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REPORT

Three decades of recurrent declines and recoveries in corals belie ongoing change in fish assemblages

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Abstract Coral reefs are increasingly being altered by a myriad of anthropogenic activities and natural disturbances. Long-term studies offer unique opportunities to understand how multiple and recurrent disturbances can influence coral reef resilience and long-term dynamics. While the long-term dynamics of coral assemblages have been extensively documented, the long-term dynamics of coral reef fish assemblages have received less attention. Here, we describe the changes in fish assemblages on Tiahura reef, Moorea, from 1979 to 2011. During this 33-yr period, Tiahura was exposed to multiple disturbances (crown-of-thorns seastar outbreaks and cyclones) that caused recurrent declines and recoveries of coral cover and changes in the dominant coral genera. These shifts in coral composition were associated with long-term cascading effects on fish assemblages. The composition and trophic structure of fish assemblages continuously shifted without returning to their initial composition, whereas fish species richness remained stable, albeit with a small increase over time. We detected nonlinear responses of fish density when corals were most degraded. When coral cover dropped below 10 % following a severe crown-of-thorns sea star outbreak, the density of most fish trophic groups sharply decreased. Our study shows that historical contingency may potentially be an important but largely underestimated factor explaining the contemporary structure of reef fish assemblages and suggests that temporal stability in their structure and function should not necessarily be the target of management strategies that aim at increasing or maintaining coral reef resilience.

Keywords Resilience · Threshold · Tipping point · Coral fish assemblages · Historical contingency · Shifting baseline

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Introduction

Most coral reefs are undergoing rapid changes due to an increase in both anthropogenic and natural disturbances (Chin et al. 2011). Some anthropogenic disturbances such as overfishing, habitat destruction and climate change are largely contributing to the overall degradation of these ecosystems (Bellwood et al. 2004; Pandolfi et al. 2005; Mora 2008; Alvarez-Filip et al. 2009; De'ath et al. 2009; Mora et al. 2011; Ban et al. 2014). For instance, the prevalence of these disturbances in the Caribbean has caused a gradual regime shift from a coral- to a macroalgal-dominated state that has persisted over decades, thus reflecting a dramatic loss in resilience (Hughes 1994; McClanahan and Muthiga 1998; Ostrander et al. 2000; Gardner et al. 2003; Hughes et al. 2010, 2013). Alternatively, natural disturbances also play an important role in

the long-term dynamics of coral reefs, and there is mounting evidence that they can often cause succession between periods of decline in coral cover and periods of recovery (Wilson et al. 2006; Adjeroud et al. 2009; Osborne et al. 2011; Speed et al. 2013; Graham et al. 2015).

Undoubtedly, long-term dynamics of coral reefs, and ultimately their resilience, are influenced by both natural and anthropogenic disturbances. However, to understand coral reef resilience, many studies compare snapshots of coral reef state along a disturbance gradient ignoring their inherent temporal dynamics (Christensen et al. 1996; Dayton et al. 1998; Knowlton and Jackson 2008; Sandin et al. 2008; D'agata et al. 2014). Multi-decadal studies are required to gain insight into coral reef resilience, as decline and recovery periods operate at scales of one to several decades (Hughes et al. 2010). To date the available long-term surveys of coral reefs have primarily documented either the gradual regime shift occurring in the Caribbean (e.g., Hughes 1994; McClanahan and Muthiga 1998; Gardner et al. 2003) or the loss of coral occurring on the Great Barrier Reef (GBR) over the last 27 yr (e.g., Bellwood et al. 2004; De'ath et al. 2012). Other long-term surveys have reported changes in coral assemblages in other parts of the globe, such as Taiwan (26 yr of survey: Kuo et al. 2012), Kenya (McClanahan and Graham 2005; Darling et al. 2010), Hawaii (Coles and Brown 2007), Western Australia (Speed et al. 2013), the Indo-Pacific region (Bruno and Selig 2007), South Pacific (Adjeroud et al. 2002, 2009), or the Indian Ocean (Ateweberhan et al. 2011). These studies mostly focused on coral assemblages; however, it is also essential to understand whether changes in coral assemblages can induce long-term cascading effects on fish assemblages, as many fish species depend on corals for food or shelter.

