

How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations

Thomas C. Adam · Andrew J. Brooks ·
Sally J. Holbrook · Russell J. Schmitt · Libe Washburn ·
Giacomo Bernardi

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Abstract Global climate change is rapidly altering disturbance regimes in many ecosystems including coral reefs, yet the long-term impacts of these changes on ecosystem structure and function are difficult to predict. A major ecosystem service provided by coral reefs is the provisioning of physical habitat for other organisms, and consequently, many of the effects of climate change on coral reefs will be mediated by their impacts on habitat structure. Therefore, there is an urgent need to understand the independent and combined effects of coral mortality and loss of physical habitat on reef-associated biota. Here, we use a unique series of events affecting the coral reefs around the Pacific island of Moorea, French Polynesia to differentiate between the impacts of coral mortality and the degradation of physical habitat on the structure of reef fish communities. We

found that, by removing large amounts of physical habitat, a tropical cyclone had larger impacts on reef fish communities than an outbreak of coral-eating sea stars that caused widespread coral mortality but left the physical structure intact. In addition, the impacts of declining structural complexity on reef fish assemblages accelerated as structure became increasingly rare. Structure provided by dead coral colonies can take up to decades to erode following coral mortality, and, consequently, our results suggest that predictions based on short-term studies are likely to grossly underestimate the long-term impacts of coral decline on reef fish communities.

Keywords Habitat loss · Resilience · Storms · *Acanthaster planci* · Coral bleaching · Climate change

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T. C. Adam (✉) · A. J. Brooks · S. J. Holbrook · R. J. Schmitt ·
L. Washburn
Coastal Research Center, Marine Science Institute,
University of California, Santa Barbara, CA 93106, USA
e-mail: adam@lifesci.ucsb.edu; thomas.adam@lifesci.ucsb.edu

S. J. Holbrook · R. J. Schmitt
Department of Ecology, Evolution and Marine Biology,
University of California, Santa Barbara, CA 93106, USA

L. Washburn
Department of Geography, University of California,
Santa Barbara, CA 93106, USA

G. Bernardi
Department of Ecology and Evolutionary Biology,
University of California, Santa Cruz, CA 95064, USA

Introduction

Key structural and functional attributes of many ecosystems are predicated on the presence of particular foundation species (Jones et al. 1997; Bruno et al. 2003), and many of these species are likely to be susceptible to escalating human impacts including those caused by global climate change (GCC) (Hoegh-Guldberg and Bruno 2010; Walther 2010; Doney et al. 2012). For example, in many temperate near-shore marine environments, kelp forests provide habitat for a wide variety of organisms, and, consequently, climate-driven increases in the frequency of severe kelp-removing storms may have cascading impacts on kelp forest communities (Byrnes et al. 2011). In the tropics, stony corals provide the foundation for highly diverse coral reef ecosystems, and the sensitivity of corals to recent environmental changes has already resulted in large-scale and wide-ranging declines in coral cover (Gardner et al. 2003;

Bruno and Selig 2007). Indeed, mass bleaching and subsequent mortality of reef-building corals in response to thermal anomalies has been one of the most visible impacts of GCC on any ecosystem to date (Hughes et al. 2003; Baker et al. 2008; Hoegh-Guldberg and Bruno 2010). Nonetheless, while much is known about the current patterns and causes of coral decline, far less is known about the impacts of these declines on functional attributes of the ecosystem (Wilson et al. 2010).

As in most ecosystems, GCC is likely to affect coral reefs through a number of different mechanisms, and there is a potential for alternate drivers to have different effects on the ecosystem services they provide. Some of the major threats faced by coral reefs, in addition to the direct effects of rising temperatures, include ocean acidification (OA) caused by increased CO₂ emissions (Hofmann et al. 2010), sea-level rise due to thermal expansion and melting of the polar icecaps (Nicholls and Cazenave 2011), and potentially increased frequency of severe storms resulting from rising atmospheric temperatures (Knutson et al. 2010). In addition to these environmental drivers, a major threat to corals in the Indo-Pacific continues to be outbreaks of corallivorous crown-of-thorns sea stars (*Acanthaster planci*; hereafter COTS), which have likely been exacerbated in recent years by increased nutrient loading in coastal oceans (Fabricius et al. 2010) and decreases in the abundances of predatory fishes due to overharvesting (Dulvy et al. 2004; Sweatman 2008). Importantly, like other foundation species, a key ecosystem service provided by corals—especially those with a branching morphology—is their function as habitat for other organisms (Schmitt and Holbrook 2000; Holbrook et al. 2002a, b; Idjadi and Edmunds 2006; Brooks et al. 2007; Messmer et al. 2011; Johnson et al. 2011). This habitat provisioning may be impaired to a greater extent by physical disturbances such as large storms that suddenly remove coral structure than by bleaching or outbreaks of COTS that kill tissue but leave the dead calcium carbonate skeletons intact (Syms and Jones 2000; Wilson et al. 2006; Emslie et al. 2008; Pratchett et al. 2008; Stella et al. 2011). However, we currently have a limited understanding of the effects of coral tissue mortality versus the loss of coral skeletal structure on reef-associated biota (Pratchett et al. 2008; Holbrook et al. 2008a, 2011; Stella et al. 2011).

Here, we focus on the effects of multiple disturbances on the structure of the reef-associated fish community. Coral reefs are home to approximately one quarter of the world's known species of fish, and as such, contribute greatly to global fish diversity (Moberg and Folke 1999; Spalding et al. 2001). In addition, reef fishes are a major source of protein for millions of people, and are an economically, aesthetically, and culturally valuable resource

throughout the tropics (Moberg and Folke 1999; Sadovy 2005). Consequently, maintenance of a diverse and abundant fish community is clearly an important ecosystem service provided by coral reefs. Further, certain fishes facilitate the recruitment, growth, and survivorship of corals, thus, potentially creating a feedback between the impacts of disturbances on fish assemblages and the likelihood that reef ecosystems will recover to a coral-dominated state following loss of coral cover (Bellwood et al. 2004; Cheal et al. 2010). In this study, we capitalize on the occurrence of two different perturbations to reefs of Moorea, French Polynesia, a COTS outbreak that—like a mass bleaching event—killed coral tissue but left skeletons intact, and a tropical cyclone that removed corals entirely. These events provided us with an unparalleled opportunity to compare the impacts on reef fish assemblages of disturbances that affect the foundation species in different ways.

