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NOTE

Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef

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Abstract Coral reefs are increasingly threatened by various disturbances, and a critical challenge is to determine their ability for resistance and resilience. Coral assemblages in Moorea, French Polynesia, have been impacted by multiple disturbances (one cyclone and four bleaching events between 1991 and 2006). The 1991 disturbances caused large declines in coral cover (~51% to ~22%), and subsequent colonization by turf algae (~16% to ~49%), but this phase-shift from coral to algal dominance has not persisted. Instead, the composition of the coral community changed following the disturbances, notably favoring an increased cover of *Porites*, reduced cover of *Montipora* and *Pocillopora*, and a full return of *Acropora*; in this form, the reef returned to pre-disturbance coral cover within a decade. Thus, this coral assemblage is characterized by resilience in terms of coral cover, but plasticity in terms of community composition.

Keywords Coral · Bleaching · Cyclone · Phase-shift · Resilience · Moorea

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Introduction

Like many marine ecosystems, in recent decades, coral reefs have been severely impacted by various types of natural and anthropogenic disturbances (Hughes et al. 2003, 2007; Pandolfi et al. 2003; Bellwood et al. 2004). While some disturbances are a routine part of coral reef dynamics, there is concern that the frequency and severity of large-scale disturbances have increased over the last three decades (Hoegh-Guldberg et al. 2007). Faced with assaults by numerous disturbances, coral reefs have been affected by widespread mortalities of keystone organisms, and in many cases have undergone a striking phase shift in community structure (McManus and Polsenberg 2006). Classically, these phase shifts have involved the replacement of stony corals by algae, which are then unable to provide the ecosystem goods and services previously supplied by corals (McManus and Polsenberg 2006).

Scleractinians provide the framework of coral reefs, and the dynamics of these ecosystems are largely influenced by changes in the population structure of corals, the detection of which requires long-term monitoring efforts, with frequent sampling necessary to resolve rapidly occurring events such as episodic recruitment, sudden-onset lethal diseases, or transient population perturbations (Connell et al. 1997; Coles and Brown 2007). The temporal resolution of time-series analyses is particularly germane to testing coral communities for resistance (i.e., the capacity to remain unchanged following disturbances), describing recovery trajectories (i.e., patterns of recolonization following disturbances), and assessing resilience (i.e., the capacity to return to a reference state following disturbances; West and Salm 2003).

The coral reefs along the north shore of Moorea have been studied at the Tiahura Outer Reef Sector (TORS) since the early 1970s, but starting in 1991, a new quantitative program began to record changes with annual resolution (Adjeroud et al. 2002). Between 1991 and 2006, TORS has been impacted by one cyclone (1991), and four bleaching episodes (1991, 1994, 2002, 2003) that were associated with high sea-surface temperatures (Penin et al. 2007; Fig. 1). Prior to 1991, TORS experienced two bleaching events (1984 and 1987), and outbreaks of the coral predator *Acanthaster planci* (1980–1982), which caused coral cover to decline from ~45% in 1979 to ~12% in 1982 (Bouchon 1985; Berumen and Pratchett 2006). The 37-year history of TORS constitutes one of the longest records of coral reef dynamics, and the trajectories of change are marked by striking differences compared to those dominating contemporary literature. Notably, while TORS has sustained multiple severe losses of coral cover, this reef has repeatedly regained coral cover to levels similar to pre-disturbance levels, and has shown no sign of a persistent phase shift to macroalgal dominance. Here, we focus on the most recent 15 years of TORS, and compare the effects of five disturbances in the context of better understanding the roles of resilience and recovery in determining the trajectory of change in coral communities.