Current evidence suggests that periods of coral decline can have contrasting effects on fish assemblages, with studies reporting both decreases (Halford et al. 2004; Jones et al. 2004; Graham et al. 2006; Halford and Caley 2009; Paddack et al. 2009) or no change (Bellwood et al. 2006, 2012; Cheal et al. 2008; Wilson et al. 2009) in fish richness and/or density due to declines in coral cover. However, most long-term surveys (one to two decades) have revealed that coral declines can have long-lasting effects on the composition of fish assemblages (Halford et al. 2004; Jones et al. 2004; Bellwood et al. 2006, 2012; Graham et al. 2006; Cheal et al. 2008; Halford and Caley 2009; Wilson et al. 2009). Most of these studies have focused on single disturbances, and therefore, our knowledge of how fish assemblages respond to recurrent disturbances is unknown. In addition, as the effects of disturbances on fish assemblages can vary greatly among taxonomic and trophic groups of fishes, and among locations, it is important to

incorporate a wide range of fish assemblages in different locations. To date, the majority of studies have focused on the GBR while other locations have received less attention (e.g., Seychelles: Graham et al. 2006, 2015; Tanzania: Garpe et al. 2006).

Here, we focused on Tiahura reef (Moorea, French Polynesia). The coral (Bouchon 1985; Adjeroud et al. 2009; Pratchett et al. 2011; Trapon et al. 2011) and fish assemblages (Galzin and Legendre 1987; Berumen and Pratchett 2006) of this coral reef have been intensively studied since the early 1980s. However, previous studies have focused on either short timescales (Trapon et al. 2011), only coral assemblages (Adjeroud et al. 2009; Pratchett et al. 2011), or specific groups of fish (Berumen and Pratchett 2006). Hence, we seized the opportunity to bring together all existing data on both coral and fish assemblages to document their joint long-term dynamics over the past three decades. During this period, Tiahura reef was exposed to multiple disturbances including cyclones, outbreaks of the coral predator crown-of-thorns seastar (COTS; *Acanthaster planci*), and coral bleaching. These are among the most important natural disturbances influencing coral reef ecosystems in the insular South Pacific, the GBR and elsewhere (Osborne et al. 2011; De'ath et al. 2012; Kayal et al. 2012; Leray et al. 2012; Baird et al. 2013). In this study, we aimed at documenting the long-term dynamics of coral cover in response to multiple disturbances. We further assessed whether recurrent declines and recoveries in coral cover led to cascading effects on the long-term dynamics of fish assemblages. Finally, we assessed whether there were early signals or thresholds of major changes in the density of six key fish trophic groups in response to change in coral cover.

Materials and methods

Study system—Tiahura reef

Tiahura reef is located on the northwestern coast of Moorea Island in the Society archipelago (French Polynesia). This reef has been extensively studied since the early 1980s (e.g., Bouchon 1985; Galzin and Legendre 1987; Adjeroud et al. 2002, 2009) offering a unique opportunity to document its long-term dynamics over several decades. Moorea is the second largest inhabited island in French Polynesia. Its coral reefs support many recreational activities (e.g., scuba diving) as well as subsistence fishing. Moorea is not exempt from anthropogenic pressures such as nutrient input and increased sedimentation but these are mostly contained within the lagoon. Here we focus on the fore reef, outside the lagoon, which is the part of the reef most exposed to COTS outbreaks and cyclones.

Data collection

The coral and fish assemblages of Tiahura reef were surveyed over five transects located on the fore reef at 12 m depth. Initially, a 50 × 2 m permanent belt transect marked by iron stakes hammered in the substrate every 10 m was used to estimate fish assemblages in 1983 and annually from 1987 to 2011. Four additional 25 × 8 m belt transects were used to estimate fish assemblages from 1991 to 2011. Consequently, fish composition at Tiahura was assessed in 1983 and on a yearly basis from 1987 to 2011. Coral cover was estimated within each of the fish transects using the point-intercept method along the center of each transect. Coral cover was estimated by scoring presence of corals at 50 equally spaced points (i.e., at 1-m intervals) along the 50-m transect. The percent cover of coral genera and algal turf (heterogeneous assemblage of filamentous algae) were estimated at 100 points located every 25 cm along the 25-m transects. To gain a better understanding of the long-term dynamics in coral cover at Tiahura, we also retrieved its percentage coral cover in 1979 and 1982 from a previous study (Bouchon 1985) allowing us to document the temporal dynamics in coral cover over a longer period (1979–2011). Note, however, that identification of coral composition at the genus level only started in 1991. Visual census counts of 219 fish species were performed by the same two observers between February and April of each year.