Methods

Study site

Moorea, in the central south Pacific, is a high volcanic island with an offshore barrier reef that encloses a shallow lagoon. The three sides of the triangular shaped island experience different wave climates with swell prevailing from the SW during the Austral winter and from the North in the summer. Between 2007 and 2010, the reefs offshore of the barrier reef crest (the exposed fore reef) were severely impacted by a COTS outbreak, with live coral cover declining precipitously from an island-wide average of ~40 to <5 % (Adam et al. 2011; Kayal et al. 2012). In addition, during February 2010, a category 4 tropical cyclone (Oli) passed to the Southwest of Moorea creating anomalously large waves and removing large amounts of coral structure at some fore reef sites but not others (see Results). Over the same period, total coral cover on the reefs in the shallow lagoons and their associated fish assemblages have remained relatively constant (Adam et al. 2011; Figure S1). This sequence of events constitutes an unprecedented opportunity to compare impacts of multiple large-scale (e.g., impacting multiple km² of reef) disturbances on reef fish communities. Here we focus on the shallow (10–12 m depth) exposed fore reef.

Data collection

Since 2005, the Moorea Coral Reef Long Term Ecological Research site has collected biological time series data, including surveys of corals and fishes, at six sites (two sites on each of the island's three shores), and physical data,

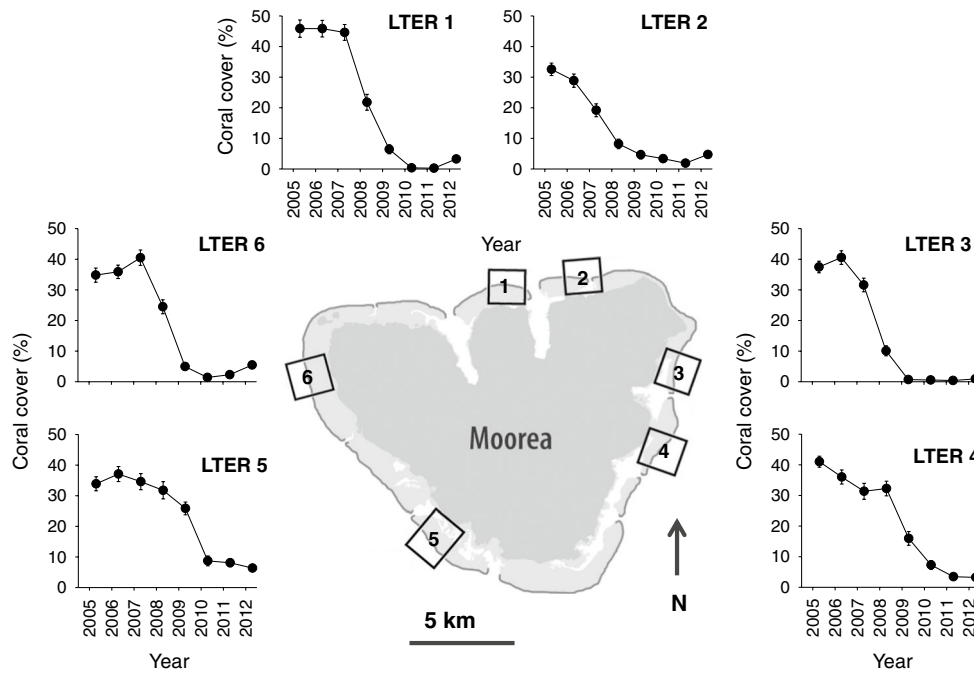


Fig. 1 Dynamics of cover of live coral (mean ± SE) at 10 m depth on the fore reef ($n = 40$ quadrats per site each year) with map of the island Moorea indicating locations of sites (LTER 1–LTER 6). Note that two sites are sampled on each of the island’s three shores (N facing, SE facing, and SW facing). Consistent with the observa-

tion that the COTS outbreak began in the N and moved southward (Kayal et al. 2012), coral decline at the two southernmost sites (LTER 4 on the SE facing shore and LTER 5 on the SW facing shore) began ~1 year after decline at the more northern sites (LTER 1, 2, 3, 6)

including wave energy, at three of these sites (one site on each shore) (Fig. 1). Biological data are collected annually by SCUBA divers, while physical data are collected continuously by bottom-mounted and moored oceanographic instruments. Data on coral cover and fish are obtained from fixed transects that were established using a stratified random design. Coral data are collected in April and fish counts are conducted four months later in August. At each site, coral cover is quantified in fixed 0.5×0.5 m photo quadrats ($N = 40$) located randomly along five 10 m transects with CPCe software (Kohler and Gill 2006) using 200 random point contacts per quadrat. Fish are counted on four adjacent 50 m transects at each site. Fish transects extend from the seafloor to the surface of the water column and consist of two swaths surveyed sequentially. To account for differences in the behavior and detectability of fishes, divers first count mobile fish on a 5 m wide swath and then count cryptic benthic fish on a 1 m wide swath. Wave energy is quantified with bottom-mounted Wave & Tide recorders (SBE 26plus; Sea-Bird Electronics, Inc., Bellevue, WA, USA) and moored Acoustic Doppler Current Profilers (Sentinel ADCP; Teledyne RD Instruments, Poway, CA, USA). MCR time series data are publicly available; further details about sampling protocols can be obtained by accessing the data sets (Edmunds 2013; Brooks 2013; Washburn 2013).

