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REPORT

Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia

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Abstract Coral reefs are often subject to disturbances that can cause enduring changes in community structure and abundance of coral reef organisms. In Moorea, French Polynesia, frequent disturbances between 1979 and 2003 caused marked shifts in taxonomic composition of coral assemblages. This study explores recent changes in live cover and taxonomic structure of coral communities on the north coast of Moorea, French Polynesia, to assess whether coral assemblages are recovering (returning to a previous *Acropora*-dominated state) or continuing to move towards an alternative community structure. Coral cover declined by 29.7% between July 2003 and March 2009, mostly due to loss of *Acropora* and *Montipora* spp. Coral mortality varied among habitats, with highest levels of coral loss on the outer reef slope (7–20 m depth). In contrast, there was limited change in coral cover within the lagoon, and coral cover actually increased on the reef crest. Observed changes in coral cover and composition correspond closely with the known feeding preferences and observed spatial patterns of *Acanthaster planci* L., though observed coral loss also coincided with at least one episode of coral bleaching, as well as persistent populations of the corallivorous starfish *Culcita novaeguineae* Muller & Troschel. While climate change poses an important and significant threat to the future structure and dynamics coral reef communities, outbreaks of *A. planci* remain a significant cause of coral loss in Moorea. More importantly, these recent disturbances have followed long-term shifts in the structure of coral assemblages, and the relative abundance of both *Pocillopora* and *Porites* continue to increase due to disproportionate losses of *Acropora* and *Montipora*. Moreover, *Pocillopora* and *Porites* dominate assemblages of juvenile corals, suggesting that there is limited potential for a return to an *Acropora*-dominated state, last recorded in 1979.

Keywords Disturbance · Resilience · Coral reefs · *Acanthaster planci* · Bleaching · Pacific

Introduction

Disturbances have an important influence on the structure and dynamics of shallow marine environments (Hughes et al. 2003; Worm et al. 2006), especially for coral reef ecosystems, which are subject to a diversity of different disturbances, including severe tropical storms, freshwater plumes, over-fishing, and infestations of invertebrate corallivores (Karlson and Hurd 1993; Hughes et al. 2003). Importantly, the incidence and severity of episodic disturbances has increased greatly in recent years, as climate-related disturbances are compounding upon numerous pre-existing natural and anthropogenic disturbances (Jackson et al. 2001; Gardner et al. 2003; Hughes et al. 2003). Increased frequency, severity and diversity of disturbances

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on coral reefs are contributing to declines in abundance of reef-building corals (Bellwood et al. 2003), which may be associated with strong directional shifts in taxonomic structure of coral communities (Berumen and Pratchett 2006; McClanahan et al. 2007). Coral depletion and changes in coral assemblages also affect reef-associated fishes and invertebrate communities (Pratchett et al. 2008, 2009b), which could undermine biodiversity, ecosystem function, fisheries production, and other critical goods and services provided by coral reef ecosystems.

Since 1998, effects of climate change on coral reefs, including widespread coral bleaching (Hughes et al. 2003) and increasing prevalence of coral disease (Bruno et al. 2007), have caused extensive coral loss and contributed greatly to coral reef degradation throughout the world (Knowlton 2001) and will only get worse in coming decades (Sheppard 2003; Donner et al. 2005). However, further increases in the frequency and severity of disturbances may not necessarily favour those corals that are most resistant (or least vulnerable) to local disturbances (Baker et al. 2008). Rather, the persistence of different corals may depend largely upon their capacity for recovery following successive disturbances (Knowlton 2001; Baker et al. 2008). On some reefs, highly susceptible corals (e.g., *Acropora*) have become even more dominant in the aftermath of severe bleaching (Kayanne et al. 2002), owing to their potential for rapid recolonisation and recovery (e.g., Kayanne et al. 2002; Sheppard et al. 2002; Pratchett et al. 2009a). In the central Great Barrier Reef, 5 years after coral bleaching killed virtually all corals along exposed reef fronts, *Acropora* is recovering rapidly and now accounts for >90% of coral cover (Pratchett et al. 2009a). Elsewhere (e.g., the Persian or Arabian Gulf), recent disturbances have caused marked declines in the abundance of *Acropora*, leading to increases in the abundance of relatively robust corals, such as *Porites* and Faviidae (Sheppard et al. 2010), thereby revealing limited resilience among local coral assemblages.

Resilience and the potential of coral assemblages to effectively reassemble following major disturbances depends on a host of factors, including: (1) the spatial scale and intensity of disturbances, (2) the temporal pattern of disturbances (Riegl and Purkis 2009) and (3) whether these disturbances have unique, common, or interacting effects, (4) the availability of remnant populations for the replenishment of degraded populations, and (5) the functional integrity of the system (e.g., Wilson et al. 2006). The threat of climate changes has therefore generated renewed interest in other large-scale disturbances, such as outbreaks of *Acanthaster planci*, that also contribute to extensive and widespread coral mortality.

Periodic infestations of corallivorous starfishes, such as the coral-feeding crown-of-thorns sea star, *Acanthaster planci* (L.) and the pincushion sea star, *Culcita novaeguineae* Muller & Troschel, represent a significant biological disturbance to coral reefs in the Indo-Pacific (e.g., Moran 1986; Birkeland and Lucas 1990). The crown-of-thorns starfish is renowned for its capacity to cause large-scale devastation on tropical coral reefs. At very high densities, during outbreaks, *A. planci* can kill up to 80% of corals across large reef areas (Chesher 1969; Pearson and Endean 1969). Even at moderate densities, *A. planci* has the potential to greatly modify coral community structure by selectively feeding on certain corals (Branham et al. 1971; Glynn 1987; Pratchett 2010). Similarly, *C. novaeguineae* exhibits strong preference for certain corals (Glynn and Krupp 1986) and could potentially contribute to directional shifts in species composition of coral assemblages. Normal densities of *C. novaeguineae* are typically higher than for non-outbreak populations of *A. planci*, such that *C. novaeguineae* may represent a persistent force in structuring coral communities (e.g., Quinn and Kojis 2003). However, few studies have ever considered the ecological impacts of *C. novaeguineae* (cf. Glynn and Krupp 1986).