Fish species were categorized among six trophic groups corresponding to: (1) herbivores; (2) planktivores; (3) corallivores; (4) fishes feeding on small invertebrates (microcarnivores); (5) fishes feeding on large and mobile invertebrates (macrocarnivores); and (6) piscivores (see Electronic Supplementary Material, ESM, Table S1). One detritivore, *Crenimugil crenilabis*, was not included in any of the above trophic guilds. These classification categories have been used in several recent studies (e.g., Mouillot et al. 2013, 2014) and are representative of the food web structure that mediates energy flow in the system. It is well known that most reef fish species have complex diets and that fishes adapt their diet to available resources (but see Leray et al. 2015) and may also shift their diet as they grow (e.g., Kulbicki et al. 2005). However, such changes in diet are of low amplitude and, due to the low number of trophic group categories, this classification strategy is robust to misclassifications (Mouillot et al. 2014).

Statistical analysis

The long-term dynamics of Tiahura reef were first assessed by documenting the temporal changes in coral cover over 33 yr (1979–2011). Because coral cover at Tiahura was characterized by recurrent declines and recoveries over this time span (see "Results"), the survey was further divided into three periods of decline and two periods of recovery (Table 1). For each of these periods, we computed the magnitude of the change in coral cover ($\Delta CC = CC_e - CC_s$; where CC_s and CC_e are the coral cover at the start and at the end of the period, respectively). To determine whether this succession of declines and recoveries involved changes in coral composition, we further assessed the temporal dynamics in coral composition from 1991 to 2011 using nonmetric multidimensional scaling (NMDS) on the percentage-difference coefficient of arcsine square-root-transformed percent cover of the different coral genera.

To assess whether long-term dynamics in coral cover could have cascading effects on fish composition from 1983 to 2011, we similarly performed a NMDS on the percentage-difference coefficient of log-transformed density of all fish species. To test whether fish composition differed among periods of decline and recovery in coral cover, we performed an analysis of variance based on the distance matrix of all pairwise observations and used 999 permutations to test for significant differences. We further assessed variability in fish composition within each period as the mean distance between observations and their respective centroids using an analysis of multivariate homogeneity of group dispersions. Pairwise contrasts between periods were further analyzed using parametric Tukey's HSD.

Finally, we tested whether recurrent periods of decline and recovery in coral cover could lead to abrupt responses in fish densities. To this aim we modeled the density of all fish species and the six fish trophic groups as a function of coral cover for each period separately using either linear models (LMs) or piecewise linear models (PLMs). PLMs were fitted to the data using the R function *piecewise.linear* from the package SiZer. This function fits a spline with one breakpoint of unknown location and uses a bootstrap procedure to estimate an empirical confidence interval of the breakpoint by resampling the raw data points 1000 times. The model with the lowest Aikake information criterion (AIC) value by over at least two units was considered the best fit (Burnham and Anderson 2002). Models were reported only when the coefficient of determination (R^2) exceeded 10 %. All analyses were done using R 2.15.1 (R Core Team 2012).

Results

Coral cover on Tiahura reef varied tremendously over the three decades of survey ($F_{25,84} = 29.931$, $P < 0.0001$; Fig. 1; Table 1) and was characterized by recurrent periods of decline and recovery. Four major natural events contributed to the three declines: a COTS outbreak in 1979; a

Table 1 Description of the different periods of decline and recovery in coral cover at Tiahura from 1979 to 2011

Period	Disturbance	Start	End	CC_s	CC_e	ΔCC
Decline 1	COTS	1979	1982	46.27	11.74	−34.53
Recovery 1	–	1982	1991	11.74	48.96	37.22
Decline 2	Cyclone	1991	1993	48.96	21.56	−27.4
Recovery 2	–	1993	2006	25.04	46.81	21.77
Decline 3	COTS + cyclone	2006	2011	46.81	1.18	−45.63

