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REPORT

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Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea

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Abstract Disturbances have a critical effect on the structure of natural communities. In this study long-term changes were examined in the reef community at Tiahura Reef, on the northern coast of Moorea, which had been subject to many and varied disturbances over the last 25 years. Tiahura Reef was subject to an outbreak of crown-of-thorns starfish (*Acanthaster planci*) in 1980–1981, causing significant declines in the abundance of scleractinian corals and butterflyfishes. By 2003, the abundance of corals and butterflyfishes had returned to former levels, but despite this apparent recovery, the species composition of coral communities and butterflyfish assemblages was very different from those recorded in 1979. Ongoing disturbances (including further outbreaks of crown-of-thorns starfish, cyclones, and coral bleaching events) appear to have prevented recovery of many important coral species (notably, *Acropora* spp.), which has had subsequent effects on the community structure of coral-feeding butterflyfishes. This study shows that recurrent disturbances may have persistent effects on the structure and dynamics of natural communities.

Keywords Community structure · Alternate stable states · Chaetodontidae · Scleractinia · Coral reefs · Corallivore

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Introduction

Disturbances occur frequently during the lifespan of most organisms and are a significant factor determining community structure (reviewed by Sousa 1984; Pickett and White 1986; Petraitis et al. 1989). In general, communities appear to be fairly resilient to small-scale or moderate disturbances, readily returning to their pre-disturbance structure (Connell and Sousa 1983). Such disturbances generate significant spatial and temporal heterogeneity in the structure and dynamics of natural communities (Pickett and White 1986) but rarely have long-lasting effects on community structure. Large-scale or severe disturbances, or the combined effects of multiple disturbances, however, may lead to permanent or long-term shifts in community structure (Scheffer et al. 2001). Permanent shifts in community structure (often referred to as "phase shifts") tend to be associated with environmental degradation, whereby communities exhibit characteristic shifts in the dominance of species with different life-histories. The sequence of degradation is often fairly uniform within certain ecosystems (e.g. Bellwood et al. 2004) such that previously distinct communities may show considerable convergence when subject to high levels of disturbance (Aronson et al. 2004).

Coral reef ecosystems are frequently subject to severe and large-scale disturbances (reviewed in Karlson and Hurd 1993) and appear very susceptible to phase shifts (Bellwood et al. 2004). In coral reef environments, phase shifts tend to be characterised by a transition from hard coral dominance to algal dominance of reef substrates (e.g. Hughes 1994). Such shifts can occur very quickly, sparked by a single disturbance event (e.g. mass-bleaching, Ostrander et al. 2000), though the lack of resilience in such systems is often attributed to a prior history of recurrent disturbances and anthropogenic influences (Nyström et al. 2000; Bellwood et al. 2004). For example, in the absence of anthropogenic interference, coral communities appear fairly resilient to acute "natural" disturbances (Connell 1997; Halford et al. 2004).

Phase shifts in the structure of benthic reef habitats have significant effects on a wide range of taxa, especially coral reef fishes (Halford et al. 2004). The structure of reef habitats plays a strong modifying role in the structure of fish communities, and thus fish communities may be very resilient if and when reef habitats return to predisturbance states (Sano et al. 1987; Halford et al. 2004). Among those fishes most closely related to the structure of the reef habitat are the butterflyfishes (family Chaetodontidae), many of which rely solely on the living tissue of scleractinian corals for food (Harmelin-Vivien and Bouchon-Navaro 1983). Declines in the abundance of butterflyfishes often follow extensive coral mortality (Sano et al. 1987; Halford et al. 2004). As certain butterflyfishes exhibit very specific feeding preferences (Berumen et al. 2005), disturbances that disproportionately affect certain coral species may significantly alter the species composition of butterflyfish communities (Shibuno et al. 1999). Long-term alterations in the coral community could thus lead to a significant change in the structure of the butterflyfish communities.