Coral reefs on the north coast Moorea, in the Society Islands, French Polynesia, have been subject to frequent disturbances over the last 30 years (Adjeroud et al. 2002, 2009; Berumen and Pratchett 2006; Penin et al. 2007). Most notably, severe episodes of coral bleaching have been reported every 2–5 years since 1991, corresponding with positive temperature anomalies (Hoegh-Guldberg 1999; Penin et al. 2007). These reefs have also been subject to a major outbreak of *A. planci* in 1980–1981, as well as at least one major cyclone in 1991 (Adjeroud et al. 2002; Berumen and Pratchett 2006). In 2003, coral cover on the north coast of Moorea (mainly Tiahura) was equivalent to that recorded in 1979, before the first recorded outbreak of *A. planci* (Berumen and Pratchett 2006). However, coral composition in Moorea has changed markedly over this period. Most notably, *Porites* and *Pocillopora* replaced *Acropora* as the dominant coral genera (Berumen and Pratchett 2006). However, it is unknown whether this change in composition reflected a permanent shift in community structure, or an early successional stage of coral recovery. The purpose of this study was to investigate changes in coral cover and composition from 2003 to 2009. Specifically, we wanted to test whether the local abundance of *Acropora* is increasing, and the community structure of coral assemblages is tending towards an *Acropora*-dominated state, last recorded in 1979 (Bouchon 1985). Alternatively, recovery may have been further retarded by ongoing disturbances. Most notably, there was a major infestation of *A. planci* recorded in 2006–2009, but the ecological effects of this recent disturbance are yet to be reported.

Materials and methods

Study site

This study was conducted on the northern coast of Moorea (17°30′ S, 149°5′ W), Society Islands, French Polynesia. Sampling was conducted at two locations, Vaipahu and Tiahura, separated by approximately 2 kilometres on the north coast of Moorea (Fig. 1). Coral assemblages were sampled in July 2003, May 2007, and March 2009. On each occasion, sampling was conducted in six distinct reef zones: (1) the inner reef flat (1–2 m depth); (2) the outer reef flat (1–3 m depth), (3) the reef crest (3–5 m depth), (4) the shallow reef slope (7–9 m depth), (5) the mid-slope (10–12 m depth), and (6) the deep slope (18–20 m depth). Within each zone, percentage cover of individual corals was recorded using 5 replicate 50-m-long point-intercept transects, whereby coral or substratum types were recorded directly beneath 100 uniformly spaced points (50 cm apart) along the transect line. All transects were run from haphazardly selected starting points and run parallel to the reef crest within each zone. In this study, we distinguished four major coral genera: *Acropora*, *Pocillopora*, *Porites*, and *Montipora*. All other genera were pooled into a single category “other hard corals”.

Variation in coral cover was analysed using 3-way ANOVA to test for variation in total coral cover among sampling occasions (3-levels, fixed factor), between locations (2-levels, fixed factor), and among reef zones (6-levels, fixed factor). Proportional cover of scleractinian corals on 50-m point-intercept transects was arcsine transformed, as is appropriate for proportion data (Sokal and Rohlf 1987). Variation in the relative abundance of the different coral genera (*Acropora*, *Pocillopora*, *Porites*, *Montipora*, and other hard corals) was analysed using MANOVA, also testing for differences among samples, between locations, and among reef zones. Mostly, we were interested in establishing whether there was significant variation in rates and/or direction of change in percentage cover among different coral genera, reflective of selectivity in disturbances and/or differential recovery during this period.

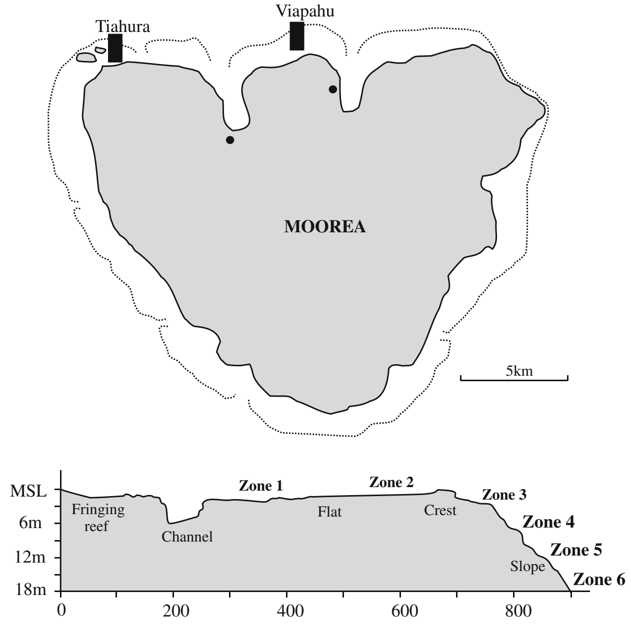


Fig. 1 Map of study sites (Tiahura and Viapahu) in Moorea, French Polynesia, as well as stylised drawing of the reef profile to indicate the relative proximity of reef zones within each study site