For each period, we indicate the year and corresponding percent of coral cover when the disturbance started and ended (CC_s and CC_e, respectively). We also provide the magnitude of coral cover lost or gained (ΔCC). Note that the survey of fish assemblages only started during the first period of recovery
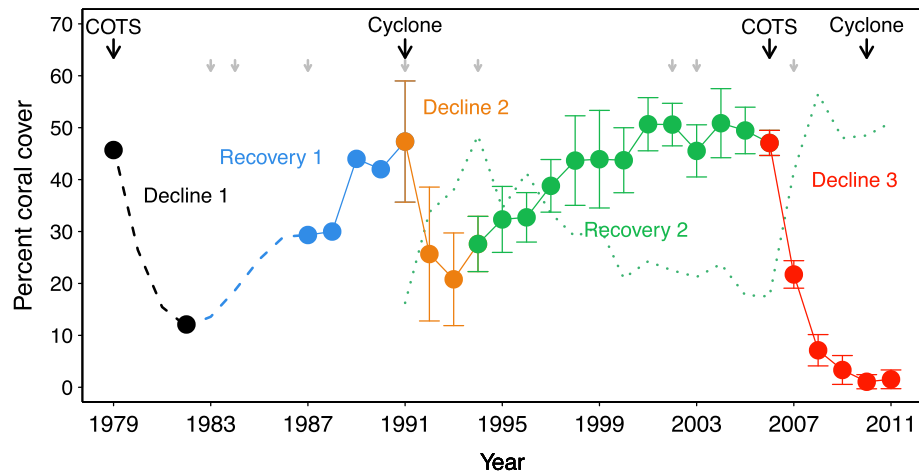

Fig. 1 Temporal dynamics in coral cover at Tiahura reef from 1979 to 2011. *Colors* refer to three periods of decline and two periods of recovery in coral cover. Periods of decline were associated with different natural disturbances shown as *black arrows*: one COTs outbreak in 1979; one cyclone in 1991; and both a COTs outbreak in 2006 and a cyclone in 2010. *Gray arrows* correspond to the various bleaching events that occurred at Tiahura. *Hashed lines* indicate cubic spline interpolation of coral cover provided for illustrative purposes, while *vertical bars* are 95 % confidence intervals (CI). The *green dotted line* represents the percent cover of algal turf. Note that fish monitoring started in 1983

cyclone in 1991; and a COTS outbreak in 2006 coupled with a cyclone in 2010. Coral cover had dropped by 75, 56, and 97 % at the end of the three periods of decline, respectively (Fig. 1; Table 1). Smaller declines that were not associated with any of the two major natural disturbances also occurred, for instance in 1990 and in 2003. The percent cover of algal turf showed the opposite temporal trend to coral cover, and they were strongly negatively correlated over the entire survey ($r = -0.91$, $P < 0.001$; Fig. 1). Although periods of recovery always resulted in similar maximum levels of live coral cover (~ 50 %), the NMDS on coral genera revealed changes in coral composition between the two recovery periods (Fig. 2a). Most of the variation in coral composition captured by the first dimension of the NMDS can be explained by the changes in total coral cover (r between the first-dimension coordinates and coral cover = −0.94), so that changes occurring along the first dimension mimic those occurring in coral cover (Fig. 1). Changes occurring along the second dimension of the NMDS were independent from those of

coral cover and reflected long-term changes in coral composition. In particular, in 1991, at the end of the first recovery following a COTS outbreak in 1979, *Pocillopora* became the most widespread coral genus (25.0 ± 7.1 % SD; ESM Table S2). In contrast, in 2006, at the end of a second recovery following a cyclone in 1991, the coral assemblage cover was shared evenly among three genera: *Pocillopora* spp. (15.9 ± 3.7 %), *Acropora* spp. (11.1 ± 2.8 %) and *Porites* spp. (11.8 ± 3.3 %).

