Research Article

Comparative Effects of Different Disturbances in Coral Reef Habitats in Moorea, French Polynesia

Mélanie L. Trapon,[1] Morgan S. Pratchett,[1] and Lucie Penin[1, 2]

[1] *ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia*
[2] *USR CNRS-EPHE 3278 CRIOBE Centre de Recherches Insulaires et Observatoire de l'Environnement, Université de Perpignan, 66860 Perpignan Cedex, France*

Correspondence should be addressed to Morgan S. Pratchett, morgan.pratchett@jcu.edu.au

Degradation and loss of critical coastal habitats has significant ramifications for marine fisheries, such that knowledge of changes in habitat quality and quantity are fundamental to effective ecosystem management. This study explores changes in the structure of coral reef habitats, specifically changes in coral cover and composition, in Moorea, French Polynesia, to assess the independent and combined effects of different disturbances since 1979. During this period, reefs on the north coast have been subject to coral bleaching, severe tropical storms, as well as outbreaks of *Acanthaster*. Coral cover varied significantly among years, showing marked declines during some, but not all, disturbances. The greatest rates of coral loss coincided with outbreaks of *A. planci*. Moreover, successive disturbances have had differential effects among coral genera, leading to strong directional shifts in coral composition. *Acropora* is declining in abundance and coral assemblages are becoming increasingly dominated by *Pocillopora and Porites*. Observed changes in the cover and composition of corals are likely to have further significant impacts on the reef fish assemblages. Given that significant disturbances have been mostly associated with outbreaks of *A. planci*, rather than climate change, effective ecosystem management may reduce and/or delay impending effects of climate change.

1. Introduction

Disturbances play an important role in the structure and dynamics of marine communities and are a necessary part of ecosystem dynamics [1–4]. On coral reefs, moderate levels of disturbance make an important contribution to increasing biodiversity [5]. In many locations, however, natural acute "pulse" disturbances have combined with chronic "press" [6] anthropogenic stresses (e.g., overfishing, pollution and eutrophication) to cause excessive disturbance and degradation of coral reef environments [7, 8]. On a global scale, it is estimated that 30% of coral reefs have now lost >90% of reef-building corals and there is little to no prospect of recovery [9]. Moreover, 60% of coral reefs around the world may face a similar fate by 2030 [9, 10]. The loss of reef-building corals is likely to have major impacts on the biodiversity, productivity, and biological functioning of coral reef ecosystems [11, 12]. In some locations, changes in the

structure and quality of benthic reef habitats are now the most important driver of changes in the abundance of reef fishes (including some large piscivorous species), having a greater influence than extractive fisheries [13, 14].

Major contributors to coral loss and coral reef degradation vary regionally [15], but most reef areas are exposed to multiple disturbances [12]. Areas in which coral reef degradation is most pronounced (the Caribbean, SE Asia, and the western Indian Ocean) are characterized by a long history of heavy exploitation of coral reef resources and other chronic disturbances [9], which may have increased vulnerability to recent acute disturbances, such as severe tropical storms [16–20], El Niño Southern Oscillation (ENSO) events [21, 22], coral bleaching events [23–28], high and low temperature extremes, freshwater plumes from heavy rainfall and runoff events [29], coral diseases [30], and outbreaks of coral predators (mainly, the corallivorous sea star *Acanthaster planci* in the Indo-Pacific, [31–39], and

tidal fluctuations [40]). More importantly, coral loss and associated degradation of coral reef habitats is expected to worsen over the next 2-3 decades, due to climate related increases in temperature [41] and ocean acidification [42].

Effects of acute disturbances on coral assemblages vary greatly, both within and among different types of disturbance. Disturbances that result in an immediate loss of habitat complexity (e.g., severe tropical storms) tend to have a greater impact on fishes from all trophic levels, compared with disturbances that kill corals, but do not immediately compromise the structure of reef habitats (e.g., coral bleaching and outbreaks of *Acanthaster planci*) [12]. Disturbances of a similar type (e.g., cyclones) may also differ in terms of the spatial scale of impact on habitat, intensity, magnitude, and duration of effect [5, 6]. Moreover, responses to disturbances will vary among locations, according to the history of disturbances that have already modified community structure [3], the stage of recovery since the last major disturbances [43–45], as well as inherent differences in community structure at large geographical scales [46]. Despite these differences, increases in the diversity, frequency, and intensity of disturbances in many reefs throughout the world tend to be causing clear directional changes in the structure of coral reef habitats [8, 47]. In general, increasing disturbances cause declines in the abundance of habitat-forming corals, which may, in some situations, be replaced with macroalgae (e.g., [48]). Even if coral cover does not decline there may be marked changes in community structure of coral assemblages (e.g., [49]).