Causes of coral loss

To account for recent changes in the abundance and/or composition of scleractinian corals, densities of coral-feeding asteroids were also recorded in each habitat at each location. Densities of both *Acanthaster planci* and *Culcita novaeguineae* were recorded by carefully searching for both these coral-predators within 2 m either side of the 50-m coral transects. To maximise detection of sea stars, divers moved very slowly (<5 m per minute) along each side of the transect tape carefully searching within and under all coral colonies for cryptic individuals. Divers also recorded the incidence of coral bleaching, by recording the proportion of corals sampled along 50 × 4-m belt transects that exhibited conspicuous signs of bleaching. The severity of bleaching for different coral genera was assessed based on the proportion of colonies that were (1) healthy, (2) partly bleached, (3) completely bleached, and (4) recently dead, following Marshall and Baird (2000). For recently dead corals, it is important to recognise that mortality may be due to either severe coral bleaching or coral predation by corallivorous starfishes.

Juvenile corals

Densities of juvenile corals, defined as small corals (<5 cm diameter) that had settled on natural substrates and were visible with the naked eye (Rylaarsdam 1983), were recorded in March 2009 to assess whether the proportional replenishment of different coral taxa is reflective of the adult assemblage, following Penin et al. (2010). Densities of juvenile corals were quantified within a 1-m-wide belt along the first 10-m transects deployed to quantify benthic composition. As such, five replicate transects were surveyed in each zone at each location. However, densities of juvenile corals were not measured within the lagoon (zones 1 and 2) due to the lack of consolidated carbonate substrates upon which larval corals typically settle. In these habitats, fragmentation is likely to have greater importance in the production of new colonies, which would lead to strong taxonomic biases in patterns of recruitment (Highsmith 1982). For data collected from zones 4–6, variation in the densities of juveniles for each coral genera (*Acropora*, *Pocillopora*, *Porites*, *Montipora*, and other hard corals) were analysed using MANOVA, testing for differences between locations (Tiahura and Viapahu), and among reef zones (zones 3, 4, 5 and 6). Count data was log-transformed to normalise the data.

Results

Coral cover and composition

Overall coral cover declined by 44.2% across the two study locations (Tiahura and Viapahu), from 34.8% (±2.0 SE) in July 2003 down to 19.4% (±1.6 SE) in March 2009. However, temporal variation in coral cover was conditional upon both zone and location (ANOVA, Table 1). Declines in coral cover were most pronounced on outer reef slope, with greatest loss (93.7% decline) recorded in zone 6. In zone 4, coral cover declined significantly at Tiahura, but not Viapahu. In shallow reef habitats (zones 1, 2, and 3), coral loss was generally negligible, except at zone 2 for Tiahura, which experienced marked declines in coral cover from 2003 to 2007, but no further change to 2009. In zone 3, coral cover tended to increase throughout the course of this study (Fig. 2).

Declines in coral cover were not equally apportioned among different coral genera. In general, *Acropora* and *Montipora* declined in abundance from 2003 to 2009, leading to increases in the proportional abundance of *Pocilllopora* and/or *Porites* (Fig. 3). Analyses of community structure revealed a significant interaction between year, location, and zone (MANOVA, Table 2), whereby changes in the relative abundance of the major coral taxa varied among zones and between locations. Absolute cover of *Montipora* declined by 50.1%, mostly between 2003 and 2007, and declines were apparent across all zones (Fig. 3). For *Acropora*, overall cover declined by 39.8%, but greatest declines occurred in zones 4, 5, and 6 (Fig. 3). Conversely, the proportional cover of *Pocillopora* and *Porites* increased by 16.3 and 18.0%, respectively. In March 2009, *Pocillopora* and *Porites* accounted for 38.7 and 33.1%, respectively, of overall coral cover. However, the dominant coral varied by zone, whereby *Pocillopora* was dominant in zones 3 and 4, whereas *Porites* dominated in zones 1, 2, 5, and 6 (Fig. 3).

Table 1 ANOVA to test for variation in (a) percentage cover of all scleractinian corals (arcsine-squareroot transformed), (b) mean abundance of *A. planci* ($\log_{10}$ transformed), and (c) mean abundance of *C. novaeguineae* (raw data), among years (July 2003, May 2007, March 2009), between locations (Tiahura and Viapahu), and among zones (1–6)

Source	*df*	Coral cover		*A. planci*		*C. novaeguineae*	
		MS	*F*	MS	*F*	MS	*F*
Year (Y)	2	5.77	442.37***	0.45	24.26***	0.07	0.37
Location (L)	1	0.16	12.09**	0.08	4.10	0.14	0.77
Zone (Z)	5	0.04	2.91*	0.29	15.48***	1.70	9.43***
Y × L	2	0.01	0.07	0.06	30.6	0.09	0.49
Y × Z	10	0.06	4.74***	0.08	4.53***	0.20	1.11
L × Z	5	0.10	7.92***	0.08	5.38**	0.20	1.21
Y × L × Z	10	0.06	4.66***	0.06	3.39**	0.09	0.50
Error	144	0.01		0.02		0.18	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Bleaching versus coral predation