The purpose of this study was to explore long-term changes (over 25 years) in coral communities and butterflyfish assemblages at Tiahura Reef, Moorea, and assess resilience of these interrelated communities following multiple disturbance events. Tiahura Reef has been subject to many acute disturbance events over the last 25 years, the most significant of which was a major outbreak of crown-of-thorns starfish (*Acanthaster planci*) in 1980–1981 that reduced live coral cover by 61%, and indirectly caused significant declines in the abundance of coral-feeding butterflyfishes (Bouchon 1985; Bouchon-Navaro et al. 1985). The current study documents the structure of coral communities and butterflyfish assemblages at Tiahura Reef in 2003, more than 20 years after the first documented disturbance at Tiahura Reef. Live coral cover and total abundance of butterflyfish was found to have returned to similar levels recorded prior to the disturbance. There were, however, notable differences in the species composition of coral communities and butterflyfish assemblages compared to those recorded in 1979. This apparent change in coral communities and butterflyfish assemblages is attributed to persistent disturbance in the aftermath of the initial outbreak of crown-of-thorns starfish, including additional outbreaks of crown-of-thorns starfish, cyclones, and bleaching events, which greatly modified the structure of coral communities at Tiahura Reef.

Materials and methods

This study was conducted at Tiahura Reef (17°30′S, 149°50′W), on the northern coast of Moorea, in the Society Islands (see map in Galzin and Pointier 1985). Sampling was conducted in four distinct reef zones at Tiahura Reef: (1) the lagoonal reef flat (1.5–2 m depth) on the shoreward side of the barrier reef, (2) the exposed reef crest (3 m depth) along the seaward margin of the shallow reef platform, (3) the reef slope (8–10 m depth) along a gently sloping continuous section of reef matrix, and (4) the reef base (18–20 m depth) where the continuous reef matrix is replaced by a spur-and-groove system. The position of these four zones corresponds with 4 of the 12 zones sampled by Bouchon (1985) and Bouchon-Navaro et al. (1985).

Total live coral cover and species composition of scleractinian corals were quantified using replicate 10-m line-intercept transects, recording the species and intercept length (in centimetre) of all corals underlying the line transect. Five replicate transects were sampled in each zone, giving a total of 20 transects. Densities of butterflyfishes were measured using five replicate 50 m × 4 m visual belt transects in each of the four zones at Tiahura reef. The species and number of adult individuals [>5 cm total length (TL)] was recorded on each transect. For both coral and fish surveys, the total area sampled was the same as that in Bouchon (1985) and Bouchon-Navaro et al. (1985), although sampling of fish densities was achieved with five replicates while Bouchon-Navaro et al. (1985) measured fish density with a single transect in each zone. *Chaetodon lunulatus* was previously known as *C. trifasciatus*, including in Bouchon-Navaro et al. (1985). We are not aware of any other changes in taxonomy of fishes or corals that would impact the comparability of these data sets.

Variation in the composition of both coral and butterflyfish communities was analysed using multivariate analyses of variance (MANOVA) (sensu Syms and Jones 2001). Univariate homogeneity was tested using Cochran's test and residual plots were examined to confirm MANOVA assumptions of multivariate homogeneity and normality. Pillai's Trace statistic was used to determine the significance of MANOVA results, following Olsen (1976). Canonical discriminant analysis (CDA) was then used to display variation in the structure of coral and butterflyfish communities among years (sensu Syms and Jones 2001). In the analysis of coral communities, coral data were pooled in five categories (Table 1) to enable direct comparisons with Bouchon (1985). In the analysis of butterflyfish communities, we used only the 15 most abundant species; *Chaetodon bennetti*, *Heniochus monoceros*, and *Hemitaurichthys polylepis* were not included in community analysis because they were each recorded in only one of 3 years surveyed (Table 1).

