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REPORT

Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia

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Abstract The reefs surrounding the island of Moorea, French Polynesia, experienced two large pulse perturbations between 2008 and 2010, an outbreak of the crown-of-thorns seastar (*Acanthaster planci*) followed by a cyclone, that resulted in the reduction in live coral cover on the fore reef from ~40 to <5 %. Live coral cover in back reef and fringing reef habitats initially remained relatively stable, but began a gradual decline around 2010. We assessed the changes in the functional composition of the herbivorous fish community following the pulse perturbations and during the time of gradual coral decline on the back reef and fringing reef. Forty-nine species of herbivorous fishes quantified in yearly surveys between 2006 and 2014 were assigned to six functional groups: browser, detritivore, excavator, farmer, grazer/detritivore, and scraper. Non-metric multidimensional scaling analyses revealed that despite unique functional assemblages initially existing among the fringing reef, back reef, and fore reef habitats, the herbivorous fish communities in all three habitats responded in a qualitatively similar fashion to coral decline by moving toward functional communities characterized by an increased representation of excavators and scrapers. Island-wide scraper biomass increased by ~sevenfold in the post-disturbance time period, while excavator biomass increased by nearly threefold. The biomass of detritivores and grazers/detritivores also increased over the same time period, but to a much lesser degree, while the biomass of browsers and farmers remained essentially unchanged. Macroalgae remained a relatively minor space holder (<10 % cover) in lagoon habitats and on the fore reef through 2014, enabling recruitment of juvenile coral and initiating coral recovery on the fore reef. Results suggest that a functional community with a substantial biomass of herbivores and the capacity for the biomass of scrapers and excavators to increase rapidly in response to landscape-scale declines in coral cover may enhance resilience by preventing the widespread establishment of macroalgae.

Keywords Coral reef fish · Ecological resilience · Herbivore responses · Control of macroalgae

Introduction

Coral reefs face a variety of chronic and acute perturbations ranging from effects associated with global climate change, ocean acidification, and cyclones to more localized effects resulting from disease, coral predator outbreaks or anthropogenic disturbances (Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Anthony et al. 2008; Pandolfi et al. 2011). In some cases, the loss of live coral is followed by an increase in macroalgae due to the sudden availability of suitable substrata. The response of benthic meso-herbivores, especially sea urchins and fishes, can be crucial to the suppression of macroalgae, which is necessary for a return to a coral-dominated community state (Bellwood

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et al. 2004; Hughes et al. 2007; Ledlie et al. 2007). Because the frequency and intensity of perturbations are predicted to increase over the next century, there is a pressing need to more fully understand how assemblages of reef herbivores respond to landscape-scale disturbances that generate open space suitable for colonization by foliose algae (Wilson et al. 2010).

Numerous studies of the effects of disturbances on coral reef fishes have reported that species reliant on live coral for food or shelter frequently decline following loss of live coral cover (Munday 2004; Garpe et al. 2006; Wilson et al. 2006; Graham et al. 2007; Adam et al. 2014; but see Holbrook et al. 2008, 2015), whereas herbivores and detritivores often increase (Garpe et al. 2006; Wilson et al. 2006; Gilmour et al. 2013; Adam et al. 2014; Russ et al. 2015). Disturbances that destroy structural architecture of the reef (e.g., intense wave activity) tend to have greater negative impacts on the fish assemblage as a whole compared to disturbances that kill coral tissue but leave their skeletal structures intact [e.g., bleaching, crown-of-thorns seastar (*Acanthaster planci*) outbreaks] (Sano et al. 1987; Wilson et al. 2006; Garpe et al. 2006; Graham et al. 2006; Adam et al. 2014). Disturbances can vary greatly in magnitude, intensity, and spatial scale of effects among reef habitats (fore reef, back reef, fringing reef), and as a result, these communities may be impacted differently by the same disturbance.