Materials and methods

The study site is located on the outer reef slope at the Tiahura sector at the western end of the north shore of Moorea (17°30′S, 149°50′W). The Tiahura reef slope is largely free of direct anthropogenic disturbances, as demonstrated by sediment and water quality analyses (Schrimm et al. 2004). The percent cover of algal turf (heterogeneous assemblage of filamentous algae that typically is <10 mm in height), macroalgae (macroscopic fleshy algae, represented mostly by the genera *Turbinaria*, *Halimeda*, and *Sargassum*) and scleractinian corals was recorded along four permanent transects of 25 m length, oriented parallel to the reef front, and placed at 10–12 m depth on the outer slope. For the purpose of the present analyses, each transect

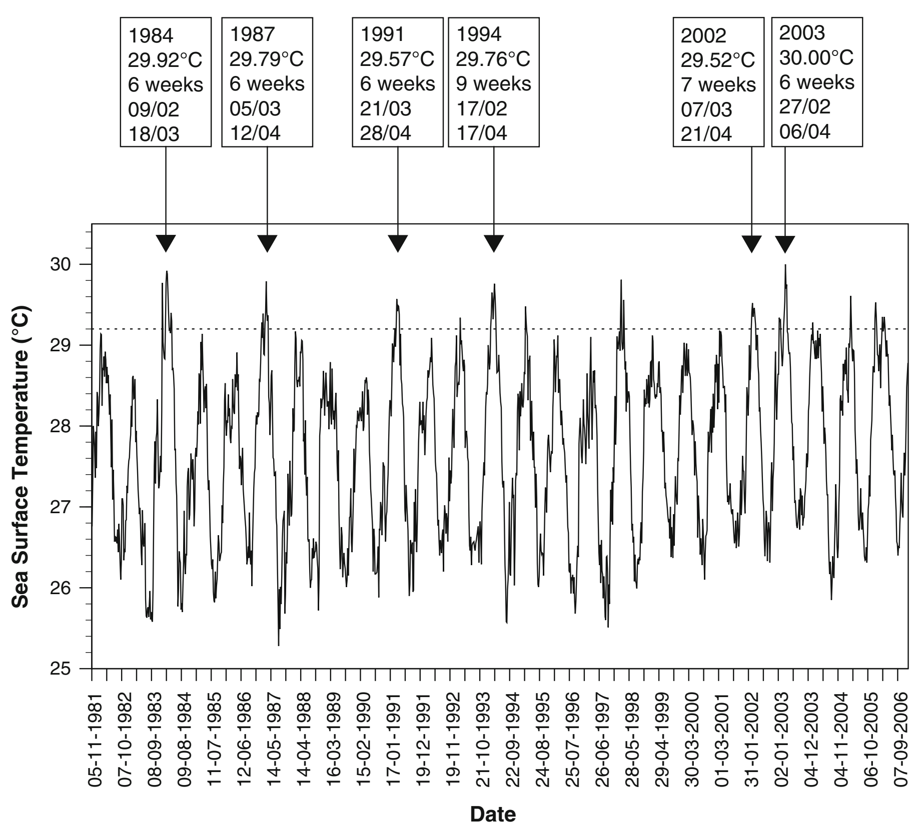

Fig. 1 Weekly sea surface temperature around Moorea from November 1981 to December 2006. IGOSS-nmc data courtesy of the Lamont-Doherty Climate Center. Arrows indicate bleaching events, and the horizontal dotted line indicates the thermal threshold for Moorea (29.2°C). For each event, the amplitude of the temperature anomaly (highest temperature) and its duration (number of consecutive weeks with temperature higher than the threshold, and dates) are indicated in boxes

was treated as a statistical replicate ($n = 4$) in all temporal contrasts. We used the Point Intercept Transect Method, with points placed every 0.25 m, to estimate cover of each category of benthic organisms. Data were collected once a year in March–April. For further details on the sampling design and methodology, see Adjeroud et al. (2002).

The significance of the interannual variability was evaluated using the nonparametric test of Friedman, because of the absence of normality in the data, and because these data were not independent. The Wilcoxon test was used in an a posteriori fashion to compare values of two different years. We used Kruskal's non metric multidimensional scaling (MDS) to examine the interannual variation in the composition of the coral assemblage based on the Bray–Curtis dissimilarity index.

