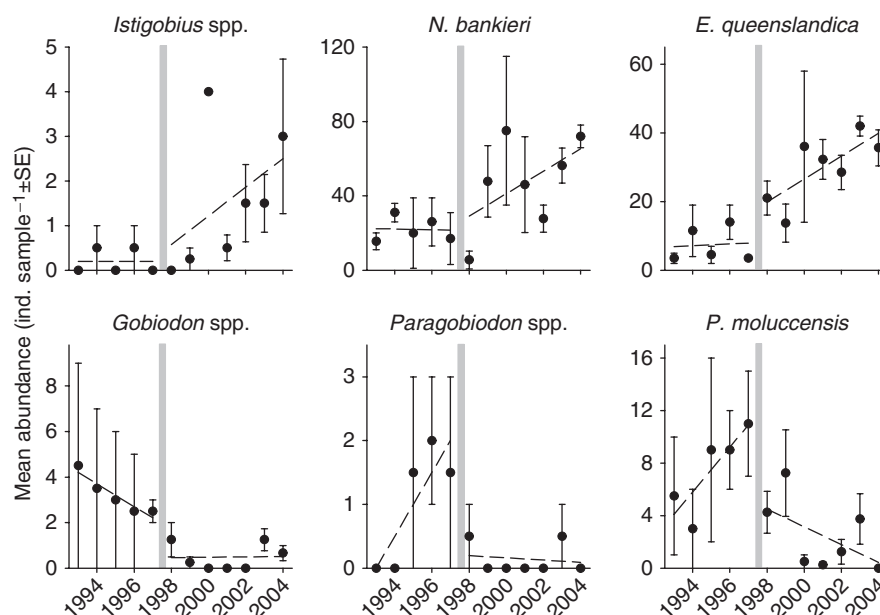
Fig. 4 Changes in the abundance of six cryptobenthic fish species in relation to the 1998 coral bleaching event (marked by the vertical grey line). The data contrast increases in three generalist species (the planktivore *Neopomacentrus bankieri* and the omnivorous/detritivorous *Istigobius* spp. and *Eviota queenslandica*) and decreases in three coral-associated species (*Pomacentrus moluccensis*, *Gobiodon* spp. and *Paragobiodon* spp.).

In contrast to the only other long-term studies (Jones et al., 2004; Munday, 2004), we found no decrease in diversity, richness or abundance in reef fishes over the 12-year study period. Indeed, as in most previous studies, the three main metrics, species richness, diversity (H′) and total abundance showed no response to a major disturbance (in this case the 1998 coral bleaching event). At face value this could be taken as strong evidence for resilience – the reef fish fauna remained intact in the face of what was arguably the greatest impact on global coral reefs in living memory. This single event resulted in extensive bleaching, with approximately 40% of the world's reefs exhibiting serious damage. This damage contributed significantly to the widespread decline in coral cover on reefs in all tropical oceans (Wilkinson, 2004; Agardy et al., 2005). Our study site suffered an estimated 75% mortality in *Acropora* species and almost total loss of the dominant structure providing species *Montipora* (Marshall & Baird, 2000), yet, the reef fishes appeared to fare well. Indeed, in terms of overall abundance, fish numbers in the study area have almost doubled since the 1998 bleaching event. In terms of reef processes, one may thus assume that little has changed and that the critical controlling functions and processes provided by fishes remain intact.

This apparent stasis or resilience is misleading: There were marked changes in community structure. The traditional metrics did not detect a major, yet cryptic, change in community composition, which marked a distinct and relatively stable shift from a prebleaching to a postbleaching reef fish assemblage. Our findings emphasize the need for caution when evaluating the resilience of reef ecosystems, and highlight the potential insensitivity of common metrics used for measuring responses of fishes to bleaching.