From 1983 to 2011, we characterized significant changes in fish assemblages (Figs. 2b, 3), both in term of species composition ($F_{25,109} = 4.15$, $P = 0.001$) and trophic structure ($F_{25,109} = 8.34$, $P = 0.001$). Variability in fish species composition depended on whether coral cover was declining or recovering. Changes in fish composition were larger during periods of decline in coral cover than during periods of recovery ($P = 0.001$ based on 999 permutations; Fig. 2c). Importantly, these changes were constantly driving the assemblages away from their initial state in 1983 (Fig. 2b). Fish composition exhibited little change
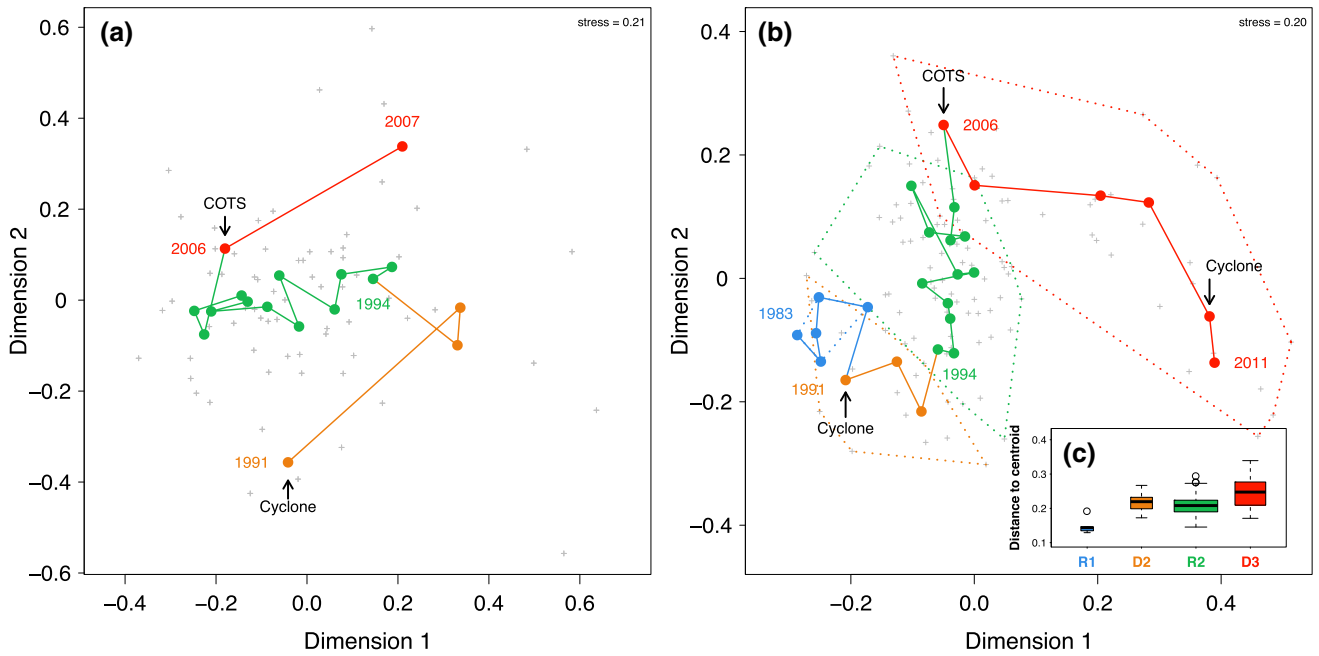
Fig. 2 Temporal dynamics in coral and fish assemblages at Tiahura reef. **a** Long-term trajectory of coral assemblages (1991–2007) resulting from a two-dimensional nonmetric multidimensional scaling (NMDS) on the percentage-difference coefficient of arcsine square-root-transformed percent cover of the different coral genera. The last 4 yr (2008–2011) are not shown because most transects had zero coral cover (see Fig. 1). **b** Long-term trajectory of fish assemblages resulting from a two-dimensional NMDS on the percentage-difference coefficient of log-transformed fish density. *Gray crosses* represent individual transects, and *points* represent year centroids.