Herbivorous reef fishes constitute a functionally diverse group (e.g., browsers, grazers/detritivores, scrapers, excavators, farmers, detritivores), with different functional groups important for (1) preventing the establishment of macroalgae after a disturbance, (2) removing mature macroalgae if it becomes established, and (3) facilitating settlement, growth, and survival of coral recruits (Bellwood et al. 2004). While the contribution of different functional groups to resilience of coral reefs has been highlighted by several studies (Burkepile and Hay 2008; Green and Bellwood 2009; Hoey and Bellwood 2009; Cheal et al. 2010, 2013), many studies of the role of herbivorous fish in the prevention of coral-to-macroalgae phase shifts have focused on the changes in abundance or biomass of individual species or the total herbivore assemblage (Hart et al. 1996; Halford et al. 2004; Ledlie et al. 2007; Wismer et al. 2009; Lamy et al. 2015). This makes it challenging to assess how dynamic responses of the herbivore assemblage—particularly with respect to the different functional roles played by groups of herbivores—may influence the capacity for a community to return to its pre-disturbed, coral-dominated state.

Recent dynamics of the reef community on Moorea, French Polynesia, provide an unparalleled opportunity to assess island-wide changes in the functional composition of the assemblage of herbivorous fishes to acute disturbances, which in turn can provide insight into how such responses might strengthen or weaken reef resilience. The reefs of Moorea have been subjected to several large perturbations in the past four decades, including a recent outbreak of crown-of-thorns seastars (COTS) in 2008–2009 and large, high energy waves associated with Cyclone Oli in 2010 (Adjeroud et al. 2009; Pratchett et al. 2011a; Adam et al. 2011, 2014; Kayal et al. 2012). Prior to these recent perturbations, the coral community on the fore reef displayed high resilience to earlier disturbances, returning to pre-disturbed coral cover (~40–50 %) within about a decade without undergoing a shift to high cover of macroalgae or other persistent community state (Adjeroud et al. 2009; Trapon et al. 2011; Pratchett et al. 2011a). In contrast to the fore reef, coral cover has historically been more stable within the lagoon habitats (i.e., back reef and fringing reef) of Moorea (Trapon et al. 2011). Nonetheless, some lagoon reefs have transitioned to a state where macroalgae persisted following disturbances that reduced the cover of coral (Done et al. 1991). Thus, while the lagoon habitats of Moorea appear to be much less susceptible to periodic pulse disturbances that can rapidly reduce coral cover on the fore reef, they also appear to be less resilient to disturbance, with even small perturbations potentially resulting in a persistent increase in macroalgae. Whether a system will undergo a coral-to-macroalgae regime shift is partly dependent on the response of the herbivore community immediately following a disturbance (Bellwood et al. 2004; Hughes et al. 2007; Cheal et al. 2010).

In Moorea, both observational and experimental evidence suggests herbivorous fishes prevent the widespread establishment of macroalgae on the fore reef, the habitat most affected by the recent set of disturbances (Adam et al. 2011, 2014; Mumby et al. 2015). By contrast to the fore reef and similar to previous disturbances impacting the reefs around Moorea, the cover of corals in lagoon habitats (i.e., back reef inshore of the barrier crest; fringing reef adjacent to the shore) was reduced less uniformly in space and far less overall in the recent disturbances (Adam et al. 2011, 2014). The herbivore assemblage typically differs among these major coral reef habitats (Russ 1984; Fox and Bellwood 2007), and this, coupled with spatial differences in the degree to which coral cover was affected, may result in spatially varying responses of the herbivore assemblages. Spatial differences in the structure and/or dynamics of the herbivore assemblage could be one of the factors contributing to the lower historical resilience in the lagoons of Moorea compared with the fore reef.

Here, we assessed changes in the herbivore functional community assemblage following the two large-scale disturbances at two different spatial scales—within a specific habitat type and island-wide. The goals were to (1) measure differences in functional composition of the herbivore assemblage among the three major reef habitats (fore reef, back reef, and fringing reef), (2) assess the island-wide responses of herbivorous fishes at the level of functional groups, and (3) evaluate whether functional group responses were likely to strengthen or weaken reef resilience.