Results

In 2003, mean coral cover was 37.6% at Tiahura Reef, which was slightly higher than was recorded in 1979, just prior to the 1981 outbreak of *A. planci* (Fig. 1). Coral cover declined by 62.1% during this outbreak of *A. planci* from 37.4% in 1979 to 14.5% in 1982 (Table 1). Moreover, *A. planci* had a disproportionate impact on the most abundant coral genus, *Acropora*. In 1979, *Acropora*

Table 1 Butterflyfish and coral abundances from four zones at Tiahura Reef, Moorea

Species	Zone 1			Zone 2			Zone 3			Zone 4			Total (all zones)		
	1979	1982	2003	1979	1982	2003	1979	1982	2003	1979	1982	2003	1979	1982	2003
No. of individuals per 200 m^2															
Chaetodon auriga (NC)	0.5	0.2	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.1	0.0	0.0	0.25	0.05	0.00
Chaetodon bennetti (OC)	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.03	0.00	0.00
Chaetodon citrinellus (FC)	3.8	2.0	5.4	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	1.05	0.50	1.45
Chaetodon ephippium (NC)	0.1	0.0	0.0	0.0	0.4	0.4	0.2	0.0	0.0	0.2	0.2	0.2	0.13	0.15	0.15
Chaetodon lunula (FC)	1.3	0.0	0.0	0.2	0.4	0.0	0.5	0.0	0.0	0.4	0.4	0.0	0.60	0.20	0.00
Chaetodon lunulatus (OC)	1.3	1.2	0.8	0.0	0.0	0.0	0.7	1.0	0.0	0.4	0.4	0.0	0.60	0.65	0.20
Chaetodon ornatissimus (OC)	0.9	0.0	1.6	1.1	0.4	2.6	1.3	0.0	0.2	1.0	0.0	0.0	1.08	0.10	1.10
Chaetodon pelewensis (OC)	0.0	0.0	0.0	0.0	0.0	0.8	3.8	1.2	9.8	3.9	1.6	5.8	1.93	0.70	4.10
Chaetodon quadrimaculatus (OC)	0.0	0.0	0.0	1.5	0.6	5.0	0.5	0.2	0.4	0.0	0.0	0.0	0.50	0.20	1.35
Chaetodon reticulatus (OC)	1.7	0.8	1.0	0.8	0.8	1.8	8.0	1.4	5.4	1.3	1.0	4.8	2.95	1.00	3.25
Chaetodon trifascialis (OC)	3.6	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.4	0.95	0.00	0.10
Chaetodon ulietensis (SC)	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.2	0.0	0.4	0.4	0.6	0.33	0.15	0.15
Chaetodon unimaculatus (SC)	0.7	0.0	0.8	0.6	0.8	1.0	0.4	0.4	0.8	0.1	0.4	0.0	0.45	0.40	0.65
Chaetodon vagabundus (NC)	0.8	0.4	0.6	0.7	0.0	0.0	0.2	0.4	0.0	0.0	0.6	0.0	0.43	0.35	0.15
Forcipiger longirostris (NC)	0.3	0.2	0.0	0.0	0.4	0.0	2.3	0.2	1.2	1.3	0.8	0.8	0.98	0.40	0.50
Heniochus chrysostomus (FC)	0.4	0.6	0.8	0.0	0.0	0.0	0.0	0.2	0.0	2.9	2.4	4.0	0.83	0.80	1.20
Heniochus monoceros (NC)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.00	0.05	0.00
Hemitaurichthys polylepis (NC)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.8	0.00	0.00	0.25
Mean butterflyfish/200 m^2	15.4	5.4	11.0	5.6	3.8	12.0	19.2	5.2	18.0	12.0	8.4	17.4	13.1	5.7	14.6
Percent cover															
Acropora spp.	16.7	0.0	5.8	3.0	3.5	0.8	18.4	2.6	10.4	1.3	0.1	9.7	9.9	1.6	6.7
Pocillopora spp.	3.0	0.0	15.4	7.8	3.8	16.5	9.5	4.1	15.1	0.8	2.3	5.2	5.3	2.5	13.0
Montipora spp.	4.7	0.1	1.2	3.7	5.1	3.0	0.4	0.7	5.2	0.8	0.2	5.7	2.4	1.5	3.8
Porites spp.	21.1	21.4	24.2	0.6	0.3	1.0	3.2	1.1	7.5	12.1	2.3	6.0	9.2	6.3	9.7
Other genera	2.6	0.4	0.0	2.3	1.8	0.0	14.2	3.5	6.4	23.1	4.5	11.0	10.5	2.6	4.4
Mean coral cover	48.2	22.0	46.6	17.4	14.4	21.3	45.7	12.1	44.7	38.1	9.4	37.7	37.4	14.5	37.6