Observations are colored by periods of decline and recovery following the color code used in Fig. 1. Convex hulls surround all observations within a given period. Note that the two dimensions of the NMDS are arbitrary. **c** *Boxplot* of the mean distance of observations within a given period to their centroid. *Boxes* represent the lower and upper quartiles and are drawn with widths proportional to the number of observations per period. *Error bars* are 95 % confidence limits and *open circles* represent outliers. *R1, R2* period of recovery 1 and 2; *D2, D3*: period of decline 2 and 3
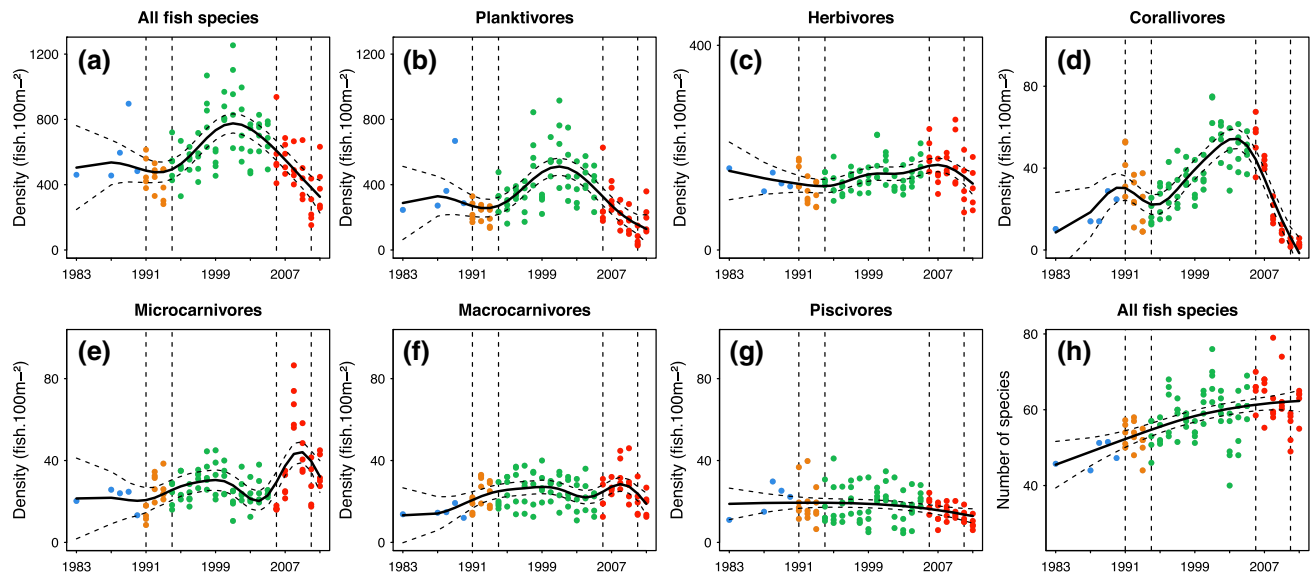

Fig. 3 Temporal dynamics in fish density from 1983 to 2011 for **a** all fish species; **b** planktivores; **c** herbivores; **d** corallivores; **e** microcarnivores; **f** macrocarnivores; **g** piscivores; and **h** temporal dynamics in fish richness. *Points* represent individual transects colored by periods of decline and recovery following the color code used in Fig. 1. For

each panel a generalized additive model was fitted to the data to provide the general temporal trend along with its 95 % CI. *Dashed bars* correspond to limits between periods. Note that units and scales of the *y*-axis change across panels

during the first period of recovery in coral cover (1983–1991; Fig. 2b, c). Fish composition showed greater variability during the first period of decline in coral cover triggered by the cyclone compared to periods of recovery (1991–1993; Fig. 2c) and consistently changed along the first dimension of the ordination (Fig. 2b). During the second period of recovery in coral cover (1993–2006), fish composition continued to change, consistently following a new trajectory along the second dimension of ordination although the rate of change decreased compared with the previous period (Fig. 2b, c). Fish composition was the most variable during the third period of decline in coral cover (2006–2011) and followed a new trajectory along the first dimension of ordination. Overall, the first dimension of the ordination appeared to reflect changes in fish composition during periods of decline in coral cover, while the second dimension appeared to reflect changes associated with period of recovery. These changes along the first dimension of the NMDS were related to shifts from corallivorous species that had negative scores to microcarnivorous, herbivorous, and planktivorous species that had generally high positive scores along this dimension (ESM Fig. S1). No differences in species scores were characterized among trophic groups along the second dimension.

Planktivores and herbivores were the most prevalent groups of fishes accounting for 57 and 25 %, respectively, of every fish observed (Fig. 3). Total fish density and density of the six trophic groups exhibited contrasting relationships with coral cover across periods of recovery and decline although the density of corallivores mirrored that of coral cover throughout the entire survey. For three periods between 1983 and 2006, corresponding to the first recovery following a COTS outbreak in 1979, a period of decline in coral cover triggered by a cyclone in 1991, and the subsequent recovery, coral cover explained a variable amount of the variation in trophic group densities (up to 61 % for corallivores). Although variation in the density of some trophic groups was poorly explained by variation in coral cover, all the significant models suggested that fish density varied linearly with coral cover (ESM Figs. S2–S4). During the last period of decline (2006–2011), most fish–coral cover relationships became nonlinear (Table 2; Fig. S5). Coral cover during this period reached such low levels that the densities of trophic groups drastically changed below different threshold levels. For example, when coral cover started to decline in 2006, corallivores declined, whereas microcarnivores and macrocarnivores increased (Table 2). Drastic declines in corallivores and planktivores were triggered below coral cover thresholds of 19 % (95 % CI 15–37 %) and 13 % (95 % CI 5–23 %), respectively. Furthermore, when coral cover dropped below 5 % (95 % CI 2–44 %), microcarnivores and macrocarnivores also started to drastically decrease.