By looking at small species with high turnover rates, and using annual censuses over 12 years, we are able to distinguish responses to bleaching from a background pattern of interannual variation. Furthermore, our observations avoid the storage effects of long-lived species where recruitment failure and declines may be masked by the presence of long-lived individuals. Many of the conspicuous reef fishes that are included in fish censuses live for one to two decades (Choat & Axe, 1996; Choat et al., 1996). The resilience reported in previous studies (e.g. Williams, 1986; Hart et al., 1996; Sano, 2000; Kokita & Nakazono, 2001; Booth & Beretta, 2002; Halford et al., 2004) may, at least in part, reflect the ability of adults of long-lived species to withstand disturbance (by movement among habitats, using stored reserves or prey switching, Pratchett et al., 2004). In contrast, most of the species in the community that we examined had maximum longevities of less than 1 year (Depczynski & Bellwood, 2005, 2007; Hernaman & Munday, 2005). This means that these species reveal the effects of bleaching on the entire life history including settlement, recruitment, juvenile and adult survival. Previously, our ability to detect changes in reef

systems may have been compromised by both limitations in the methods and the speed with which changes are likely to be manifest. If species with a maximum longevity of a few months take 3 years to reorganize into a relatively stable postbleach community, comparable reorganization in larger taxa with longevities of 5–20 years may take several decades. Indeed, if coral bleaching is manifested in coral reef fishes through a disruption of recruitment patterns then the full impact of the 1998 bleaching event may have not even begun to appear in censuses of long-lived species.

This raises the question of whether the observed shift in cryptobenthic community structure represents a stable state or merely an alternate or even transitional state. The postbleaching community is quite distinct and after 5 years and up to 35 generations later the assemblage has shown little signs of returning to anything resembling the prebleached condition. If the frequency and intensity of thermal anomalies and bleaching continues the prebleach community may never return (cf. Donner *et al.*, 2005). However, the apparent stability of the postbleach assemblage does not necessarily indicate a stable state. It is certainly plausible that with a return of significant coral cover the fish community will change again; the current community may thus represent a transitional state. Nevertheless, the nature of the shift in community composition suggests that the time frame for regeneration is likely to be decades rather than years and that there remains a strong possibility that the path to regeneration will exhibit significant hysteresis (cf. Hughes *et al.*, 2005).

The timing and nature of the observed changes in fish community structure strongly suggest that it was a direct result of the 1998 bleaching event, even though the shift was marked by changes to a wide range of fish taxa. Coral associated species were still living in bleached corals in 1998 and in small remnants in 1999, but they largely disappeared thereafter. The loss of coral remnants was probably exacerbated by changes in density-dependent coral mortality rates as a result of excessive predation by the remaining fish coralivores (up to eight *Labrichthys unilineatus* were observed feeding on a single isolated *Acropora* colony). What was most striking, apart from a decrease in species with no known association with corals, (e.g. *Eviota* sp. F (from 1.3 ± 0.1 to 0.4 ± 0.1 fish per sample $\pm$ SE) and *Pomacentrus adelus* (1.6 ± 0.5 to 0.6 ± 0.2 fish per sample $\pm$ SE)), was the marked increase in abundance in number of common, habitat and trophic generalist species (e.g. *Istigobius* spp. and *E. queenslandica* (Fig. 4); Depczynski & Bellwood, 2003, 2004). This is particularly striking as coral represents only a small, but apparently important, component of the benthic fauna (throughout the period mean live coral cover on GBR reefs was in the region of 20–30%; Bellwood *et al.*, 2004).