Results and discussion

The five disturbances had different impacts on the coral assemblages. A significant decline in coral cover followed the two disturbances of 1991. Coral cover (pooled among genera) declined from 51.0 ± 9.5% (mean ± SD) in early 1991 to 24.2 ± 14.4% in 1992, and 22.5 ± 9.3% in 1993 (Fig. 2; Table 1). In contrast, the bleaching events of 1994, 2002, and 2003 had no detectable effects on coral cover, even though the thermal anomalies causing these events and their short-term impacts in term of bleaching prevalence were similar to the 1991 bleaching event (Salvat 1992; Hoegh-Guldberg and Salvat 1995; Penin et al. 2007; Fig. 1). The decline in coral cover in the 4 years following 1991 is among the most rapid of this magnitude recorded following natural disturbances. For instance, along the north coast of Jamaica, coral cover at 7 m depth declined from ~75% in 1977–1979 to ~40% in 1980 after Hurricane Allen, and to ~5% by 1993 (Hughes 1994). The protracted loss of coral cover in Jamaica followed two hurricanes, three bleaching events, a reduction of grazing pressure and a potential pulse of nutrients which all

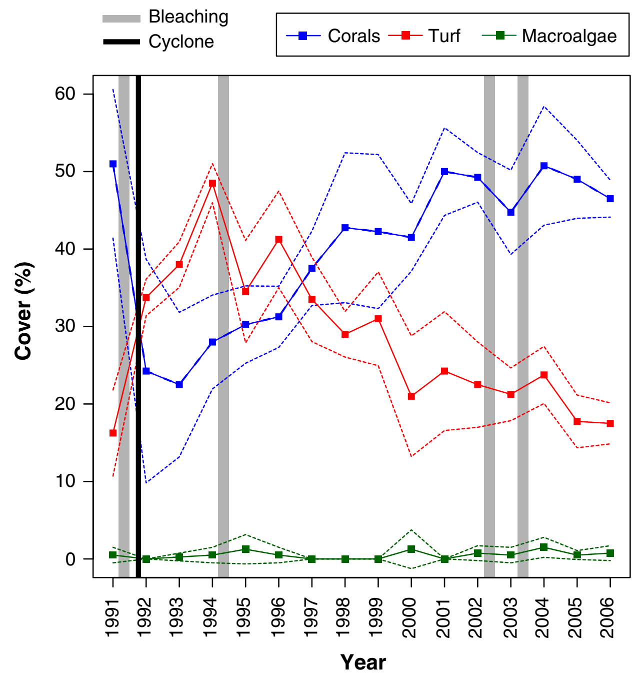

Fig. 2 Variation in coral, turf, and macroalgal cover at Tiahura between 1991 and 2006. The cyclone (December 1991) and the four bleaching events (March–July 1991, 1994, 2002 and 2003) are indicated. *Dotted lines* represent standard deviation

contributed to a dramatic increase of algal cover, from ~4% in 1977 to ~92% in 1993 (Hughes 1994). On the southern Great Barrier Reef, an "extreme" loss in coral cover was also reported as a result of cyclones, from ~80% in 1987 to ~10% in 1989 (Halford et al. 2004), and in the eastern Indian Ocean, coral cover decreased from ~48% in 1998 to ~11% in 1999 after the 1998 bleaching event (Smith et al. 2008).

Between 1991 and 1994, the decline in coral cover at TORS was accompanied by a rapid colonization by turf algae (16.2 ± 5.5% in 1991 to 48.5 ± 2.5% in 1994; Fig. 2). Turf algae are generally among the first to colonize vacant space, but are often replaced by dense growths of macroalgae (McManus and Polsenberg 2006; Done et al.

Table 1 Statistical significance (*P* value) of interannual variability in cover among years (Friedman tests), and of differences between select pairs of years (Wilcoxon tests), for major taxa of corals and algae

	All corals	*Acropora*	*Montipora*	*Pocillopora*	*Porites*	Turf algae	Macroalgae
Among years	<0.001	<0.001	0.046	0.312	<0.001	<0.001	0.449
1991 vs. 1992	0.061	0.029	0.183	0.061	0.659	0.029	0.453
1991 vs. 1993	0.030	0.029	0.055	0.030	0.559	0.030	1.000
1991 vs. 1994	0.030	0.029	0.183	0.030	0.559	0.029	1.000
1994 vs. 1995	0.661	0.369	0.306	0.194	0.659	0.028	0.620
2002 vs. 2003	0.309	0.462	0.243	0.470	1.000	0.770	0.739
2003 vs. 2004	0.465	0.301	0.766	0.243	1.000	0.442	0.278
1991 vs. 2006	0.312	0.561	0.053	0.108	0.028	0.561	0.739

2007). On TORS, however, a successional sequence of algal growth was not observed, but instead, the cover of algal turf decreased after 1994, and returned to the pre-disturbance levels within a decade. This result suggests that the availability of vacant space is not sufficient to cause a persistent increase in algal cover, and that other factors, such as a reduction in grazing pressure or an increase in nutrients—that were not present at TORS—are necessary for a phase change to macroalgal dominance (McManus and Polsenberg 2006; Mumby et al. 2007).