Table 2 Nonlinear responses of coral fish assemblages to coral degradation during the third period of decline (2006–2011)

Group	Model	R^2	Threshold	
Total density	Piecewise (NS/−)	55.2	4.7 %	[2.3–14.3]
Herbivores	Linear (−)	12.5	–	–
Plankton feeders	Piecewise (NS/–)	45.4	12.6 %	[4.6–22.7]
Corallivores	Piecewise (NS/–)	93.3	19.0 %	[14.9–37.1]
Microcarnivores	Piecewise (+/−)	53.3	5.3 %	[3.3–43.7]
Macrocarnivores	Piecewise (+/−)	51.4	5.0 %	[2.3–8.5]
Piscivores	Linear (−)	25.3	–	–

Responses were either linear or nonlinear (piecewise). (−) indicates a negative response (e.g., density of herbivores decreases as coral cover decreases) and (+) a positive response. For nonlinear responses, we give the response above and below thresholds [e.g., (NS/–) = fish density does not significantly change as a function of coral cover above the threshold of say, 4.7 %, while it decreases below this threshold]. Thresholds correspond to the estimation of coral cover at which the nature of the relationship changes. R^2 is the coefficient of determination. Responses of fish assemblages during the three other periods are either linear or nonsignificant (see Electronic Supplementary Material Figs. S2–S5). 95 % CI are given within square brackets

Consequently, the total density of all fish species declined precipitously at very low coral cover (Table 2). Nevertheless, over most of the study period, fish species richness (number of species/transect) increased through time, albeit very slightly (+0.54 species yr^{-1}, $P < 0.001$).

Discussion

Our results show that coral cover at Tiahura reef was extremely dynamic, fluctuating between periods of decline and recovery over more than three decades. Indeed, coral cover rarely stabilized at a high value (∼50 %) nor did it remain very low (<10 %) over the survey. This cyclical pattern in coral cover is similar to that described for the GBR (Osborne et al. 2011) and Western Australia (Speed et al. 2013). Coral reefs should not be defined as either 'healthy' or 'degraded' based on estimates of coral cover alone (high cover vs. low cover), as both states are transient and part of a long-term dynamic. At Tiahura, recurrent COTS outbreaks and cyclones causing severe coral mortality could partly explain this dynamic, as each major decline in coral cover was associated with one of these two types of disturbance. Other types of disturbances, including anthropogenic stressors, could potentially also contribute to the long-term dynamics in coral cover we documented, as exhibited by coral bleaching (e.g., Garpe et al. 2006; Graham et al. 2006; Halford and Caley 2009). Although several bleaching events of various intensity occurred over the past decades on Tiahura reef (Adjeroud et al. 2005),

they have had little to no impact on the cover of live corals on the exposed fore reef (Adjeroud et al. 2002, 2009; Penin et al. 2013). The impact of anthropogenic disturbances may be stronger within the lagoon where most anthropogenic threats occur than on the fore reef. At a smaller temporal scale (1991–2011), we also documented changes in coral composition. In particular, coral assemblages were different after each recovery. *Acropora* was the dominant genus in 1979 (Bouchon 1985), but decreased from recovery to recovery in favor of other compositions such as *Pocillopora, Acropora,* or *Porites* in 1991, which to some extent confirms that *Porites* is frequently favored in the face of multiple disturbances (Adjeroud et al. 2009).

Our study also suggests that long-term dynamics in coral cover and the associated changes in coral composition can have long-lasting cascading effects on the fish assemblages. We characterized a long-term trajectory in the composition of fish assemblages from 1983 to 2011. Each severe natural disturbance had a specific effect on fish composition contributing to continuous changes over time. Hence, despite the relatively rapid recoveries in coral cover, both coral and fish assemblages bear the legacy of past disturbance history, and neither has recovered the composition that was first recorded in the initial surveys. Such results highlight the importance of historical contingency in coral reef ecosystems (Hughes 1989; Jackson et al. 2001; Wilson et al. 2006). Our results also add to the growing body of evidence showing the long-lasting effects of single disturbances on the composition of fish assemblages of the GBR (Halford et al. 2004; Bellwood et al. 2006, 2012; Cheal et al. 2008; Halford and Caley 2009; Wilson et al. 2009) and other locations such as the Seychelles (Graham et al. 2006, 2015), Tanzania (Garpe et al. 2006) and Papua New Guinea (Jones et al. 2004). Although fish diversity and/or density can remain relatively stable in the face of natural disturbances (Bellwood et al. 2006, 2012; Cheal et al. 2008; Wilson et al. 2009; Emslie et al. 2011), their composition can shift without regaining their initial state even when coral cover has fully recovered (Bellwood et al. 2012). Collectively, these results suggest that fish assemblages may either need greater time between disturbances to fully recover (McClanahan and Graham 2005; Halford and Caley 2009) or may never regain their pre-disturbance composition due to changes in the benthic assemblages. Reef fish recruitment is extremely variable through time and space (Planes et al. 1993; Dufour et al. 1996; Tolimieri et al. 1998) and could combine with natural disturbances to explain the constantly evolving fish assemblage composition.