Butterflyfish abundances reflect the mean number of individuals counted along belt transects. Coral abundances reflect the mean percent cover on line-intercept transects. Zone 1 = reef flat (1.5–2 m), zone 2 = reef crest (3 m), zone 3 = reef slope (8–10 m), zone 4 = reef base (18–20 m). Totals were pooled across all zones for each year. Data for 1979 and 1982 are from Bouchon (1985) and Bouchon-Navaro et al. (1985). Designations following species names indicate trophic category: *NC* non-corallivore, *SC* soft coral feeder/generalist, *FC* facultative corallivore, *OC* obligate corallivore

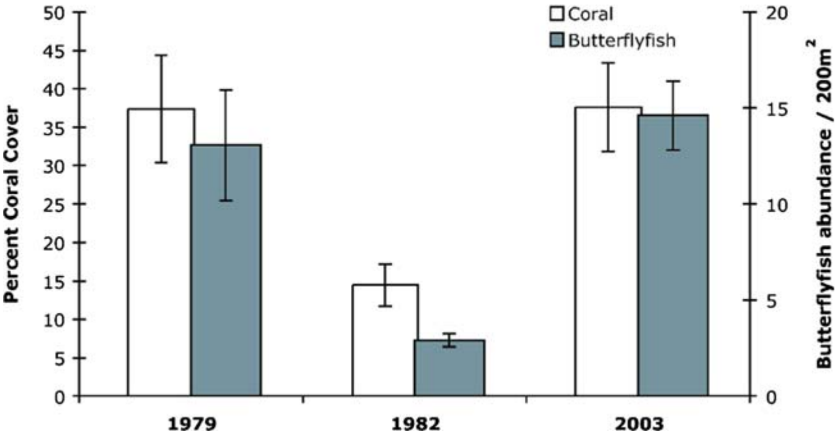

Fig. 1 Mean percent coral cover (*white bars* left axis) and abundances of butterflyfish (*shaded bars* right axis) at Tiahura Reef, Moorea, in surveys conducted in 1979, 1982, and 2003. *Error bars* indicate one standard error. Data for 1979 and 1982 are from Bouchon (1985) and Bouchon-Navaro et al. (1985)

occupied 9.9% of hard substrates at Tiahura Reef and accounted for 26.7% of coral cover. However, *Acropora* declined 79% during the 1981 outbreak of *A. planci* to a mean cover of 2.1% in 1982. Since 1982, cover of *Acropora* has increased significantly, but in 2003, cover of *Acropora* was still much lower than recorded in 1979 (Table 1). In 2003, the dominant coral genus was *Pocillopora*, which accounted for 34.6% of coral cover. The composition of coral communities varied significantly through time (MANOVA, Pillai's Trace, F = 2.46, $df = 10$, $p = 0.020$), and most importantly, the relative abundance of different coral genera at Tiahura Reef in 2003 was very different from that recorded in 1979 (Fig. 2a). Aside from changes in the dominant coral taxa (*Pocillopora* versus *Acropora*), *Montipora* was relatively more abundant in 2003 while most of the rare coral genera (including *Favia*, *Montastraea*, *Acanthastrea*, and *Astreopora*) were less abundant than in 1979.

Spatial and temporal patterns in coral abundances varied from zone to zone. On the reef flat (zone 1),