For TORS, the response of coral populations to disturbances, and their recovery trajectories, differed among the four dominant genera. *Acropora* was affected by the disturbances of 1991, declining from 11.5 ± 2.6% in 1991 to 2.5 ± 1.7% in 1992, but its cover was only slightly affected by subsequent bleaching events (Fig. 3; Table 1). *Acropora* showed a high rate of recovery after the 1991 disturbances and until 2005, with pre-disturbance cover restored by 1999. *Montipora* was also affected by the 1991 disturbances, but its cover declined further as a result of two other bleaching events (1994 and 2002), and did not show signs of recovery. *Pocillopora* was also affected by the 1991 disturbances, declining from 25.0 ± 7.0% in 1991 to 10.5 ± 8.6% in 1992, thereafter with the cover remaining relatively stable at ~15%. In contrast to other genera, the cover of *Porites* was unaffected by the five disturbances, and its cover increased between 1991 and 2005, finally reaching 12.2 ± 2.3%, when it became the second most dominant coral. Interestingly, massive *Porites* has also been identified as an ecological "winner" in Okinawa following the bleaching event of 1998 (Loya et al. 2001), and in the Caribbean, *P. astreoides* (the "massive" *Porites* of this region) has also been a relative winner over the last few decades of disturbances (Green et al. 2008). Together, this evidence suggests it would be productive to evaluate the biological characteristics favoring the success of massive *Porites* in the face of multiple disturbances.

The results of this long-term survey support the hypothesis that the algal-dominated phase can represent a state from which a rapid reversal is possible, or a transitional state along a gradient of temporal changes (Bellwood et al. 2006; Idjadi et al. 2006; Mumby et al. 2007). In addition, our results reveal that corals can recover rapidly following a dramatic decline. Such decadal-scale recovery of coral cover has been documented at some locations (Connell 1997; Halford et al. 2004, Emslie et al. 2008, Sheppard et al. 2008), but our results are novel in