Effects of disturbances on the foundation species

We aimed to first describe the impacts of the COTS outbreak and Cyclone Oli on corals on the fore reef, particularly branching corals that are the most important sources of habitat for fishes. With this goal in mind, we documented changes in the cover of all living coral at each of the six sites due to the COTS outbreak. We then quantified the magnitude of the physical disturbance experienced by the reefs as a result of Cyclone Oli by plotting the daily maximum significant wave height (H_s) recorded at each of the three sides of Moorea (N facing, SE facing, SW facing). In addition, to better understand the impact of the two disturbances on fish habitat, we quantified the amount of living and dead branching coral present at each site prior to the COTS outbreak in 2006 and 2007, again following the COTS outbreak but prior to Cyclone Oli in 2008 and 2009, and, finally, after Cyclone Oli in 2010, 2011, and 2012. This allowed us to track the immediate effects of the cyclone on coral structure, as well as the more gradual erosion of structure that occurs following the death of coral tissue. These data were obtained from a subset of photo quadrats ($N = 10$) from each site-year combination that were analyzed with the image analysis program ImageJ (Rasband, W.S., US National Institutes of Health, Bethesda, Maryland, USA). Quadrats were initially chosen

randomly and then repeatedly sampled each year. For the analysis, the total footprint of all live and dead branching corals belonging to the genera *Pocillopora* and *Acropora* (the two dominant genera of habitat-providing corals on the fore reef in Moorea) were measured. These data were converted to proportional cover, logit transformed ($\log(x/(1-x))$), and analyzed with linear mixed-effects models (random effect = quadrat, fixed effect = year), with correlation structure modeled as a first order autoregressive process. Post hoc Tukey tests were subsequently conducted in order to identify time intervals when changes in coral cover occurred.

Dynamics of the fish assemblage in response to disturbances

The previously described analyses revealed three sets of sites based on their disturbance history (see “Results”). The N shore sites (LTER 1 and LTER 2) were impacted by both the COTS outbreak and Cyclone Oli, while the SE facing (LTER 3 and LTER 4) and SW facing (LTER 5 and LTER 6) sites were impacted primarily by the COTS outbreak, with the onset of the outbreak occurring a year later at the southernmost sites on the island’s SE facing and SW facing shores (LTER 4 and LTER 5) (Fig. 1). Consequently, to investigate the impact of the disturbances on reef fish communities, we evaluated changes in the abundance, species richness, and community composition of fishes in each of three groups corresponding to different disturbance histories. These groups were cyclone-impacted sites of LTER 1 and LTER 2, early onset of COTS outbreak of LTER 3 and LTER 6, and later onset of COTS outbreak of LTER 4 and LTER 5. To evaluate changes in abundance and species richness, we used linear mixed models with year modeled as a fixed effect, disturbance history, site (nested in disturbance history), and transect (nested in site) modeled as random effects, with correlation structure modeled as a first order autoregressive process. Since we expected differences in disturbance history to drive variation in the responses of fish communities, we tested for an interaction between year and disturbance history in all models, and constructed separate models for each group when significant interactions were found. Changes in community composition were evaluated with permutational MANOVA (Anderson 2001) using the Bray-Curtis dissimilarity index. Abundances were log transformed prior to all analyses to improve distributional properties.

To visualize changes in the community composition of fishes, we used canonical analysis of principal coordinates (CAP) (Anderson and Willis 2003). CAP is a constrained ordination technique that identifies combinations of variables that best discriminate among a priori groups (e.g., sites). Similar to multidimensional scaling, CAP provides

site scores that can be used to visualize multivariate patterns, and species scores to evaluate the relative contributions of individual species. To visualize changes in the fish communities that occurred at each site, we plotted the centroids of the site scores for each site-year combination as well as the species scores for the thirty most influential species (i.e., those with the highest species scores on the two primary axes from the CAP analysis). In addition to identifying important individual species, we also tested for changes in the abundance of functional groups. To accomplish this, each species was categorized into one of seven groups (planktivores, piscivores, invertebrate consumers, roving herbivores, site-attached herbivores, corallivores, and coral dwellers) based on diet and habitat use (Randall 2005; Froese and Pauly 2012 and references therein), and changes in the total abundance of each group were evaluated with linear mixed models using the same framework described previously (for more information on functional groups see Table S1).

To directly test for relationships between coral cover and reef structure and changes to the fish assemblage, we plotted cumulative changes in the centroids of CAP 1 and CAP 2 against the cover of live branching corals and the total combined cover of live and dead branching corals (a measure of structural complexity) at each site during each sampling period. To evaluate whether coral cover or structure were better predictors of changes in the fish community, and whether relationships were best described by linear or non-linear functions we used a model selection framework. Specifically, we modeled changes in the values of CAP 1 and CAP 2 as linear functions of coral cover and structure and the log of coral cover and structure. Log-linear models were used as a general description of a decelerating relationship. Model comparison was achieved with AIC and by visually inspecting plots of actual versus predicted values. Relationships were modeled with mixed-effects models that incorporated site as a random effect. An identical framework was used to explore relationships between coral cover and structure and changes in the abundance of functional groups. As a rule of thumb, differences in $AIC < 2$ indicate that models are roughly equivalent (Burnham and Anderson 2002); thus, if ΔAIC between the best linear and log-linear model was < 2 , we concluded that we did not have strong support for a nonlinear relationship. Analyses were conducted in the R programming language (R Core Team 2013) using the vegan package (Oksanen et al. 2011) for multivariate analyses, and the nlme package for mixed-effects models (Pinheiro et al. 2013), with multiple comparisons implemented using the multcomp package (Hothorn et al. 2008). Data and model code for analyses of the relationship between coral structure and fish abundance are archived and publicly available at: <http://mcr.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-mcr.1041>.