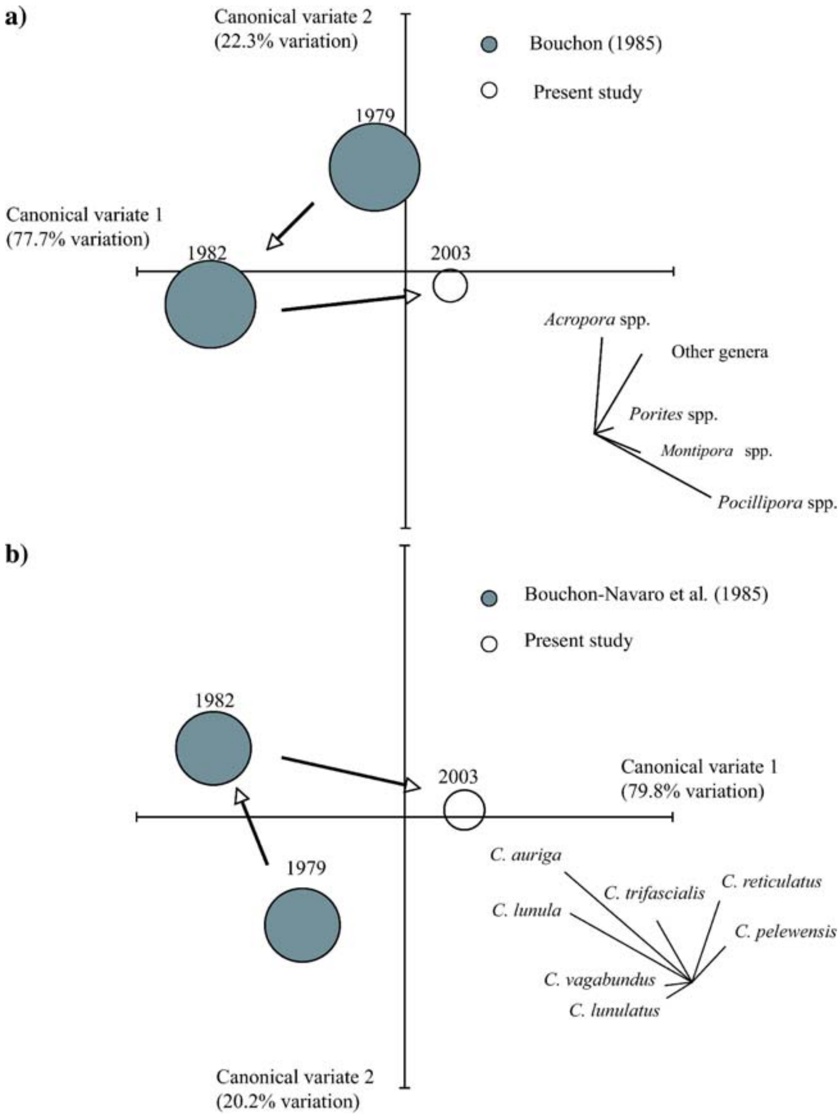

Fig. 2 Canonical discriminant analysis of temporal shifts in the structure of (**a**) coral communities (by genera groups), and (**b**) of butterflyfish communities (by species, all in the genus *Chaetodon*) at Tiahura Reef, Moorea. *Circles* plotted represent 95% confidence limits around the centroids for each genera group or species. Vectors are structural coefficients of response variables, indicating the relative abundance of each genera group or species in different years. Data for 1979 and 1982 are from Bouchon (1985) and from Bouchon-Navaro et al. (1985) (*shaded circles*)

Acropora and *Pocillopora* were both very abundant in 1979 but were completely absent in 1982 (Table 1). By 2003, cover of *Pocillopora* had increased to five times that recorded in 1979, though *Porites* was still the dominant coral in this zone. The reef crest (zone 2) was the least affected by the disturbances with only a 17% decrease in mean coral cover from 1979 to 1982. The dramatic increase in the cover of *Pocillopora* in this zone is the main cause of the overall increase in mean coral cover from 1979 to 2003. The reef slope (zone 3) showed little change in mean coral cover from 1979 to 2003, but *Pocillopora* replaced *Acropora* as the dominant coral in this zone. On the reef base (zone 4) coral assemblages are still dominated by corals in the “other” category, but cover of *Acropora* and *Pocillopora* have increased more than sixfold from 1979 to 2003.