Coral loss recorded during this study coincided with both an outbreak of *A. planci*, as well as at least one episode of coral bleaching. *Acanthaster planci* were first recorded on the outer reef slope (12 m depth) at Vaiapahu and Tiahura in April 2006 and rapidly increased in abundance at these locations throughout 2006 and 2007 (Lison de Loma, pers. comm.). In May 2007, highest densities of *Acanthaster planci* (3.60 ± 1.12 starfish per 200 m^2) were recorded along the shallow (6 m depth; zone 4) slopes of Tiahura, though starfishes were recorded in every zone on the reef slope at both locations (Fig. 2b). No *A. planci* were observed on the reef crest, and only a single starfish was recorded on the reef flat (Fig. 2b). In 2009, starfishes were still most prevalent on the outer reef slope, though overall densities had dropped significantly compared to 2007. Several starfish were recorded on the reef crest (zone 3) at Viapahu, but the greatest densities were recorded on the shallow reef slope. *Culcita novaeguineae* was found in low densities ($\leq$1 individual per 200 m^2) across all surveys, and always restricted to the reef flat (zones 1 and 2). No *C. novaeguineae* were ever recorded on the reef crest or reef slope, whereas mean densities of *C. novaeguineae* on the reef flat were 0.46 (±0.08 SE) per 200 m^2 and did vary significantly among years.

The only known occurrence of mass bleaching during this study occurred in late summer (March–April) 2007. Surveys conducted in May 2007 revealed that 26.7% (1,113/4,173) of coral colonies were bleached or partially bleached. A further 2.0% of colonies (85/4,173) had recently died (Fig. 4), though this was not necessarily due to bleaching. The incidence of bleaching was highest among *Acropora*; 59.4% (518/871) of *Acropora* colonies were either partly or completely bleached. In contrast, only 12.5% of *Pocillopora* colonies, and 17.3% of *Porites* colonies exhibited any bleaching. Similarly, the incidence of recent mortality was much higher for *Acropora*, compared

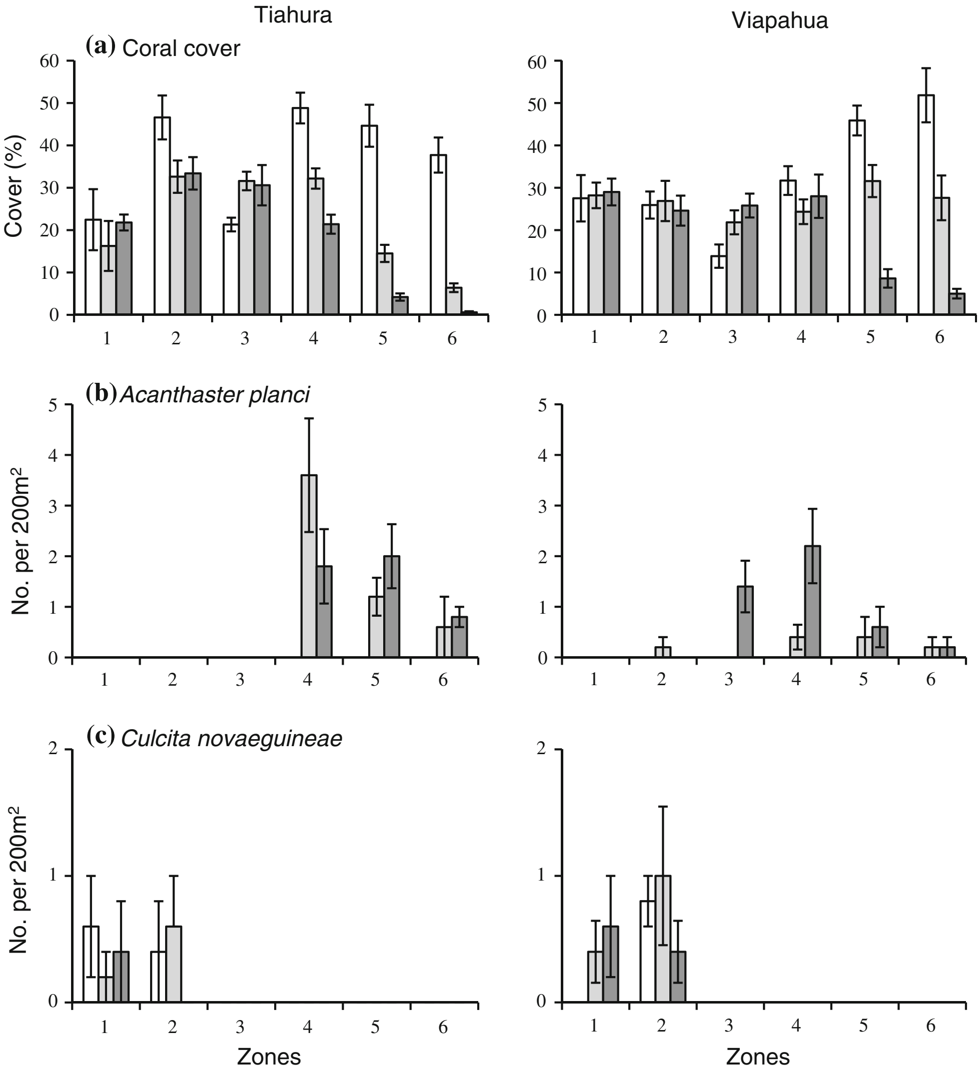


Fig. 2 Mean (±SE) of **a** percentage cover of all scleractinian corals, relative to **b** densities of the corallivorous sea star, *Acanthaster planci*, and **c** *Culcita novaeguineae* within each reef zone, in July 2003 (*white bars*), May 2007 (*light grey bars*), and March 2009 (*dark grey bars*). No *A. planci* were recorded in 2003

to any other genera (Fig. 4) and was most pronounced (22.0%) on the deep slope (zone 6).