Effects of disturbances on coral composition depend on selectivity of effects, and differential vulnerabilities among major coral taxa (common families and genera). *Acropora*, for example, is the first and worst affected genera during coral bleaching [50, 51], outbreaks of *A. planci* [52], and cyclones [20], whereas massive corals, such as *Porites* and *Favia* are resistant to all but the most severe disturbances. Consequently, erect branching corals (e.g., *Acropora*) are increasingly being replaced with encrusting and/or massive corals (e.g., *Porites*) at locations with extreme disturbance regimes (e.g., the Arabian Gulf; [53, 54]), which greatly reduced habitat availability and topographical complexity of coral reef environments. *Acropora* and other branching corals are the predominant habitat used by most coral-dwelling fishes [55], while habitats with low complexity and topographic relief support far fewer fishes (e.g., [13, 38]) owing to the critical role of topographic complexity in moderating recruitment, competition, and predation [56]. It is important therefore, to assess whether changes in the structure of coral assemblages observed in the Arabian Gulf, may ultimately occur at other locations the Indo-Pacific, especially given projected increases in the severity and/or frequency of disturbance [41].

A critical limitation in understanding effects of persistent or recurrent disturbances on coral reefs is the lack of long-term data [12]. Most studies are conducted at very limited temporal and spatial scales [57], and there are a limited number of locations around the world where there has been sufficient research conducted over an extended period to provide information on long-term changes in
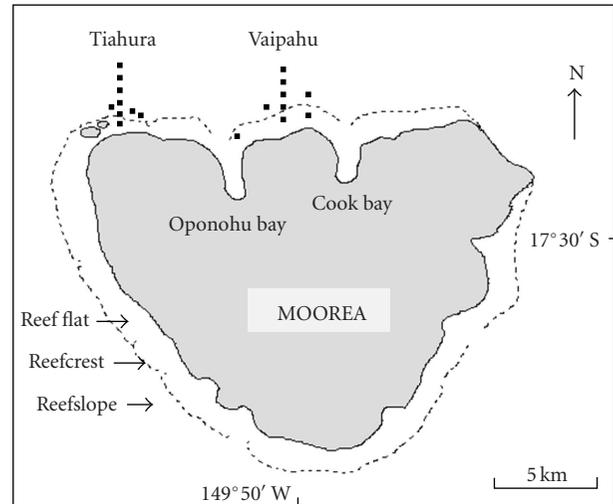
FIGURE 1: Map of Moorea (17°30′S, 149°50′W) in the Society Island, French Polynesia, showing the main study sites on the reef flat, reef crest and reef slope at Tiahura (North-West) and Vaipahu (North-East). Dashed lines represent the approximate extent of the reef front.

coral composition associated with multiple and successive disturbances [12, 16, 58]. One of the major centers for coral reef research in the central Pacific is Moorea (17°30′S, 149°50′W) in the Society Islands, French Polynesia (National Science Foundation Long-Term Ecological Research program—http://www.lternet.edu/sites/mcr/; Program "Agencement Temporel des Populations et des Peuplements", USR CNRS-EPHE3278 CRIOBE). Changes in coral cover and composition (mostly to genus) have been documented in Moorea since the 1970s by [59] and Bouchon [60], focusing on Tiahura reef on the northwest corner of Moorea (Figure 1). Since that time, extensive coral reef research and monitoring has been undertaken at Tiahura reef (and to a lesser extent at Vaipahu, situated approximately 12 km east of Tiahura, Figure 1). During this period, coral assemblages have been subject to many acute (pulse) disturbances, which are purported to have caused major changes in the community structure of coral reef communities [49]. Most notably, multispecific coral bleaching has been reported every 3-4 years since 1983 (1984, 1987, 1991, 1994, 2002, 2003, and 2007), corresponding with periods when sea surface temperature increased above 29.2°C [16, 26, 58, 61]. Then, cyclones have been reported to occur in Moorea during two El Nino events in 1983 and 1991, but in general are rare in French Polynesia (Table 1). Finally, two outbreaks of crown-of-thorn sea star occurred in Moorea, the first from 1979 to 1985, and the second one which started in 2006 was still occurring in 2009 when the reef was resurveyed by Pratchett et al. (Table 1).

The purpose of this study was to assess the recent history of disturbances affecting coral reefs of Moorea, French Polynesia, based on extensive field-based research undertaken

at this location since 1979. In addition to documenting the occurrence of distinct disturbance events, changes in cover and composition of reef-building corals were assessed following each major disturbance event. These data provide insights into the comparative effects of different disturbances, as well as revealing long-term effects of recurrent disturbances on coral reefs in the central Pacific. Assessing the major causes of coral loss is particularly important in establishing potential management strategies to address habitat-degradation (specifically, declines in habitat diversity and structural complexity) within ecosystem management frameworks.