The proximate basis for the changes is uncertain although loss of habitat, if not structure, certainly played a role (soft coral colonies were rapidly lost leaving only solid rounded bases, many hard coral skeletons are still intact). Live coral (hard and soft) was lost with the inevitable loss of habitat for coral dwelling or feeding specialists (cf. Munday, 2004). Changes in the abundance of coral-associated fishes with decreasing coral cover has been recorded in a number of studies (e.g. Booth & Beretta, 2002; Jones *et al.*, 2004). Furthermore, the presence of living coral tissue may be a critical factor in shaping patterns of recruitment or early postsettlement survivorship (Beukers & Jones, 1997; Ohman *et al.*, 1998; Holbrook *et al.*, 2000; McCormick & Hoey, 2006). The stable or gradually increasing fish abundance combined with a shift in community composition as documented the current study contrasts markedly with the only other long-term study in Papua New Guinea (PNG) (Jones *et al.*, 2004) which reported a gradual decline in fish abundance over an 8-year period (changes in community composition in PNG are likely but were not analyzed). This disparity between the two studies appears to mark a fundamental difference in the disturbance regimes. Our observations mark a distinct shift, primarily in species composition, in response to a single massive bleaching event. Subsequent bleaching events had negligible impact, as susceptible corals were absent; there were no noticeable changes in other parameters over the 12-year period. In contrast, the reefs examined in PNG were marked by ongoing bleaching events, crown-of-thorns outbreaks and concurrent increases in terrestrial runoff. The latter factor may be particularly important, as it could account for the decline in noncoral species in PNG, reflecting the impacts of terrestrial runoff on benthic dynamics including algal and detrital resources.

Finally, one must ask the question of what these changes mean for ecosystem function, and the resilience of reefs to further change. Although our knowledge of the ecology of the component taxa is limited, the shift in the fish community structure appears to reflect a distinct move from habitat and/or diet specialists to habitat or dietary generalists (cf. Depczynski & Bellwood, 2003, 2004). Prebleaching communities were characterized by the presence of several coral dwelling or associated species (*P. moluccensis*, *Gobiodon* spp., *Paragobiodon* spp.; cf. Munday *et al.*, 1997) and included *Amblygobius rainfordi*, the only herbivore in this cryptobenthic community. The density of detritivorous blennies (Wilson *et al.*, 2003) changed little over the sample period. The loss of several coral dwelling specialists reduces the potential for positive synergism between reef corals and commensal fishes (Pratchett, 2001). Postbleaching communities were dominated by the

highly abundant habitat generalist and planktivore *N. bankieri* and the benthic omnivores/detritivores *Istigobius* spp. and *E. queenslandica*. The latter is marked by having one of the broadest dietary ranges in the assemblage (Depczynski & Bellwood, 2003). The change in community structure does indeed appear to represent a phase shift in that fish-mediated ecosystem processes have probably been modified. This is not simply a case of functional redundancy, responding to change by replacing one species with a functional equivalent; there is clear evidence of trophic simplification.

This phase shift reveals the limited resilience of the prebleach community to coral bleaching. Resilience would have been characterized by either no change in the community composition (resistance) or regeneration and the return to a community with similar ecological characteristics (in terms of ecosystem processes) to those exhibited by the prebleach community. However, the community composition and ecosystem processes both appeared to change as a result of the 1998 coral-bleaching event. This shift also marked the beginning of a new and potentially more resilient postbleach assemblage. The postbleach assemblage is characterized by many generalist species (cf. Bellwood *et al.*, 2005), and as such, may be capable of withstanding future bleaching events with little further change. We may, thus, be faced with an undesirable yet resilient state: a pernicious postbleach fish assemblage.

It is sobering to note that this is the first record of a clear shift in a GBR reef fish community in response to the 1998 bleaching event and that has only been revealed by examination of exceptionally short-lived species. Furthermore, the study location lies within one of the best protected areas of the Great Barrier Reef Marine Park, with a relatively intact large fish fauna (Graham *et al.*, 2003), yet, this phase shift has persisted for over 5 years, representing 5–35 generations of these cryptobenthic fishes. The implications of global warming for coral reefs are poorly understood. However, our observations provide a clear example of the exceptional sensitivity of coral reefs to environmental change and highlight the difficulty of measuring the resilience of coral reef ecosystems. The need for sensitive metrics for evaluating resilience is of paramount importance and presents an ongoing challenge in coral reef management.

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