Juvenile corals

A total of 1,570 juvenile corals were recorded during surveys conducted on the reef crest and reef slope (zones 3–6) in March 2009, corresponding with a mean of 39.25 (±2.28 SE) juveniles per transect (10 m^2). Assemblages of juvenile corals were dominated by *Pocillopora* and *Porites*, which together accounted for 58.0% (910/1,570) of juvenile corals counted (30.4 and 27.6%, respectively). *Pocillopora* dominated juvenile assemblages on the reef crest and shallow reef slope (zone 4), but *Porites* was more or equally abundant in the deeper zones (zones 5 and 6). *Acropora* were much better represented in the juvenile assemblages than they were in adult assemblages, especially on the outer reef slope; *Acropora* comprised <1.0% of adult assemblages across zones 4–6, but comprised 9.1–12.2% of recruits recorded in these zones. However, *Acropora* accounted for only 10.1% of juvenile corals surveyed and were much less abundant compared to *Pocillopora* and *Porites* (Fig. 5).

Discussion

This study revealed significant declines in coral cover, as well as significant changes in coral composition, on the north coast of Moorea in the 6 years to March 2009. Recent coral loss and changes in coral communities at these study sites follow a long history of disturbances, including at least one major outbreak of *A. planci*, a severe cyclone, and recurrent bleaching, which have already greatly altered coral communities, if not necessarily reducing overall coral cover (Adjeroud et al. 2002, 2009; Berumen and Pratchett 2006; Penin et al. 2007). In 2003, average coral cover at Tiahura was close to the highest recorded (35%)

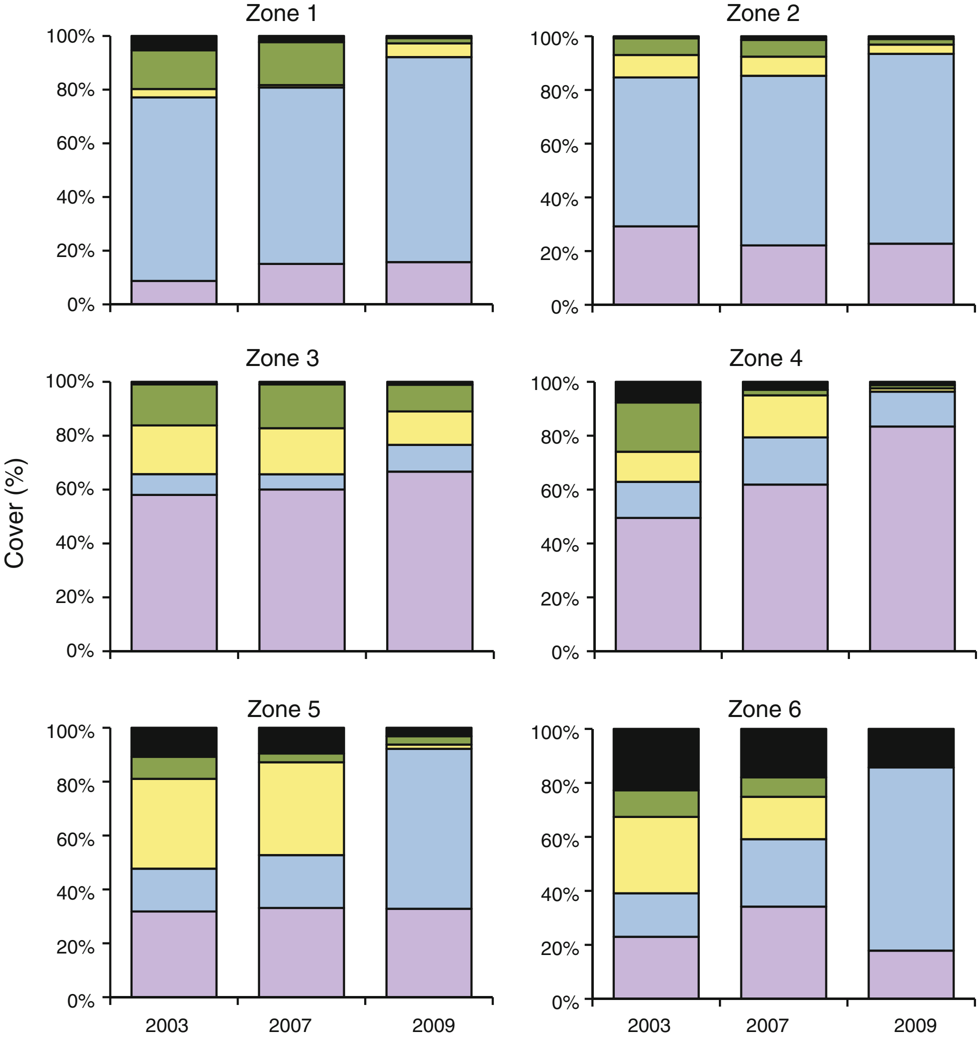


Fig. 3 Changes in proportional cover (percentage of total live coral cover) of the four major coral genera (*Pocillopora—purple*, *Porites—blue*, *Acropora—yellow*, *Montipora—green*), plus all other genera combined (*black*) within each reef zone. Data pooled across two study sites (Viapahu and Tiahura) on the northern coast of Moorea ($n = 10$ transects per zone)

Table 2 MANOVA to test for variation in the relative abundance of major coral genera (*Acropora*, *Montipora*, *Porites*, *Pocillopora*, and "others")

Effect	Pillai's trace	Hypothesis *df*	Error *df*	*F*
Year (Y)	0.68	10	282	14.44***
Location (L)	0.05	5	140	1.44
Zone (Z)	1.72	25	720	15.05***
Y × L	0.20	10	282	3.20***
Y × Z	1.13	50	720	4.23***
L × Z	0.74	25	720	4.97***
Y × L × Z	0.46	50	720	1.45*

Data were arcsine-squareroot transformed

* $P < 0.05$; *** $P < 0.001$

throughout the last 25 years, but coral communities had shifted from being *Acropora*-dominated (in 1979) to *Pocillopora*-dominated (Berumen and Pratchett 2006). This shift was caused and appears to be maintained, by the selective removal of *Acropora* corals during recurrent disturbances (Berumen and Pratchett 2006). Similarly, recent coral loss was not equally apportioned among different coral genera, and there was greater loss of *Acropora* compared to *Pocillopora*. Consequently, *Pocillopora* has become even more dominant, accounting for over 38.7% of live coral cover in March 2009, compared to 32.4% in July 2003.