2. Materials and Methods

To explore long-term changes in coral cover and community structure at Moorea, quantitative data were compiled from 15 studies conducted at Tiahura [16, 33, 49, 58, 62–70] and/ or Vaipahu [16, 62, 71, 72], located 2 kilometres apart on the north coast of Moorea [62]. Most of these studies (11 studies) directly compared changes in coral cover and composition through time, sampling coral assemblages between 2–17 years. This study also encompasses data from two previous studies, that document long-term changes in coral cover and composition [49, 58]. However, this study extends the temporal and spatial extent of these data sets. Most importantly, it includes knowledge of recent changes in coral cover and composition, from 2006–2009, during which time there was a major outbreak of *A. planci*.

To account for differences in sampling among specific habitats or depths, we pooled data across different reef zones (up to 7) to distinguish between: (i) shallow habitats (from 0 to 5 m), which encompass the barrier reef flat, the barrier reef crest, and the upper part of the outer-reef slope and (ii) deep habitats (10 to 30 m), encompassing the outer-reef slope. We calculated a mean coral cover for each of these habitats, at each site, and in each year. Whenever possible, we also considered the structure of coral communities, based on relative abundance of the major coral genera *Pocillopora*, *Acropora*, *Montipora,* and *Porites*. All other corals were then lumped into a single category, "others".

The temporal occurrence and severity of major disturbances such as coral bleaching events, cyclones, and outbreaks of *Acanthaster planci* (*A. planci*) was assessed based on a comprehensive review of published literature (Table 1). To relate changes in total coral cover to the occurrence of disturbances, we calculated annual geometric rate of change in total coral cover for each year, following Côté et al. [73]. Geometric rates of change in live coral cover are calculated based on the relative change in coral cover between respective samples, without assuming a linear decline in coral cover, which is necessary when comparing among different sampling intervals. The average annual rate of change was then compared among individual years in which different types of disturbances (bleaching, cyclones, and outbreaks of *A. planci*) occurred. It was not possible to partition effects of different disturbances that occurred simultaneously, though there were only three years (1983,

1991, and 2007), where multiple disturbances occurred within the same year. Unfortunately, however, both cyclones occurred in years with either bleaching (1991) or bleaching and outbreaks of *A. planci* (1983), making it difficult to assess the independent effect of these disturbances.

3. Results and Discussion

3.1. Episodic Disturbances and Changes in Coral Cover. Since 1979, Moorea has been subject to seven coral bleaching events, two cyclones and two major outbreaks of *Acanthaster planci* (Table 1). As such, coral assemblages have been subject to an average of one disturbance every 2.7 years. Coral cover has varied considerably throughout this period, starting with mean cover of 40.9% (± 4.9 SE) in 1979, and ending with 16.5% (± 5.9 SE) in 2009. Coral cover recorded in 2009 (especially on the reef slope) was the lowest that has been recorded since 1979. However, coral cover has not exhibited a systematic decline through time, rather live coral increased to >50% on outer reef slopes in 1991, and also in 2004, immediately prior to the most recent outbreak of *A. planci* (Figures 2 and 3). Although there is limited data on chronic disturbances affecting the study locations in Moorea (e.g., fishing pressure, sedimentation, and/or eutrophication), it appears that periodic depletion of live corals is largely explained by the occurrence of acute disturbances (Figures 2 and 3), including bleaching, cyclones, and outbreaks of *A. planci*, all of which have contributed to significant coral depletion elsewhere throughout the Pacific [7, 12].

The average annual rate of change in coral cover recorded in years during which acute disturbances were reported was -25.6 (± 11.6 SE), compared to 1.5 (± 1.8 SE) in years with no reported disturbances. Average rates of coral loss were significantly different among years in which bleaching was reported to occur, versus cyclones or outbreaks of *A. planci* (ANOVA, $F = 9.38$, $df = 3/96$, $P < .001$). Among the different types of disturbances, overall rates of coral loss (averaged across zones and locations) were greatest (mean = -33.2 ± 14.1 SE) during outbreaks of *A. planci*, and significantly higher than rates of coral loss recorded during bleaching events (Tukeys Post-Hoc, $J = 0.41$, $P = .003$). The two major cyclones affecting Moorea (in 1983 and 1991) were associated very high rates of coral loss, but these disturbances coincided outbreaks of *A. planci* and/or bleaching (Figures 2(a) and 2(b)), making it difficult to assess the individual contribution of cyclones to recorded coral loss. However, the average rate of coral loss across years with multiple disturbances was higher than for recorded during any single disturbance, suggesting that different disturbances may have additive effects on coral loss (Figure 4).