Results

Coral dynamics

Prior to the COTS outbreak in 2005, mean live coral cover on the fore reef ranged from 35 % to 45 %. Live coral cover began to decline precipitously between 2007 and 2008 at the northern sites (LTER 1, 2, 3, 6) with declines at the two southernmost sites (LTER 4, 5) beginning a year later (Fig. 1). By 2011 live coral cover had been reduced by >90 % at five of the six sites, and 76 % at LTER 5 on the SW shore (Tukey HSD 2005 vs. 2011 $P < 0.001$ for each site; Fig. 1). In 2012 coral cover remained stable at LTER 3, LTER 4, and LTER 5 and began increasing at LTER 1, LTER 2, and LTER 6 (Tukey HSD on successive years $P < 0.05$ for each site; Fig. 1).

Wave history

The three sides of the island experience very different wave climates with the SW facing shore, and to a lesser extent the SE facing shore, normally experiencing much larger wave events than the N shore (quantified as the significant wave height H_s) (Fig. 2). However, on February 4 and 5, 2010, wave heights on the N shore were elevated greatly by Cyclone Oli, with waves ~6 SDs greater than the largest waves observed in the preceding five years (Fig. 2). By contrast, Cyclone Oli did not generate anomalously large waves on the SE or SW facing shores (Fig. 2).

Impact of disturbances on fish habitat

Between 2006 and 2009, cover of live branching corals declined greatly due to the COTS outbreak at the majority of sites (LTER 1, 2, 3, 6), with significant declines at the two southernmost sites (LTER 4 and 5) occurring by 2010 (Tukey HSD 2006 vs. 2009 and 2006 vs. 2010, respectively, $P < 0.05$ for all sites; Fig. 3). However, during this time, large amounts of coral structure remained at all sites in the form of dead coral skeletons (Fig. 3). In February 2010 Cyclone Oli removed all remaining coral structure (both live and dead) from the two north shore sites, LTER 1 and LTER 2 (Tukey HSD 2010 vs. 2009, $P < 0.001$ both sites; Figs. 2, 3). In contrast, sites less impacted by Cyclone Oli still retained a large proportion (41–77 %) of their physical structure in 2010, and a moderate proportion in 2011 (17–53 %) (Fig. 3). However, by 2012, the amount of live and dead branching corals had been reduced to 25 % or less of that present prior to the COTS outbreak at all sites (Tukey HSD 2012 vs. 2006, $P < 0.05$ all sites). Further, during 2012, LTER 1, LTER 2, and LTER 6 experienced small but significant increases in the cover of live branching corals (Tukey HSD on successive years, $P < 0.05$;

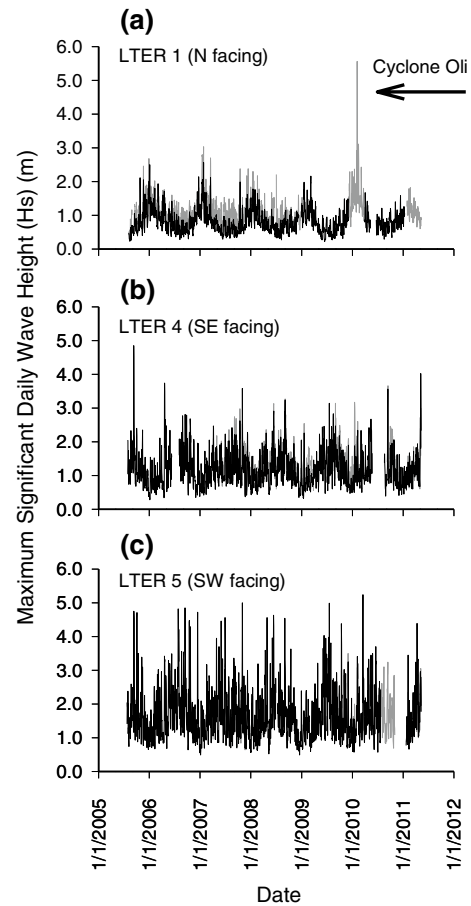


Fig. 2 Maximum daily wave heights (calculated from H_s) recorded on the **a** N (LTER 1), **b** SE (LTER 4) and **c** SW (LTER 5) facing shores of Moorea. Note that data from multiple instruments are plotted in each panel. *Black lines* are data obtained from bottom-mounted Wave & Tide recorders (SBE 26plus Sea-Bird Electronics, Inc., Bellevue, WA, USA); *gray lines* were obtained from moored Acoustic Doppler Current Profilers (Sentinel ADCP; Teledyne RD Instruments, Poway, CA, USA)

Fig. 3) suggesting that the loss of physical structure occurring at these sites was stabilizing and was in fact beginning to reverse as new corals established and grew.

Fish community dynamics

Between 2006 and 2012 all sites experienced large shifts in fish community composition (MANOVA, $P < 0.001$ for all sites, Fig. 4a) due primarily to changes in the relative abundances of common species. In contrast, there were no persistent changes in total abundance or species richness (Fig. S2, Fig. S3). The CAP analysis captured a large amount of the variation in community structure in the first two components, with the two primary axes, CAP 1 and CAP 2, accounting for 35 % and 21 % of the total variance, respectively. The largest shifts in community