Coral bleaching is widely considered as the major contributor to coral loss and coral reef degradation in many parts of the world (e.g., in the Indian Ocean, Graham et al. 2008), but recent bleaching events have caused relatively little coral mortality in Moorea (Penin et al. 2007; Adjeroud et al. 2009). Mass bleaching has been recorded in Moorea in 1984, 1987, 1991, 1994, 2002, and 2003, based on appearance of unusually pale or white corals across a range of different taxa (Hoegh-Guldberg 1999; Penin et al. 2007). However, there has not been any systematic sampling of physiological variables (e.g., zooxanthellae densities; Brown et al. 1994) to assess the severity of coral bleaching in Moorea, nor has there been any systematic

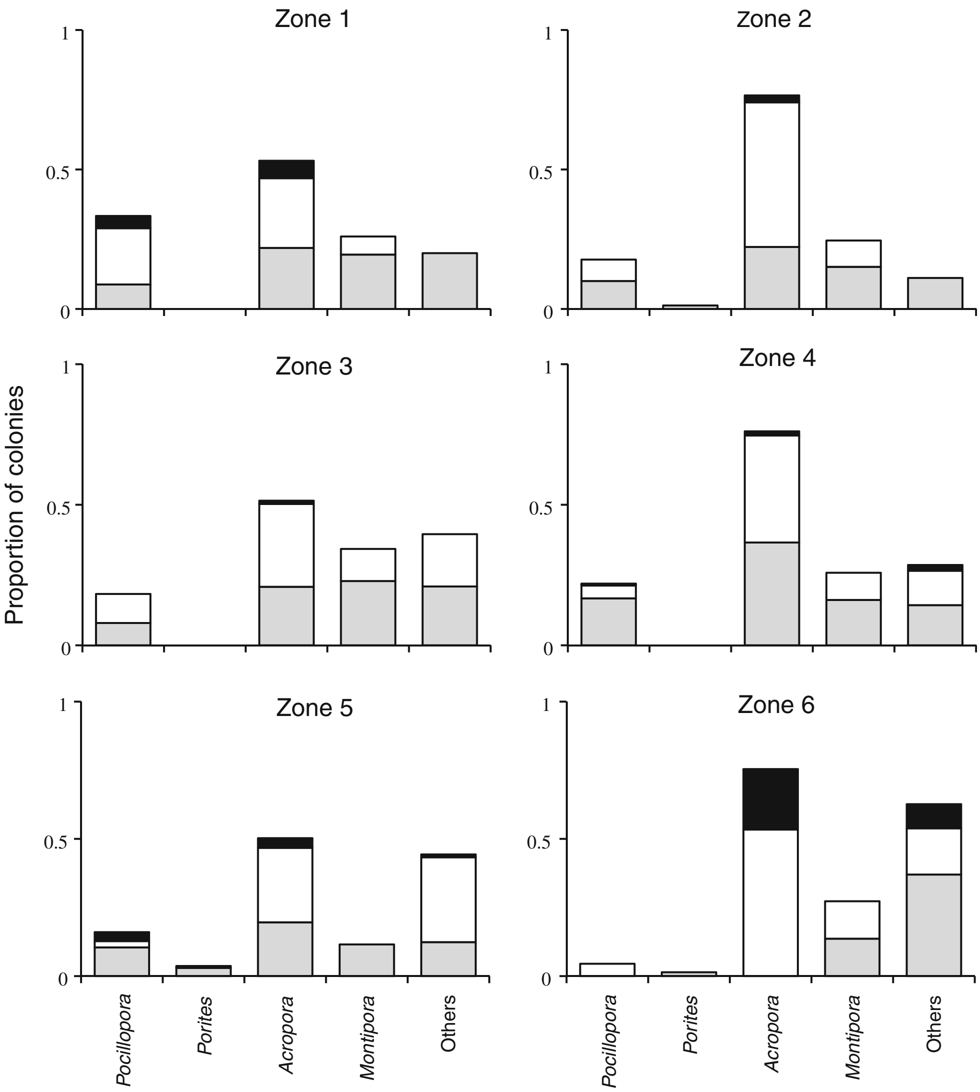
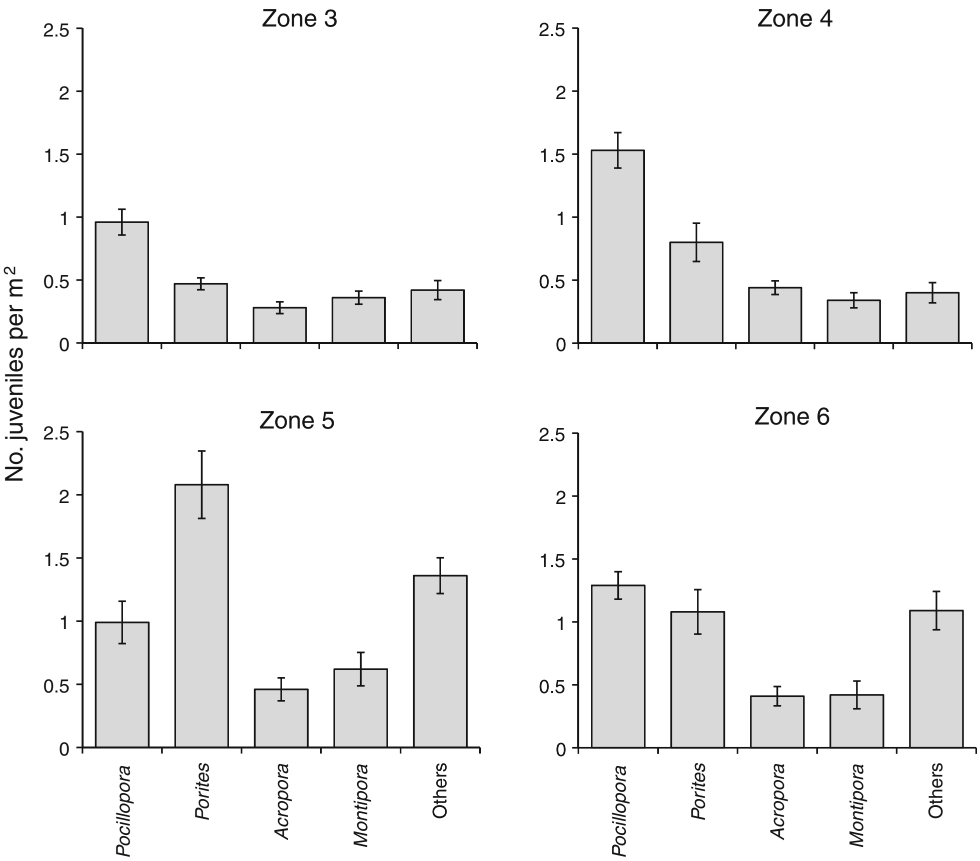