During the course of the study (1979-2009), there were two distinct outbreaks of A. planci. The first of these outbreaks began in 1979, with infestations of sea stars first observed on the deep reef slope at Tiahura reef [68]. This initial infestation seemed to have ended by 1986 at Tiahura reef [68], but there were significant ongoing outbreaks in southern parts of Moorea until 1987 [33], probably reflecting the movement of sea stars as well as increased settlement
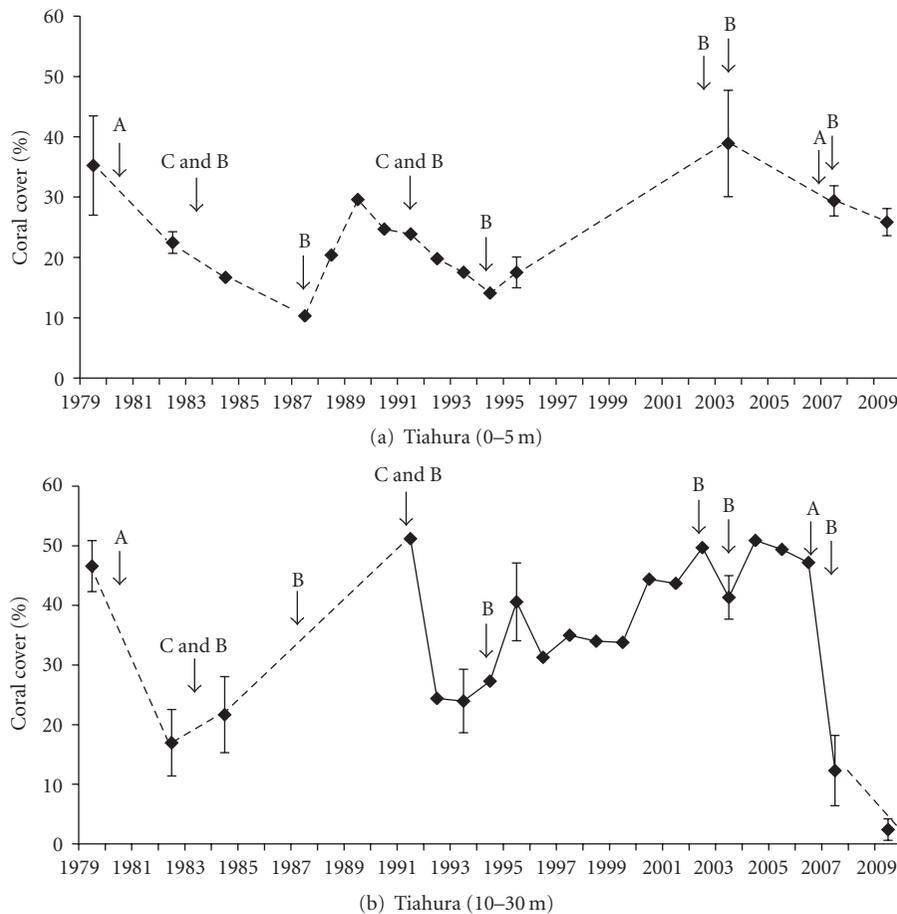
Figure 2: Interannual variation in mean (±SE) coral cover in (a) shallow habitats (0–5 m), and (b) deep habitat (0–30 m), and at the Tiahura reef, Moorea. Dashed lines indicate presumed trend across years for which no survey data are available. The occurrence of outbreaks of *A. planci* (A), coral bleaching (B), and cyclones (C) is shown.

of larval sea stars spawned by infestations of reproductively mature sea stars in northern Moorea, as reported by Pratchett [36] at Lizard Island on the northern Great Barrier Reef. The most recent and only second known outbreak of *A. planci* in Moorea started in 2006 [58], with high densities of sea stars again being recorded first on the outer-reef slope of Tiahura (23,000 sea stars km^{-2}, according to Lison de Loma et al. [74]) which was far higher than the density threshold of >1500 sea stars km^{-2}, considered to cause devastation to reef habitats by Moran and De'ath [75]. Accordingly, rates of coral loss recorded during outbreaks of *A. planci* were much higher on the reef slope, compared to the reef flat (Figure 4), which is consistent with observations of *A. planci* impacts elsewhere in the world (reviewed by Moran [76]).

Outbreaks of *A. planci* are one of the most significant biological disturbances on coral reefs [77] and remain the principal cause of short-term coral loss in the Indo-Pacific [15], often killing up to 90% of scleractinian corals, for example, on the Great Barrier Reef [36, 78, 79], in Guam [80], in Papua New Guinea [81] and in Japan [39]. After the first outbreak of *A. planci* in Moorea (1979–1986), coral cover at Tiahura increased rapidly and returned to predisturbance levels (46.6%) within less than 5 years. In

other geographic locations, recovery of coral cover following outbreaks of *A. planci* has typically taken much longer (e.g., Great Barrier Reef—10 to 15 years, [82]; 10 to 20 years, [83]; 10 to 25 years, [84] and 20 to 40 years, [32]; Guam—11 years, [85]; 20 to 30 years, [86]). Coral recovery was even more pronounced in deep water where the coral cover increased from <20% in 1982 to 51% in 1991 (Figure 2(a)). This apparent resilience in coral cover on reefs in Moorea has been reported previously and may be attributable to consistently high rates of coral recruitment [58]. However, relatively rapid increase in total coral cover may belie fundamental changes in coral composition [49] and thereby habitat structure. Moreover, the amount of remnant corals on the reef slope in 2009 was much lower compared to the end of the first *A. planci* outbreak in 1982 (Figure 2), which may suggest that recovery from the latest outbreak of *A. planci* will take substantially longer [87].