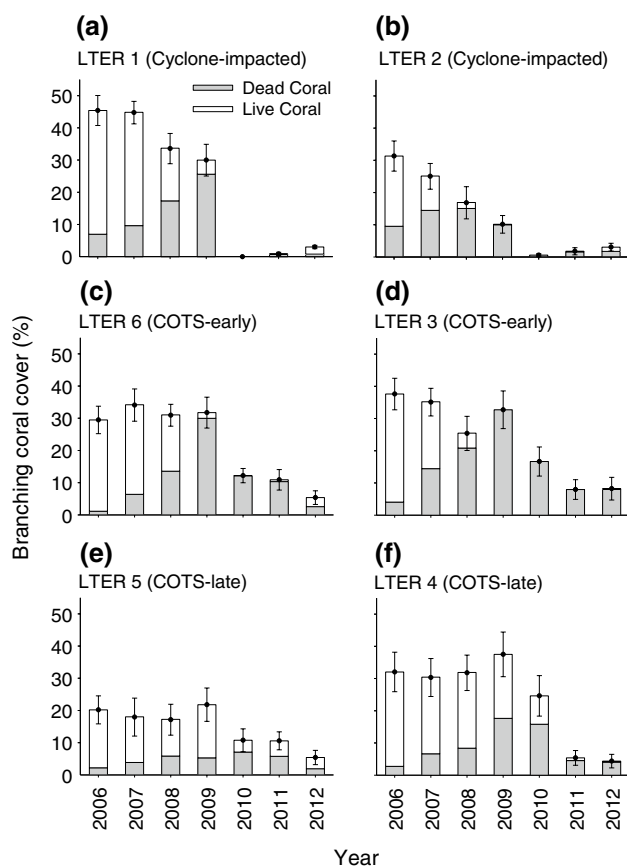


Fig. 3 Dynamics of fish habitat (mean cover of live (*white*) and dead (*gray*) branching corals \pm SE) at 10 m depth on the fore reef. Sites are organized according to disturbance history. **a, b** Sites impacted by COTS and Cyclone Oli (LTER 1 and LTER 2); **c, d** sites impacted exclusively by COTS with onset of coral decline by 2008 (LTER 3 and LTER 6); **e, f** sites impacted exclusively by COTS with onset of coral decline by 2009 (LTER 5 and LTER 4) ($n = 10$ quadrats per site each year). Note the rapid loss of structural habitat at the two N shore sites (LTER 1 and LTER 2) following Cyclone Oli

composition occurred between the 2009 and 2010 surveys at the north shore sites, LTER 1 and LTER 2, following the nearly complete removal of coral structure there by Cyclone Oli (Fig. 4). In particular, changes in the value of CAP 1 following Cyclone Oli were approximately three and a half times and two and a half times greater at LTER 1 and LTER 2, respectively, than the largest year-over-year changes observed at any other site during the study period. Changes in community composition at all sites reflected a decline in the abundance of species that depend on living coral for either food or shelter, and an increase in certain species of herbivores, invertebrate consumers, and planktivores not directly dependent on living coral (Fig. 4). The CAP analysis also revealed significant spatial structure in the fish assemblages that was well predicted by the gradient in wave intensity experienced by the sites, with the least wave-exposed sites (e.g., N facing sites—LTER 1 and

2) having lower CAP 1 and CAP 2 values than the most wave-exposed sites (e.g., SW facing sites—LTER 5 and 6) prior to the disturbance events (Fig. 4). Further, CAP 1 values increased over time at all sites following the disturbances, particularly at sites impacted by Cyclone Oli, such that by 2010 spatial structure in CAP 1 was not apparent, suggesting that the link between wave energy and CAP 1 was mediated by the physical structure of the coral habitat at these sites. Indeed, changes in CAP 1 values were most strongly related to physical structure, and accelerated as structure declined (best model: loglinear; Table S2, Fig. 4c). In contrast, changes in CAP 2 were better explained by the cover of live branching corals (Table S2). Similar to CAP 1, changes in CAP 2 accelerated as coral cover declined (best model: loglinear; Table S2, Fig. 4d).

As expected, the abundance of coral dwelling fish and corallivores declined throughout the study period. However, the timing of these declines differed among sites with different disturbance histories (ANOVA, year \times disturbance history $P < 0.0001$, $P < 0.01$, respectively). Consistent with the timing of the COTS outbreak, significant declines in coral dwellers occurred by 2009 at the four northernmost sites and by 2011 at the two southernmost sites (Fig. 5). Corallivore declines also coincided with the declines in coral dwellers (Fig. 5). In contrast to coral-associated fishes, roving herbivores and invertebrate consumers increased at all reefs, with no evidence for differences in timing among reefs with different disturbance histories (ANOVA year \times disturbance history $P > 0.4$ for both), and both groups experienced persistent increases in abundance during 2009 (Tukey HSD on successive years $P < 0.001$) (Fig. 5; Fig. S4). Unlike roving herbivores, the dynamics of site-attached herbivores varied significantly among reefs with different disturbance histories (ANOVA year \times disturbance history $P < 0.01$), with declines at the sites impacted by the cyclone on the N shore occurring following Cyclone Oli (Tukey HSD 2009 vs. 2010 $P < 0.05$) and no changes observed at the other sites (ANOVA $P > 0.1$ for both) (Fig. 5). The dynamics of piscivores and planktivores were consistent among sites with different disturbance histories (ANOVA year \times disturbance history $P > 0.3$ for both) with neither group showing persistent temporal trends (Fig. S4). Finally, changes in the abundance of coral dwelling fishes, corallivores, and territorial herbivores were all most strongly related to the total amount of physical structure present on a reef (Table S2). For coral dwelling fishes and territorial herbivores, declines in abundance accelerated as structure declined (best model: loglinear; Table S2, Fig. 6). In contrast, declines in the abundance of corallivores were linearly related to coral structure (best model: linear; Table S2, Fig. 6). Increases in the abundance of roving herbivores and invertebrate consumers were both inversely related to