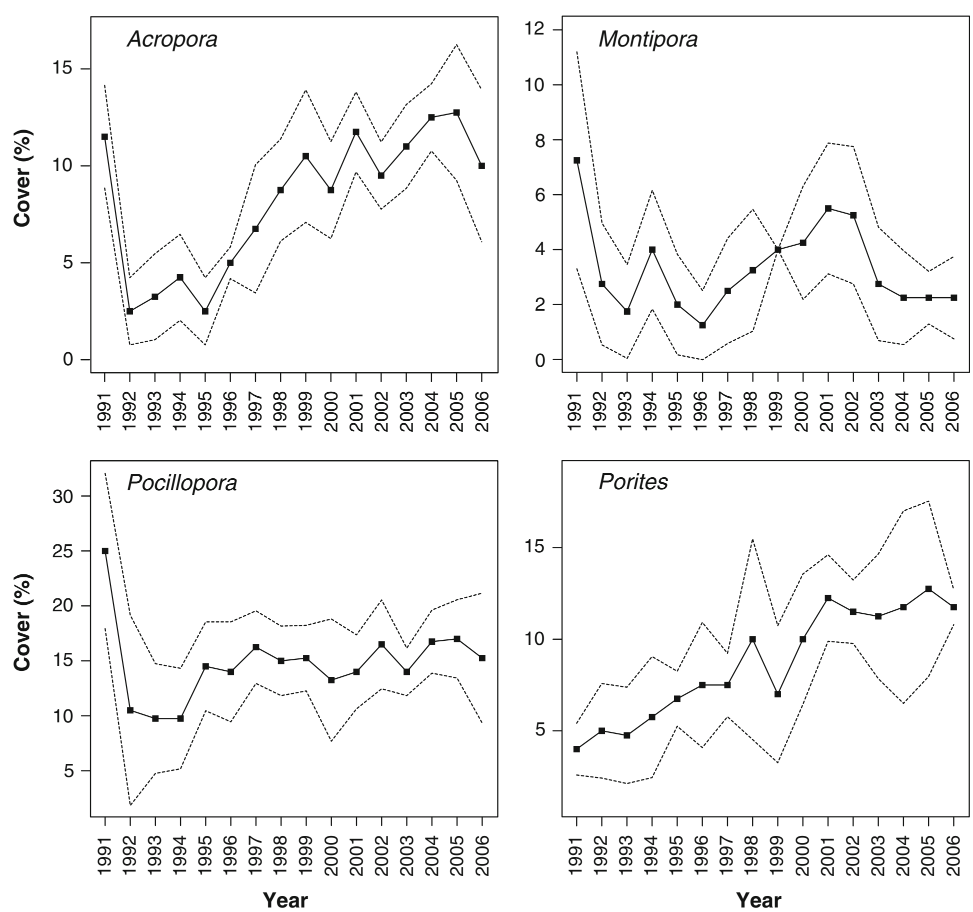

Fig. 3 Impacts of disturbances and recovery trajectories of the four dominant coral genera at Tiahura between 1991 and 2006. Dotted lines represent standard deviation

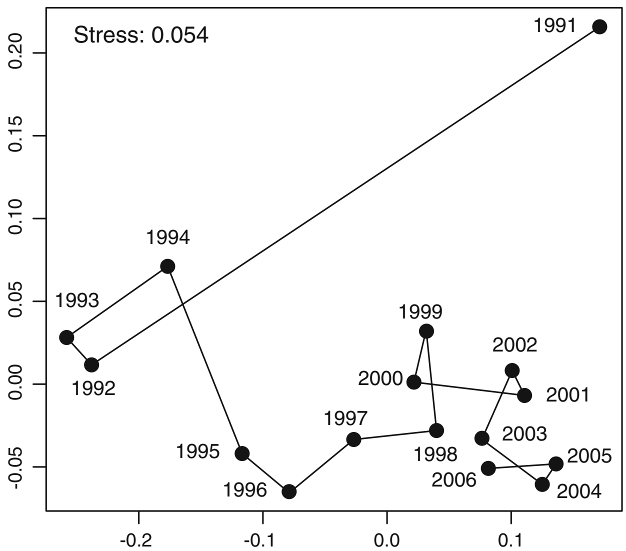

Fig. 4 Variation in composition of the coral assemblage. Kruskal's non-metric multidimensional scaling (MDS), using Bray-Curtis dissimilarity index of the coral assemblage recorded annually from 1991 to 2006 at Tiahura

demonstrating rapid recovery against a backdrop of ongoing, high frequency, and large-scale disturbances (but see Connell et al. 1997; Wakeford et al. 2008). At TORS, the post-disturbance dynamic is associated with a shift in the structure of the assemblages (Fig. 4). Thus, coral assemblages at TORS appear to be characterized by ecological resilience in terms of overall coral cover, but plasticity in terms of generic composition.

Tiahura is among the few reefs, all located in the Indo-Pacific, that have shown the capacity to recover from severe and recurrent disturbances (Connell 1997), and it supports the hypothesis that some reefs will undergo gradual changes in structure of their coral communities in response to major stress rather than collapse abruptly (Loya et al. 2001; Hughes et al. 2003; Wakeford et al. 2008). Despite the optimism that the last 15 years of coral dynamics at TORS engender, these results must be considered with caution, as most models predict an increase in the frequency and severity of disturbances over the next few decades (Pandolfi et al. 2003; Hoegh-Guldberg et al. 2007). Indeed, a significant outbreak of *A. planci* began in Moorea immediately following the period covered by this study (late 2006) (personal observation), and this ongoing outbreak has reduced the coral cover on some outer reef sites to <10% (in May 2008, PJ Edmunds, personal communication). While it is too soon to evaluate the long-term implications of this disturbance for TORS, we suspect that the coral community in this location may regrow rapidly, at least based on the abundance of coral recruits we have found at near-by sites.

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