Coral bleaching has occurred every 3-4 years at Moorea since 1983, but these mass-bleaching events have not caused consistent declines in live coral cover. The greatest rates of coral change recorded during bleaching years (1991 and 2007) both coincide with other disturbances (a cyclone and outbreak of *A. planci*, resp.), whereas in all other years that
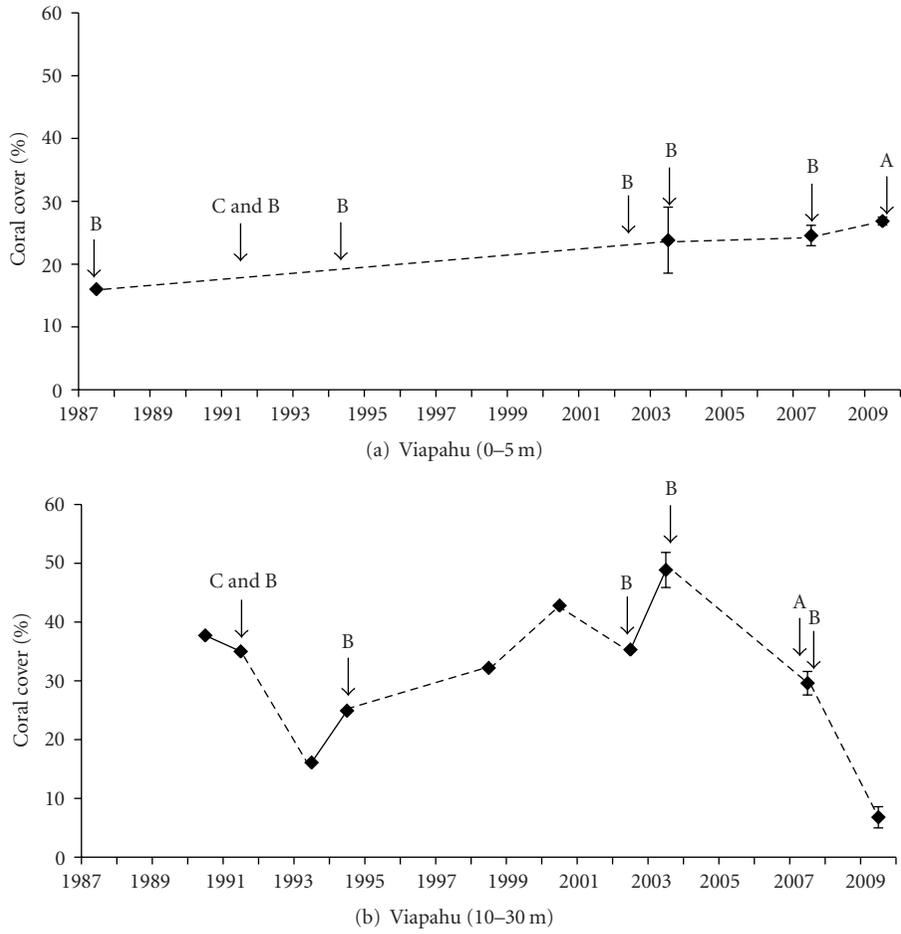
(a) Viapahu (0–5 m)

(b) Viapahu (10–30 m)