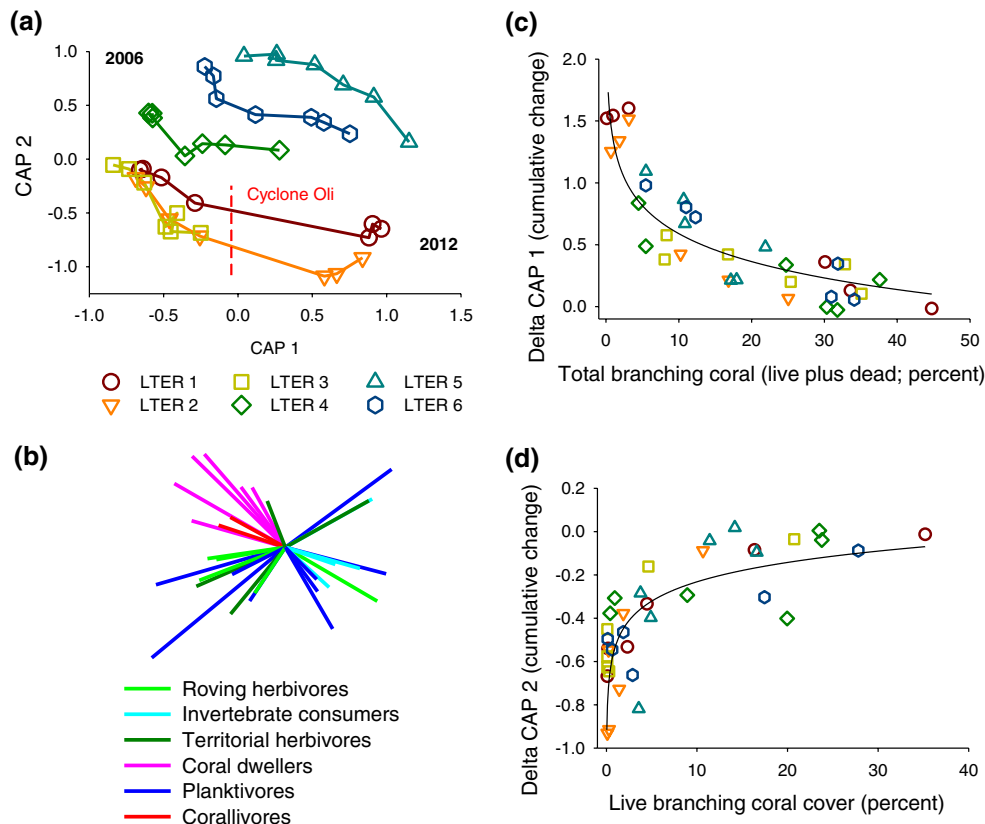


Fig. 4 **a** Canonical analysis of principal coordinates (CAP) ordination plot showing changes in composition of reef fish assemblages on the fore reef of Moorea. Note the similar trajectory of the fish assemblages at all sites and the large changes that occurred at the N shore sites (LTER 1 and 2) following the removal of coral habitat by Cyclone Oli in 2010 (indicated by vertical dashed line) ($n = 3$ transects per site each year). **b** Species loadings of the thirty most influential species, showing their relative contributions to the ordination

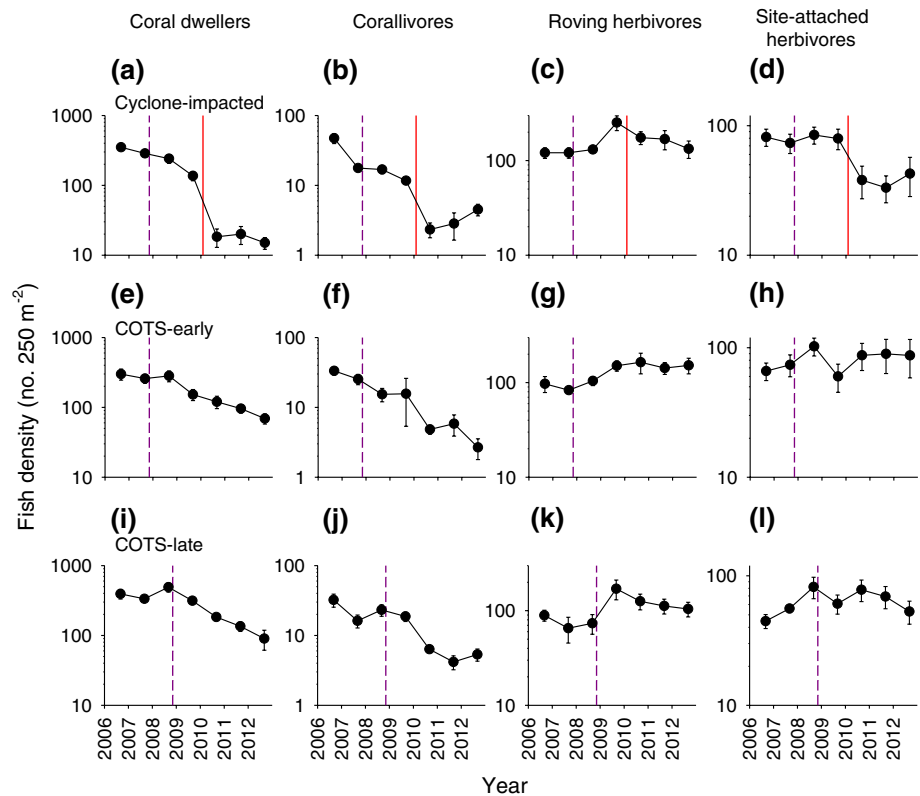
the total amount of living coral at a site with the best model being linear for invertebrate consumers and nonlinear for roving herbivores (Table S2). Changes in the abundance of piscivores and planktivores were not significantly related to the loss of live coral or structure at the site scale (best model: ANOVA $P > 0.05$).

Discussion

Our observation that a tropical cyclone had larger impacts on coral reef fish assemblages than a disturbance that killed corals but left their dead skeletons intact is consistent with recent syntheses (e.g., Wilson et al. 2006; Pratchett et al. 2008; Graham and Nash 2013), and indicates that many of the long-term effects of coral decline on reef fish communities will be delayed until the physical structure provided by corals is lost. The rate of erosion of dead coral skeletons is highly variable and complete erosion can take years to

decades (e.g., Aronson and Precht 2001), making it difficult to predict the time scales over which fish assemblages will respond to climate-driven changes in disturbance regimes worldwide. For example, it has been proposed that recent declines in the abundance of many fishes in the Caribbean—occurring nearly two decades after region-wide declines in coral cover—could be the result of protracted declines in habitat structure following initial coral mortality (Paddack et al. 2009). Similarly, delayed responses of fish communities to coral decline on Indo-Pacific reefs has led to the inference that fish assemblages respond primarily to changes in structural complexity rather than declines in living coral (e.g., Sano et al. 1987; Pratchett et al. 2011). However, delayed responses to coral decline on Caribbean and Indo-Pacific reefs could also be driven by a storage effect (sensu Warner and Chesson 1985). Thus, the events we observed on Moorea provided us with a unique opportunity to unequivocally compare the impacts of coral mortality versus the loss of structural complexity on reef fish communities.