Overall abundance of butterflyfish in 2003 (14.6 individuals per 200 m^2) was slightly higher than the abundance recorded in 1979 (Fig. 1). Butterflyfish abundance showed a sharp decline following the 1981 outbreak of *A. planci*, from an average of 13.1 individuals per 200 m^2 to less than 6 individuals per 200 m^2, but subsequently recovered (Table 1). Species most affected by the outbreak of *A. planci* were *Chaetodon trifascialis* (100% decline), *Chaetodon ornatissimus* (91% decline), *Chaetodon reticulatus* (66% decline) and *Chaetodon pelewensis* (64% decline), and only some of these species exhibited full recovery in 2003. Overall, there was significant variation in the relative abundance of different butterflyfishes among years (MANOVA, Pillai’s Trace, $F = 11.10$, $df = 24$, $p < 0.000$) and the structure of butterflyfish communities in 2003 was very different from 1979 (Fig. 2b). In 2003, the most abundant butterflyfish was *C. pelewensis*, whereas the most abundant butterflyfish in 1979 was *C. reticulatus* (Table 1). These two species were the most abundant butterflyfishes at Tiahura, and were primarily responsible for differences in community structure between 1979 and 2003 (Fig. 2b).

As with coral abundances, temporal patterns in the abundance of butterflyfishes varied from zone to zone. Butterflyfish assemblages on the reef crest (zone 2) were least affected by the 1981 outbreak of *A. planci*, while the butterflyfish assemblages on the reef base (zone 3) were most affected (Table 1). Mean abundance of butterflyfishes on the reef slope declined by 73% from 1979 to 1981, due mostly to an 82% decline in the abundance of *C. reticulatus*. On the reef flat, the abundance of butterflyfishes declined by 65% over the same period, caused by the complete disappearance of *C. trifascialis* and also a 47% decline in the abundance of *Chaetodon citrinellus*. Both *C. citrinellus* and *C. trifascialis* exhibited strong patterns of zonation, and occurred almost exclusively on the reef flat (Table 1). In 2003, however, *C. trifascialis* was only recorded on the reef base, albeit in very low numbers.

Discussion

This study has shown that both coral cover and the overall abundance of butterflyfishes at Tiahura Reef in 2003 are slightly higher than that were recorded in 1979 by Bouchon (1985) and Bouchon-Navaro et al. (1985), demonstrating significant recovery since disturbances caused by an outbreak of *A. planci* in 1981. However, despite this recovery, there has been little apparent community resilience. The abundances of some coral genera and some species of butterflyfish have increased much more than others, resulting in marked changes in community structure. Most notably, *Acropora* spp. dominated coral communities in 1979 (Bouchon 1985), but *Pocillopora* spp. are now the most abundant corals at Tiahura Reef. *Acropora* spp. were significantly affected by the 1981 outbreak of *A. planci* and have not yet returned to their original abundance. Limited recovery of *Acropora* could be due to ongoing disturbances, including episodes of coral bleaching, further outbreaks of *A. planci*, and severe tropical storms, which have affected coral communities at Tiahura Reef throughout the last 25 years (Adjeroud et al. 2002). Both *A. planci* and coral bleaching affect *Acropora* corals more than any other genera, including *Pocillopora* (e.g. Marshall and Baird 2000; Pratchett 2001). Pocilliporid corals, mostly *P. verrucosa* and *P. meandrina*, which now dominate coral communities at Tiahura reef, may also be more resistant to storm damage compared to *Acropora* corals.

As persistent disturbances affected coral assemblages, changes in prey availability were likely responsible for subsequent shifts in the community structure of butterflyfishes. Butterflyfishes most affected by the change in coral communities (e.g. *C. pelewensis*, *C. reticulatus*, and *C. trifascialis*) were all obligate corallivores, while abundances of non-coral feeding species (e.g. *Chaetodon auriga, Chaetodon ephippium*, and *Chaetodon vagabundus*) were relatively unaffected by the outbreak of *A. planci* and subsequent disturbances (see also Willams 1986; Sano et al. 1987). However, even among corallivorous butterflyfishes, there were significant differences in susceptibility to disturbance and rates of recovery, which may be related to differences in their specific diets. On the Great Barrier Reef, Pratchett (2005) showed that corallivorous butterflyfishes tend to specialise on either *Acropora* or *Pocillopora* corals, and these differences in dietary composition may influence their susceptibility to disturbance (Pratchett 2002). In French Polynesia, *C. pelewensis* appears to feed preferentially on *Pocillopora* spp., while *C. reticulatus* feeds mostly on *Acropora* (M.L. Berumen and M.S. Pratchett, unpublished data). Spatial and temporal patterns in the abundance of *C. pelewensis* and *C. reticulatus* at Tiahura Reef support these differences in their prey preferences, and differences in the availability of preferred prey may account for the changes in their relative abundance through time (see Pratchett et al. 2004; Berumen et al. 2005). On the reef slope and reef base (zones 3 and 4), temporal patterns in the abundance of *C. pelewensis* and *C. reticulatus* closely match changes in the abundance of *Pocillopora* spp. and *Acropora* spp., respectively.