FIGURE 3: Interannual variation in mean (±SE) coral cover in (a) deep habitat (0–30 m) and (b) shallow habitats (0–5 m) at the Viapahu reef, Moorea. Dashed lines indicate presumed trend across years for which no survey data is available. The occurrence of outbreaks of *A. planci* (A), coral bleaching (B), and cyclones (C) is shown.
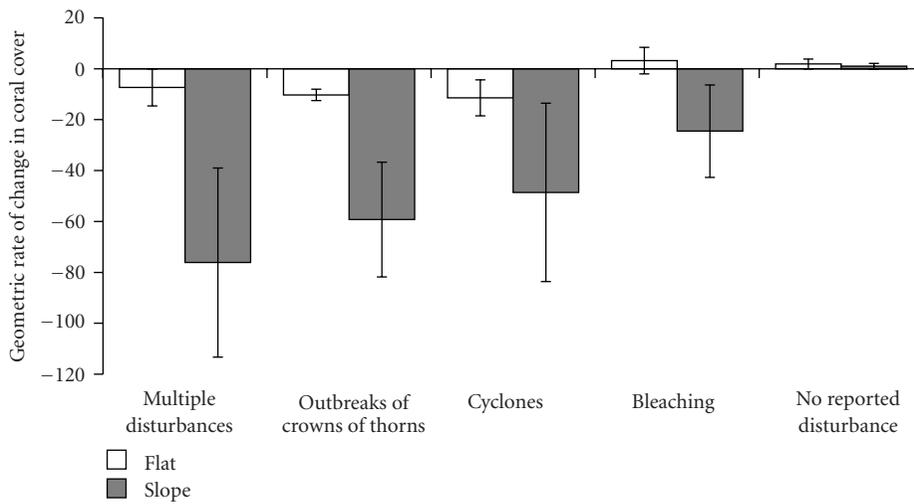

FIGURE 4: Variation in the mean (±SE) annual geometric rate of change in total cover of scleractinian corals, for years (between 1979 and 2008) during which outbreaks of *A. planci* (1979–1986, 2006–2008), cyclones (1983 and 1991), or bleaching (1983, 1987, 1991, 1994, 2002, 2003, and 2007) were reported.

TABLE 1: Episodic disturbances that have affected Moorea Island, and geometric rate of change in mean coral cover (Δ Coral cover) reported to occur between successive surveys spanning each disturbance.

| Disturbances	Period	Reference(s)	Δ Coral cover
Bleaching Events	March–May, 1983	Williams and Bunkley-Williams [28], Glynn [22], Salvat [88]	−2.2 (±13.8 SE)
	March-April, 1987	Williams and Bunkley-Williams [28], Glynn [22], Salvat [88]	21.1 (±14.4 SE)
	March-April, 1991	Salvat [88], Gleason [72], Adjeroud et al. [58]	−43.9 (±24.2 SE)
	February–April, 1994	Hoegh-Guldberg and Salvat [26], Adjeroud et al. [16, 58]	15.3 (±6.9 SE)
	April–July, 2002	Adjeroud et al. [16, 58], Penin et al. [61]	4.9 (±9.9 SE)
	January–March, 2003	Carroll et al. (unpulished data)	−0.3 (±13.9 SE)
	February–April 2007	Adjeroud et al. [58], Pratchett et al. [62], Penin et al. (unpublished data)	−59.3 (±4.0 SE)
Cyclones	April, 1983	Harmelin-Vivien and Laboute [19]	−2.2 (±13.8 SE)
	December, 1991	Gleason [72]	43.9 (±24.2 SE)
Acanthaster planci outbreaks	1979–1986	Bouchon [60], Faure [33]	−12.2 (±4.5 SE)
	2006–2009	Lison de Loma et al. [74], Pratchett et al. [62]	−64.8 (±25.4 SE)
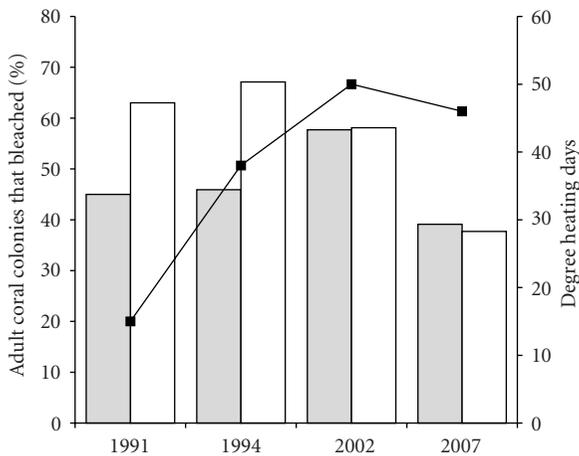
FIGURE 5: Percentage of adult coral colonies that bleached at Tiahura (grey bars) and Viaphu (white bars), versus the duration of temperature anomalies (degree heating days) during four episodes of mass-bleaching in Moorea. Degree heating days were calculated for the summer period (September–March) in each year that mass-bleaching was documented (generally between February and April), based on 4 km Pathfinder (NOAA) data for Tiahura Reef with backfilling and smoothing functions to eliminate null values.

bleaching has been recorded, coral loss was negligible. Coral bleaching generally occurs at Moorea whenever sea surface temperature (SST) exceeds the notional threshold of 29.2°C for more than several weeks [16, 26, 58, 61, 64]. There does not, however, seem to be any significant relationship between the extent of bleaching recorded during major mass-bleaching events (1991, 1994, 2002, and 2007) and the temporal duration of thermal anomalies (Figure 5). On the outer-reef slope at Tiahura and Vaipahu, the percentage of coral that bleached in 1991 was 45% and 63%, respectively,