Fig. 4 Bleaching incidence within each reef zone in May 2007, showing the proportion of colonies in each major genera that were (1) partly bleached (*grey bars*), (2) completely bleached (*white bars*), and (3) recently dead (*black bars*). Data based on surveys of 594–892 colonies per zone, pooled across two study sites (Viapahu and Tiahura) on the northern coast of Moorea

monitoring of individual coral colonies, which is necessary to assess the fate of bleached corals (e.g., Baird and Marshall 2002). Overall, there appears to have been very limited change in coral cover associated with these episodic disturbances, suggesting that while corals bleached, they probably did not die. Coral bleaching observed during this study (in May 2007) affected 16–34% of colonies across all reef zones, but bleaching incidence and corresponding loss of live coral were most pronounced on the outer reef slope and tended to increase with increasing depth. Increased incidence and severity of bleaching with depth have been reported in several oceanic locations and is attributable to disproportionate effects of solar radiation (e.g., Gleason and Wellington 1993) for corals in deeper water. Whereas shallow water corals are regularly exposed to high levels of solar radiation, prolonged periods of calm weather can significantly increase the amount of solar radiation affecting corals in deep water (up to 24 m depth). The 2007 mass bleaching corresponds with an extended period (43 days) during which sea-surface temperatures remained above 29.2°C, regarded as the local bleaching threshold (Hoegh-Guldberg 1999). This situation may have been exacerbated by calm sea conditions and associated increases in solar exposure, especially in deeper habitats. It is more likely, however, that higher levels of coral loss on the reef slope compared to the reef flat relate to differences in the abundance of *A. planci*, which were much more abundant on the reef slope. *Acanthaster planci* were almost never recorded within the lagoon (zones 1 and 2) at Moorea (see also Pratchett 2005).

Prior to 2006, the only known outbreak of *A. planci* in Moorea occurred in 1980–1981 (Bouchon 1985), and while there is limited data on the actual densities of *A. planci* that occurred during this previous outbreak, coral loss recorded at Tiahura and Viapahu was both rapid and very pronounced (Berumen and Pratchett 2006). In 2007, mean

Fig. 5 Mean (±SE) densities of juvenile corals ("recruits") on natural substrates for each of the major coral genera within reef zones 4–6, recorded in March 2009. Data pooled across two study sites (Viapahu and Tiahura) on the northern coast of Moorea ($n = 10$ transects per zone)



densities of *A. planci* exceeded threshold densities (0.3–0.8 starfish per 200 m^2) used to define outbreaks on Australia's Great Barrier Reef (Moran and De'ath 1992; Pratchett 2005). However, the maximum density recorded during this study was only 3.6 starfish (±1.12 SE) per 200 m^2, which is substantially lower than has been recorded during major outbreaks elsewhere in the Pacific (Moran 1986). Accordingly, coral loss was fairly moderate. There was, however, significant loss of *Acropora* and *Montipora*, which is consistent with reported feeding preferences of *A. planci* (Keesing 1992; De'ath and Moran 1998; Pratchett 2001, 2007). Recent coral loss was also most pronounced on the outer reef slopes (zones 4–6), corresponding with zones where *A. planci* tended to be most abundant (Fig. 2).