We showed that the density of several key fish trophic groups abruptly decreased when coral cover dropped below a threshold of 10 %. In the Indo-Pacific, fish assemblages and coral cover frequently exhibit linear relationships when coral cover is greater than 10 % (Bell and Galzin 1984; Bozec et al. 2005; Komyakova et al. 2013; but see Wilson et al. 2009; McClanahan et al. 2011; Pratchett et al. 2014; Beldade et al. 2015). However, we observed that although the decrease in fish density was slow at first, it decreased much faster when coral degradation was the most severe (coral cover <10 %), after the succession of a COTS outbreak and a cyclone (2006–2011). This result suggests and reinforces the notion that there is a threshold when coral cover gets lower than 10 % (e.g., Beldade et al. 2015). Corallivores were the most sensitive to variation in coral cover and exhibited the highest threshold value in coral cover during this period of decline, revealing their tight trophic dependency on corals. Coral specialists, either coral feeders or coral dwellers, are usually more sensitive to variation in coral cover (Jones et al. 2004; Wilson et al. 2009), while other habitat features such as coral diversity (Komyakova et al. 2013) or habitat complexity (Friedlander and Parrish 1998; Wilson et al. 2007; Emslie et al. 2008; Pratchett et al. 2014) may be more important to explain variation in other species. The combination of both a COTS outbreak in 2006 and a cyclone in 2010 may have driven the nonlinear relationship between coral cover and fish assemblages during this period that was absent when each disturbance occurred individually.

We documented little change in species richness (number of species/transect) but large changes in both density (fish m^{-2}) and trophic structure (relative densities of trophic groups). Interestingly, besides corallivores whose density closely mirrored that of coral cover, the density of the other trophic groups exhibited loose relationships when coral cover was higher than 10 %. This may suggest that the carrying capacity at Tiahura reef is weakly linked to coral cover when coral is abundant, but below a given threshold there is a loss in carrying capacity which is directly linked to coral cover. This result accords with recent broad-scale studies outlining a general lack of fluctuation in local diversity (Hobbs et al. 2006; Graham et al. 2014) but major compositional changes over time (Vellend et al. 2013; Dornelas et al. 2014).

We clearly showed that recurrent disturbances can shape the long-term trajectory of coral reef ecosystems. This can have serious consequences on coral reefs worldwide as natural disturbances are predicted to increase in frequency and magnitude in the near future (Harley et al. 2006; Karl et al. 2008; Turner 2010; van Hooidonk et al. 2013). In our study, both COTS outbreaks and cyclones appear to be important drivers of this dynamic, but it is more difficult to determine the additional influence of anthropogenic activities occurring either at the local (e.g., fishing, agriculture) or global (climate change) scales. In addition, the frequency or magnitude of natural disturbances can be indirectly modulated by anthropogenic activities. For instance,

both fishing (Dulvy et al. 2004) and terrestrial nutrient inputs (Fabricius et al. 2010; Lane 2012) can contribute to an increase in the frequency of COTS outbreaks. Tiahura is probably increasingly impacted by such anthropogenic disturbances which may explain part of the long-term dynamic outlined in our study.

While a great deal of effort is devoted to improving management for the sustainable future of coral reefs, studies that lack a temporal component ignore the potentially large magnitude of changes naturally occurring in coral reefs. Coral reefs are naturally dynamic systems and have been subject to various anthropogenic impacts for several centuries (Jackson et al. 2001; Pandolfi et al. 2003; Norris et al. 2013). Historical contingency may potentially be an important, yet largely underestimated, factor explaining the contemporary structure of reef fish assemblages. Management strategies should be framed within this context and require long-term surveys even if decision-makers often wish to be provided with shorter-term information.

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