[72, 88], compared to 45.9% and 67.1% in 1994 [26], 57.7% and 58.1% in 2002 [61], and 39.1% and 37.7% in 2007 (Penin et al. unpublished data). As such, the severity of bleaching appears to have declined, even though the severity of temperature extremes (degree heating days) has increased among this bleaching events (Figure 5). Declines in the response of corals, despite similar or worsening thermal stresses, suggest that corals and/or the zooxanthellae may have acclimatized or adapted to increasing temperature, and may therefore, be less susceptible to future thermal anomalies [89, 90]. Alternatively, successive disturbances are likely to cause changes in the structure of coral assemblages, increasing the proportional abundance of species and genotypes that are most resistant to bleaching [25, 91]. If the latter is true, then severe bleaching and high rates of coral mortality may result with further increases in the severity and/or duration of temperature stresses.

3.2. Persistent Shifts in Coral Composition. Aside from causing marked changes in live cover, acute disturbances occurring in Moorea from 1979 to 2009 have caused significant and persistent shifts in coral composition (Figures 4(a) and 4(b)). In 1979, coral communities at Tiahura were mostly dominated by *Acropora* (Figures 4(a) and 4(b)). However, the *A. planci* outbreaks in late 1970s greatly affected *Acropora* corals which declined by 84.3% throughout the reef by 1982. While coral cover increased rapidly following the initial outbreak of *A. planci*, the postoutbreak coral composition was very different compared to the composition recorded in 1979 [60]. Berumen and Pratchett [49] described apparent recovery of coral cover despite marked temporal changes in coral composition as evidence that recurrent disturbances were causing a pronounced shifts in the structure of local coral assemblages. In 2003, *Pocillopora* was the most abundant genus in Moorea (Figures 4(a) and 4(b)), probably

(a) Deep habitat (10–30 m)
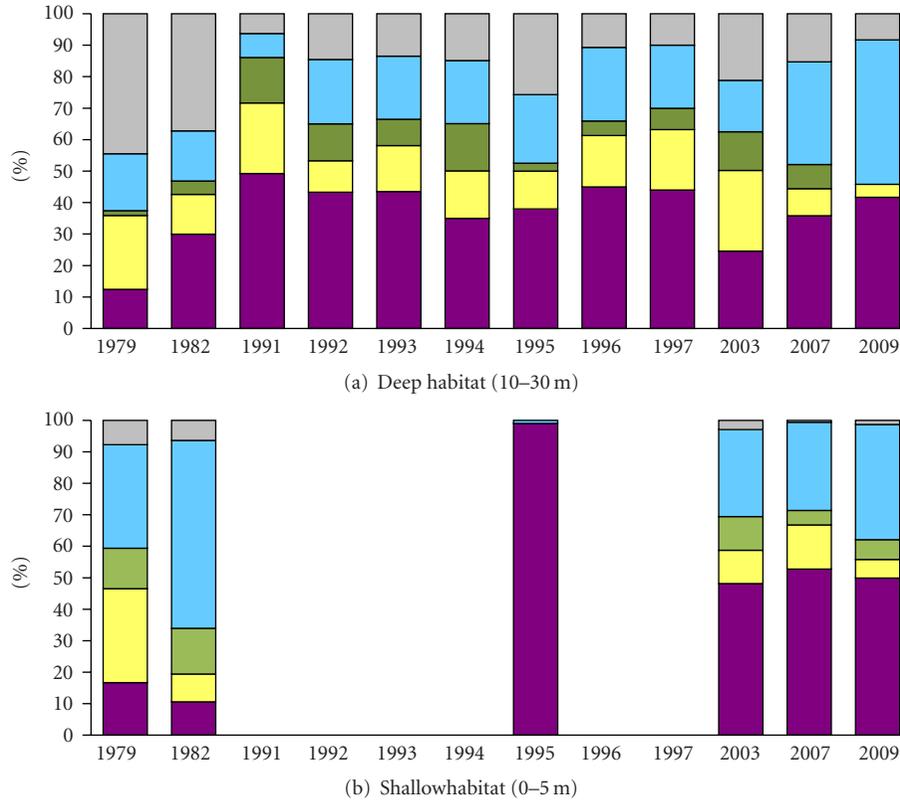
(b) Shallowhabitat (0–5 m)

FIGURE 6: Interannual variation in relative abundance of major coral genera at Tiahura reef, Moorea Island.

because it is less affected by coral bleaching, outbreaks of *A. planci* [92, 93], and tropical storms [49], especially compared to *Acropora* corals. *Pocillopora* corals increased in their relative abundance after the initial outbreak accounting for 30% and 49.2% of the coral cover on the reef slope (10 to 20 m) in 1982 and 1991, respectively, and remained the dominant coral until 2009 (Figure 4(a)). Similarly, in shallow waters habitats, the dominant coral genera changed from *Acropora* to *Porites* after the first outbreak of *A. planci* in 1982 (Figure 4(b)).