The abundance of *Porites* spp. was not as greatly affected by the disturbances, especially in the reef flat (Zone 1), where it is most common. *Porites* spp. are known to be a non-preferred food of *A. planci* (De'ath and Moran 1998) and are also somewhat resistant to storm damage (Done and Potts 1992). Few butterflyfish consume or prefer *Porites* spp. (Pratchett 2005) and it is therefore unlikely that these corals influence butterflyfish communities as much as *Acropora* spp. and *Pocillipora* spp. Likewise, non-corallivorous butterflyfishes, such as *C. auriga*, *C. ephippium*, *C. vagabundus*, and *Forcipiger longirostris* (Allen et al. 1998; Pratchett 2005), did not follow trends of coral abundances. Other species may be examined in the context of what is known of their feeding behaviours (compiled from Allen et al. 1998; Kuiter 2002; Pratchett 2005, summarised in Table 1). *Chaetodon ulietensis* and *Chaetodon unimaculatus* are generally classified as soft-coral feeders, occasionally consuming hard corals and frequently consuming non-coral prey. *C. ulietensis* does not track the pattern of change in coral abundance, which may be predicted for a fish with no obligate dependence on coral as a food source. *C. unimaculatus*, however, shows an interesting trend of a slight decline followed by an increase in abundance to a level exceeding its 1979 abundance. Although Allen et al. (1998) and Pratchett (2005) both categorise this species as a generalist feeder (non-obligate coral feeder), Cox (1994) found *C. unimaculatus* to specialise on corals in the genus *Montipora* in Hawaii. Based on the change in abundance we observed, we would suggest that *C. unimaculatus* might be likewise reliant on *Montipora* spp. for at least some component of its diet at Tiahura reef as the abundance patterns track each other closely. Facultative corallivores also may consume corals but are generally considered not to have an obligate reliance on them for food. *Heniochus chrysostomus* and *C. lunula* show changes in abundance that do not follow patterns of change in coral communities, similar to what was observed for non-corallivorous butterflyfishes.

In some cases, the abundance changes may indicate potential regional feeding preferences. Allen et al. (1998)

describe *C. quadrimaculatus* as a *Pocillopora* specialist. Our data seem to confirm that this is the case at Tiahura reef. This species returned in greater numbers in 2003 than were originally recorded in 1979. Additionally, *C. citrinellus* may be a *Pocillopora* specialist on Tiahura reef. Although generally categorised as a facultative corallivore, Pratchett (2005) found that *C. citrinellus* mainly consumed *Acropora* spp. when it ate corals. It may be possible that there is a geographic difference in the feeding behaviour of *C. citrinellus*. *C. lunulatus*, although an obligate corallivore, has been found on Australia's Great Barrier Reef to be one of the most generalised of the obligate corallivores (Berumen et al. 2005). At Tiahura reef, though, *C. lunulatus* showed an overall decline in abundance from 1979 to 2003. While *C. trifascialis* probably declined for reasons of its extreme specialisation on *A. hyacinthus* (Irons 1989), the reason for the decline of *C. lunulatus* is less clear. A generalist would perhaps be predicted to be most able to adjust to a change in prey availability, and, indeed, *C. lunulatus* shows a slight increase in abundance immediately following the initial *A. planci* outbreak. It is also possible that *C. lunulatus* made a switch to a low-quality food source such as *Porites* spp. (Gochfeld 2004) and suffered sub-lethal consequences that were not manifested in the population until after the 1983 survey (sensu Pratchett et al. 2004; Berumen et al. 2005). An additional possibility is that *C. lunulatus* persisted past the initial coral declines but was subsequently out-competed in the zones where it was common when other butterflyfishes recovered. *C. lunulatus* appears to be competitively subordinate to several other corallivorous butterflyfishes (Berumen and Pratchett 2006) and may have been out-competed by *C. citrinellus* in zone 1 and by *C. pelewensis* and *C. reticulatus* in zones 3 and 4.