Fig. 5 Changes in the abundance (mean \pm SE) of four functional groups of reef fishes (coral dwellers, corallivores, roving herbivores, and site-attached herbivores) on the fore reef of Moorea on reefs impacted **a–d** by COTS and Cyclone Oli, **e–h** exclusively by COTS with onset of coral decline by 2008, and **i–l** exclusively by COTS with onset of coral decline by 2009 ($n = 6$ transects per region per year). *Dashed vertical lines* indicate approximate onset of coral decline due to COTS (note that coral cover declined for approximately two years following the onset of the COTS impact at all sites). *Solid vertical lines* indicate timing of Cyclone Oli. Note the log scale on the y-axes



We found reef structure eroded rapidly on the highly wave-exposed fore reef of Moorea, but the rate of decline slowed as habitat structure reached low levels. In addition, fish communities responded nonlinearly to declines in habitat structure such that the impacts of declining structure accelerated at low levels. This is consistent with recent spatial studies that have found similar nonlinear (decelerating) relationships between coral cover and reef fish assemblages (Holbrook et al. 2008a; Chong-Seng et al. 2012). The existence of a decelerating relationship between habitat structure and fish communities might explain why declines in the abundance of many Caribbean fishes have lagged decades behind regional reductions in coral cover (Paddack et al. 2009) despite little evidence for similar lags in the decline of structural complexity on these reefs (Alvarez-Filip et al. 2011). Indeed, our results suggest that reef fish assemblages may be initially highly resistant to coral mortality, but then experience large shifts in community composition as reef structure degrades to very low levels. Similar nonlinear responses to environmental change have been observed in a wide variety of systems and can lead to abrupt transitions between contrasting ecosystem states, which are sometimes difficult to reverse (Scheffer and Carpenter 2003, Bestelmeyer et al. 2011).

The fact that reef fish assemblages may be initially resistant to coral mortality, but then experience large shifts in community composition in the final stages of habitat

degradation, raises two important questions: (1) what are the causes of the nonlinear (accelerating) response to coral decline and the loss of physical structure, and (2) what are the likely consequences for the long-term dynamics of the system? Elucidating the mechanisms by which coral decline impacts reef fish assemblages requires understanding the potential direct and indirect effects of coral on different species and trophic groups. Like others (e.g., Bouchon-Navaro et al. 1985; Sano et al. 1987; Emslie et al. 2011; Kayal et al. 2012), we observed rapid declines in the abundance of fishes dependent on coral following widespread coral mortality that were likely a direct consequence of the loss of their main source of food and shelter. In contrast, large roving herbivores and invertebrate feeders increased in abundance, likely due to increases in food availability (e.g., algal turfs and invertebrates associated with coral rubble) resulting from the decline in living coral (Adam et al. 2011; Gilmour et al. 2013).

In addition to understanding the direction of the response of different functional groups to coral decline, we were interested in understanding the functional form of the relationship between coral and physical structure and fish abundance. Of the five functional groups that responded to the declines in abundance of living corals and physical structure that occurred over the study period, three of these (coral dwellers, corallivores, and territorial herbivores) exhibited significant negative relationships between coral

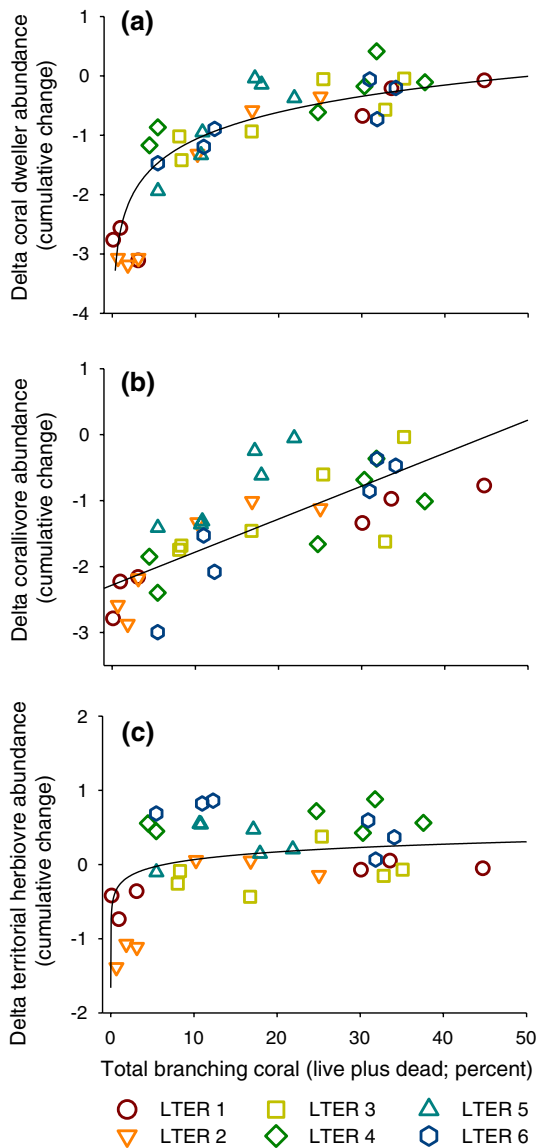


Fig. 6 Relationship between coral structure and the cumulative change in the abundance of **a** coral dwellers ($R^2 = 0.75$), **b** corallivores ($R^2 = 0.57$), and **c** territorial herbivores ($R^2 = 0.27$). Note that decreases in physical structure have increasingly large impacts on the abundance of coral dwellers and territorial herbivores as structure declines to low levels; in contrast, the relationship between physical structure and the abundance of corallivores is approximately linear (see Table S2 for competing models)