Acanthaster planci selectively feed on certain coral species, mostly *Acropora* [93, 94]. Accordingly, the proportional cover of *Acropora* (relative to all other genera) declined from (26.5%) in 1979, before the first reported outbreak of *A. planci*, down to 11.0% in 1982 (Figure 4). Further changes in coral composition were apparent in 1991, whereby the prevalence of *Acropora* coral was further diminished, probably due to their disproportionate susceptibility to both coral bleaching and storm damage [72]. Both *Pocillopora* and *Porites* have tended to increase in prevalence through time at the expense of *Acropora* corals and other coral genera (Figure 4). The most recent outbreak of *A. planci* (2006–2009) has further reduced proportional and absolute abundance of *Acropora* corals which accounted for only 4.2% of the coral cover in deep habitat and 5.9% in shallow habitat in 2009 (Figure 4, Pratchett et al. unpublished data). In contrast, *Porites* and *Pocillopora* corals accounted for 45.8% and 41.7% of the coral cover in deep habitat, respectively,

and 36.6% and 49.9% in shallow habitat in 2009. Despite an increase in proportional cover of *Porites* and *Pocillopora* corals, absolute cover of these genera has also declined during the latest outbreak of *A. planci*. This is consistent with observed feeding habitats of *A. planci* whereby starfishes will tend to consume more of their less preferred prey corals when the overall abundance of the preferred prey drops [94].

Although not measured in Moorea, declines in the abundance of branching corals, especially *Acropora* and *Pocillopora*, are likely to cause reductions in diversity and topographical complexity of coral reef habitats [95]. This will, in turn, affect many other reef-associated species [13, 96]. *Acropora* and other branching corals are the predominant habitat used by coral-feeding and coral-dwelling species, and specialized species may disappear following declines in abundance of these microhabitats [96, 97]. Moreover, any declines in habitat diversity and complexity are likely to reduce the number of species that cooccur in coral reef habitats [13, 38], owing to the role of topographic complexity in moderating competition and predation [56]. In Moorea, these effects may be partly offset, by increases in the abundance of *Pocillopora* (Figure 6). However, declines in abundance of *Acropora* from 1979 to 2003 have already caused significant declines in the abundance of (coral-feeding) butterflyfishes that specialize on *Acropora* [49], and these fishes (*C. reticulatus* and *C. trifascialis*) may now be facing localized extinction (especially on the reef slope) given

further declines in abundance of both *Acropora*, as well as other potential coral prey.

4. Conclusion and Management Implications

Coral reefs on the north coast of Moorea have been subject to several periods of extensive coral loss since 1979, caused by outbreaks of *A. planci*, cyclones, and/or bleaching. The greatest rates of coral loss recorded occurred during two major outbreaks of *A. planci* in 1979–1982 and 2006–2009, which caused particularly severe coral loss on the outer-reef slope. Moreover, coral loss was greatest among *Acropora* corals, thereby contributing to a marked shift in the composition of coral assemblages. Until now, effects of coral bleaching on local coral cover appear to have been fairly minor, especially compared to outbreaks of *A. planci*. However, projected increases in ocean temperatures, as well as ocean acidification, may yet cause significant coral loss in Moorea, and throughout the Pacific [98]. Hoegh-Guldberg et al. [98] predict that average coral cover on reefs in the Pacific will decline by 30%–40% in the coming decades, due to increasing effects of global climate change. Moreover, robust species such as *Porites* and *Favia* are expected to replace branching species, mostly *Acropora,* as the dominant coral genera [98].

Coral reef ecosystems are fundamental to coastal fisheries, and the provision of fresh seafood, throughout the Pacific. However, increasing disturbances, and the associated degradation of coral reef habitats threaten to undermine the capacity of these ecosystems to yield sufficient food and resources [99]. Climate change will, therefore, represent a major challenge for Pacific countries in the coming decades. However, in locations where major cause(s) of coral loss relate to more direct anthropogenic disturbances (e.g., fishing and eutrophication), improved local management may serve to reduce and/or delay effects of climate change. There is considerable controversy relating to the role of anthropogenic activities in causing and/or exacerbating outbreaks of *A. planci*. However, on the Great Barrier Reef, it is suggested that outbreaks result from increased nutrient loads [100] and/or overfishing of predatory fishes [101, 102]. There is a potential, therefore, that reduced fishing and/or improved water quality will minimize the occurrence and impacts of outbreaks of *A. planci*. In this instance, ecosystem management may provide an effective strategy to reduce a major contributor to coral loss in Moorea, and thereby improve ecosystem resilience to future climate change.

Acknowledgments

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