The three remaining species (*C. bennetti*, *Heniochus monoceros*, and *Hemitaurichthys polylepis*) were each only recorded in one of the 3 years surveyed and were even then occurring in such low numbers that meaningful analysis is not possible. Knowledge of specific chaetodontid diets is badly lacking and this study highlights the need for more detailed work in this area. Some caution must be taken when using feeding categorisations established at other locations as regional differences may occur (e.g. Cox 1994; Pratchett 2005).

The rate of increase in abundance observed among coral and fish communities at Tiahura reef (20–25 years) is slightly slower than that has been recorded in the Ryukyu Islands (13–15 years, Sano 2000) and in the Australia's Great Barrier Reef (10–12 years, Halford et al. 2004) following disturbances of similar magnitude. Recovery at Tiahura Reef may have been limited due to persistent disturbances (Adjeroud et al. 2002) and also due to limited connectivity to other relatively undisturbed reefs (McClanahan et al. 2002; Halford et al. 2004). The evidence found in this study does not indicate that this reef community can return to predisturbance structure within several decades. At Tiahura Reef, the question remains whether changes in coral communities from *Acropora*- to *Pocillopora*-dominated assemblages represent a permanent shift (i.e. a phase-shift) or a transitional phase in a successional sequence. Also, if coral communities do return to their previous community state, will butterflyfish assemblages show a similar recovery of composition?

Benthic assemblages at Tiahura Reef have persisted in a coral-dominated state despite persistent and often very severe disturbances, which is in stark contrast to dramatic phase-shifts observed on many coral reefs (Bellwood et al. 2004). However, the current *Pocillopora*-dominated state may be a transitional phase, indicative of either continuing degradation or recovery (Aronson et al. 2004). In time, *Pocillopora* may become even more abundant and increasingly dominant, or *Acropora* corals may eventually re-establish themselves as the dominant group. Alternatively, this new community structure may represent a stable and resilient state that will persist through time. Interestingly, coral communities elsewhere in the central and eastern Pacific (e.g. Hawaii and Panama) are characterised by high cover of *Pocillopora* and very low cover of *Acropora* (Glynn 1976). However, this new community state may also be susceptible to future "ecological surprises" (sensu Paine et al. 1998; see also Hughes 1989). For example, any disturbance that has a disproportionate impact on *Pocillopora* will now have serious ramifications for the community at Tiahura Reef. Butterflyfish communities may be likewise functionally marginalised if some aspect of redundancy has been compromised.

If coral communities do exhibit strong community resilience and return to an *Acropora*-dominated state, it may be expected that butterflyfish assemblages will exhibit similar resilience. Coral reef fish assemblages are strongly influenced by the structure of benthic habitats (e.g. Holbrook et al. 2000), and this is especially true for corallivorous butterflyfishes (Pratchett 2002). As such, population size of *C. reticulatus* would be predicted to increase with increasing abundance of *Acropora*, while densities of *C. pelewensis* would decline with decreasing abundance of *Pocillopora*. Continued monitoring of this community is essential to add to our broader understanding of long-term recovery (of both abundance and composition) from disturbances on coral reefs (sensu Halford et al. 2004).

This study demonstrates that apparent recovery of coral and fish abundances can occur without recovery of community structure. This distinction is likely to become more important as an increasing number of studies focus on long-term changes in population size and community structure (sensu Gunderson 2000). Today's ecosystems are subject to increasingly frequent disturbances, and these can be expected to have multiplicative effects (Paine et al. 1998). In coral reefs, disturbances are expected to become both more frequent and more extreme (e.g. coral bleaching, Hoegh-Guldberg 1999) while most reefs are already highly degraded or in a weakened state (Bellwood et al. 2004). It is vital, therefore, that there is ongoing research of disturbances to coral reef communities, with a particular focus on synergistic effects of combined or sequential disturbances.

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