structure and abundance at the site scale. For all three functional groups, loss of physical structure was a better predictor of declines in abundance than the loss of living coral alone. Further, for the two groups that depend on coral primarily for shelter (coral dwellers and territorial herbivores), declines in abundance accelerated at low levels of structure, suggesting that habitat becomes more limiting as physical structure becomes increasingly rare. In contrast to coral dwellers and territorial herbivores, whose dynamics were

tightly linked to the local scale (e.g., within site) dynamics of coral habitat, increases in the abundance of larger roving herbivores and invertebrate consumers were less strongly related to local changes in the benthos, suggesting that mechanisms operating at larger spatial scales may have been important in mediating their responses. The timing of the increases, which were synchronous among sites and occurred approximately one year after the major declines in coral cover at most of the sites (LTER 1, 2, 3, 6) raises the possibility that mechanisms operating at an island scale (such as increased reproductive output in response to greater food availability) could be important. These observations highlight the need to develop a better understanding of how different disturbance types impact the demographic rates of different types of fishes and how changes in these rates affect abundances at various spatial scales.

Predicting the long-term consequences of disturbances on reef fish assemblages requires knowing whether fish assemblages will eventually return to their predisturbance state. The few studies that have documented dynamics of reef fish assemblages in response to coral recovery have generally found that fishes track changes in the composition of the benthic community, suggesting that return of similar coral communities will likely herald the return of similar fish assemblages (e.g., Sano 2000; Berumen and Pratchett 2006; Halford and Caley 2009; but see Bellwood et al. 2012). However, many reef fishes strongly impact the recruitment, growth and survivorship of corals, and this creates the potential for strong feedback loops that could influence the dynamics of coral recovery (e.g., White and O’Donnell 2010; Holbrook et al. 2008b, 2011; Dixon and Hay 2012; Burkepile et al. 2013) and ultimately the resilience of the fish assemblage. Herbivorous fishes in particular, which often exert strong top-down control on algae that compete with corals for space, are important for the proper functioning of coral reef ecosystems (Bellwood et al. 2004; Burkepile and Hay 2008; Adam et al. 2011). If herbivorous fishes were to become limited by habitat following the loss of physical structure, it could allow for the establishment of macroalgae that can prevent coral recruitment and cause reefs to become locked into an algae-dominated state (Hughes et al. 2007; Blackwood et al. 2011; Bozec et al. 2013). In Moorea, we observed large declines in the abundance of small site-attached herbivores following the severe habitat degradation caused by Cyclone Oli. However, large roving herbivorous fishes—which are primarily responsible for controlling algae on the fore reef of Moorea—did not decline significantly following the loss of coral structure, likely because many initially recruit into the lagoon where habitat was largely unaltered by the COTS outbreak and cyclone, and only move to the fore reef after becoming less dependent on coral structure (Adam et al. 2011).

Feedbacks between habitat structure, herbivorous fishes, and the capacity of reefs to recover to a coral-dominated state could result in strong synergies between multiple stressors (Anthony et al. 2011). For example, chronic environmental drivers such as OA that will slow coral growth (Hofmann et al. 2010) may have the largest impacts on reef ecosystems following an acute pulse disturbance such as a major bleaching episode. By slowing the rate that new habitat is formed (or accelerating the rate at which old habitat degrades), OA could cause herbivores to become habitat-limited following a disturbance, eventually causing the collapse of herbivore populations and pushing the ecosystem into a self-reinforcing algae-dominated state.

At first glance, our results appear to suggest that tropical cyclones will have larger impacts on reef fish communities compared to less physically destructive disturbances. While this may be true in the short term, this view fails to account for the spatial scales over which these disturbances operate, and how this will influence the potential for recovery over the long term. Cyclone damage tends to be much less spatially extensive than the mortality caused by a mass bleaching event (Wilkinson 2004). As a result, reefs impacted by a cyclone are more likely to maintain connectivity with intact reefs that can supply larval corals and fishes, and, thus, are more likely to recover to a coral-dominated state. In Moorea connectivity between the disturbance-prone fore reef and the lagoon likely contributes greatly to the resilience of the ecosystem by providing the fore reef a stable supply of herbivorous fishes following a disturbance (Adam et al. 2011). This suggests that reef recovery will be impeded when disturbances impair connectivity, as is likely to occur on some isolated islands (especially those with limited habitat diversity) or following spatially extensive disturbances such as mass bleaching episodes that can affect multiple reef habitats across entire archipelagos (Graham et al. 2006). Finally, we emphasize that the effects of disturbances on reef fish assemblages are likely to vary with the attributes of the diverse systems they impact. For example, disturbances may have the biggest impacts on reef fish assemblages on the most diverse reefs (i.e., those in the western Pacific and Indian Ocean) since these reefs often harbor many species of specialized fish that can be highly susceptible to disturbances (e.g., Jones et al. 2004; Munday 2004).

By capitalizing on two landscape-scale disturbances impacting a very well-studied set of reefs, we were able to differentiate, for the first time, between the impacts of coral mortality and declining structural complexity on reef fish communities at a reef-wide scale. Our results indicate that disturbance type greatly influences the rate at which structural complexity declines following coral mortality, which in turn strongly affects the reef-associated fish community. Further, because many species that can facilitate coral

recovery are not reliant on living coral but only require the physical structure it provides, reefs may be less likely to recover to a coral-dominated state following the erosion of coral structure. In addition, we found that changes in the reef fish assemblage accelerate as coral and physical structure decline to low levels. This observation suggests that the impacts of coral decline on reef fish communities are likely to be underestimated by all but the longest-term studies, making ecological surprises likely as reefs reach their final stages of degradation. In addition to serving as a stark warning about the potential impacts of GCC on reef fish assemblages, our results suggest that local management actions aimed at enhancing the resilience of reefs may have the highest chance of success if they are enacted early, before physical structure becomes limiting for many functionally important fishes.

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