The relative contribution of coral bleaching versus infestations of *A. planci*, as well as other possible agents of coral mortality, in localised coral depletion in Moorea is difficult to discern. However, it is clear that coral depletion in zones 5 and 6 commenced in 2003–2007, before the occurrence of mass bleaching. Also, there was comparatively little change in coral cover in zones (reef flat and reef crest) where *A. planci* were rarely, if ever, recorded. Declines in coral cover that were apparent on the reef flat were caused by persistent reductions (before and after the bleaching) in the abundance of *Pocillopora*, *Acropora*, and *Montipora*, potentially caused by *C. novaeguineae*. In laboratory experiments, *C. novaeguineae* exhibits strong preference for *Pocillopora* (Glynn and Krupp 1986), and Quinn and Kojis (2003) reported that they were commonly found feeding on *Pocillopora* corals around Rota, in the western Pacific. These starfish are widespread throughout the lagoon in French Polynesia, and though found in low abundance (≤1 individual per 200 m^2), their continual removal of live coral (~28 cm^2 of coral tissue each day; Glynn and Krupp 1986) is likely to have a significant selective effect on coral composition, if not coral cover. However, coral loss recorded in zones 1 and 2 may have also resulted from coral bleaching (Fig. 2). Most notably, declines in the cover of both *Acropora* and *Montipora* occurred between 2007 and 2009, especially in zone 2, where 74.0% of *Acropora* and 24.5% of *Montipora* were at least partially bleached.

Selectivity of major disturbances is a major determinant of community structure for coral assemblages (Jackson and Hughes 1985) and also has a significant influence on other reef-associated species (Pratchett et al. 2008). *Acropora*, for example, is extremely vulnerable to most major episodic disturbances, including bleaching (Loya et al. 2001; Baird and Marshall 2002), storms (Jackson and Hughes 1985; Madin and Connolly 2006), and outbreaks of

A. planci (Pratchett 2010), but is also the favoured coral for many coral-dwelling and corallivorous fishes (Pratchett et al. 2008). Accordingly, Berumen and Pratchett (2006) have documented significant changes in the relative abundance of corallivorous butterflyfishes associated with shifts in the structure of coral assemblages. Replacement of erect branching corals (e.g., *Acropora*) with encrusting and/or or massive corals (e.g., *Porites*) will also greatly reduce habitat availability and topographical complexity of coral reef environments, thereby reducing biodiversity and productivity. Reefs with low habitat complexity and topographical relief support far fewer fishes (e.g., Sano et al. 1987, Graham et al. 2006), owing to the critical role of topographical complexity in moderating recruitment, competition, and predation (Coker et al. 2009). Thus, the interplay between *Acropora* and other major coral genera is of key importance for contemporary and future ecology of tropical coral reefs.

Recent disturbances have further augmented shifts in the structure of coral assemblages in Moorea, which have been ongoing since the early 1980s (Berumen and Pratchett 2006). However, the key question is whether the current dominance of *Pocillopora* and *Porites* represents either: (1) a transitional community state, indicative of either continuing degradation or recovery (Aronson et al. 2004), or (2) an entirely new, stable, and resilient community structure that will endure until there is a fundamental change in local conditions. In Guam, outbreaks of *A. planci* caused similar shifts in species composition of corals (from *Montipora* and *Acropora* to *Porites* and *Leptastrea*), but it took <12 years for coral cover and composition to return to pre-disturbance levels (Colgan 1987). In Moorea, however, there was limited recovery of *Acropora* >20 years after the first recorded outbreak of *A. planci* (Berumen and Pratchett 2006), and the current coral assemblages (dominated by *Pocillopora* or *Porites*) are likely to persist.

One indicator that a shift has occurred from one persistent assemblage of species to another is the existence of positive feedback mechanisms, which reinforce and sustain the altered community structure (Knowlton 1992; Nyström et al. 2008). Differences in the abundance juvenile corals among major coral taxa were strongly reflective of patterns of adult abundance and will therefore reinforce and further advance observed shifts in community structure. Although *Acropora* were relatively more abundant in juvenile assemblages compared to adult assemblages, juvenile *Acropora* were much less abundant than either *Pocillopora* or *Porites*. Further, Penin et al. (2010) showed that taxonomic differences in juvenile abundance (cf. patterns of settlement) are often reflected in subsequent patterns of abundance of adult abundance at sites around Moorea, thereby suggesting that the observed dominance of *Pocillopora* and/or *Porites* is likely to persist.

This study demonstrates that recent disturbances have compounded previous disturbances in Moorea (Berumen and Pratchett 2006), further augmenting community shifts in coral assemblages. Moreover, episodic disturbances, such as those associated with ongoing climate change, are expected to become both more frequent and more severe in coming decades (e.g., Hoegh-Guldberg 1999). It is likely, therefore, that changes in community structure of coral assemblages will become increasingly apparent throughout the world. The extent to which disturbances favour those species that are most resistant to disturbances (e.g., *Porites* and *Favia*, Riegl and Purkis 2009) versus those species that recover rapidly in the aftermath of each disturbance (e.g., *Acropora*: Pratchett et al. 2008; Kayanne et al. 2002) appears to depend upon the overall frequency of different disturbances (Riegl and Purkis 2009). Whereas infrequent disturbances may promote increased abundance of corals capable of rapid recolonisation and recovery (e.g., Pratchett et al. 2008), recurrent disturbances lead to shifts in community structure towards robust coral species that are more resistant to most major disturbances (Riegl and Purkis 2009). Locations where the latter has occurred, such as the Persian or Arabian Gulf (Sheppard et al. 2010) and Moorea (Berumen and Pratchett 2006; this study), tend to be subject to a diversity of different disturbances, suggesting that reductions in incidence and/or severity of more manageable disturbances may provide the effective tool to reduce (or at least delay) the effects of ongoing climate change, following Hughes et al. (2003). It is also possible that resilience of coral assemblages varies regionally due to differences in population and community dynamics.

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