Methods

Study site

Moorea (17°30′S, 149°50′W) is a high volcanic island with an offshore barrier reef and narrow (~0.8–1.5 km wide) lagoons (mean depth ~5–7 m) that surround its ~60 km perimeter (Electronic Supplementary Material, ESM, Fig. S1). Between 2008 and 2009, offshore reefs experienced a severe COTS outbreak (Adam et al. 2011; Kayal et al. 2012), which resulted in a decline in the cover of live coral on the fore reef from an island-wide average of ~40 % pre-disturbance to <5 % by 2010. In February 2010, a Category 4 cyclone (Cyclone Oli) passed to the southwest of Moorea. Waves associated with this storm removed large amounts of dead coral structure from the fore reef, but only on the north shore of the island (Adam et al. 2014). Immediately following these disturbances, macroalgae remained a relatively minor space holder on the fore reef which was maintained in a highly grazed state dominated by sparse turfs and crustose coralline algae (Adam et al. 2011). In contrast to the fore reef, and similar to previous disturbances impacting the reefs around Moorea, the COTS outbreak and Cyclone Oli appeared to have a relatively minor impact on corals in the back reef and fringing reef habitats (Adam et al. 2011; Trapon et al. 2011; Kayal et al. 2012).

Categorization of herbivores and functional roles

Classifying all fishes that consume algae regardless of the type of algae consumed or mode of consumption (i.e., simply as herbivores) ignores the different role each functional group may play in sustaining or enhancing coral reef resilience. Based on extensive work by Bellwood and colleagues on similar herbivore assemblages on Indo-Pacific reefs (e.g., see Green and Bellwood 2009 and references therein), we recognized six functionally distinct groups of herbivores:

1. Detritivores—species that feed primarily on detritus, but may also consume turf algae.
2. Grazers/detritivores—species that feed intensely on epilithic algal turf and associated detritus without scraping or excavating the substratum. Both grazers/detritivores and detritivores are important in the prevention of the establishment and growth of macroalgae by removing detritus, sediments, epilithic algal turf and associated macroalgal recruits (Diaz-Pulido and McCook 2002; Cheal et al. 2010; Pratchett et al. 2011b).
3. Scrapers—species that consume epilithic algal turf and associated detritus and remove small portions of the reef substratum (Green and Bellwood 2009).
4. Excavators—species that eat epilithic algal turf and associated detritus and remove large amounts of the calcium carbonate substratum. Like grazers/detritivores, scrapers and excavators can help prevent the establishment of macroalgae by removing young recruits. In addition, by removing substratum and dead coral, scrapers and excavators are important to coral reef recovery by providing settlement space for crustose coralline algae and coral recruits (Bellwood et al. 2004).
5. Browsers—fishes that feed on macroalgae and associated epiphytic material. Browsers can prevent macroalgal overgrowth and shading of corals by consuming standing macroalgae and, therefore, can play an important role in the reversal of phase shifts once macroalgae become established (Nash et al. 2013).
6. Farmers—highly site-attached, territorial species that weed unpalatable macroalgae from their territories and maintain algal farms by excluding invading herbivores (Ceccarelli et al. 2001; Hata and Umezawa 2011; Johnson et al. 2011). The farming of turf algae and removal of macroalgae within farmerfish territories can enhance post-disturbance coral recruitment and diversity compared to non-farmed areas (Done et al. 1991; Gleason 1996).

Data collection

The Moorea Coral Reef Long Term Ecological Research project has collected data island-wide on the abundances of fore reef and lagoon fishes annually since 2006 (Brooks 2014, 2015a). Surveys are conducted by SCUBA divers between 0900 and 1600 h during late July or early August of each year. Abundances of all mobile taxa of fishes observed are recorded on four replicate 5 × 50 m permanent transects that extend from the surface of the reef to the surface of the water column. The abundances of all non-mobile or semi-cryptic taxa of fishes then are counted along the same transect lines using a transect width of 1 m. Our analyses use data from three replicate transects that have been surveyed by the same three observers each year since 2006 on the fore reef, back reef, and fringing reef habitat at each of six sites (two on each of Moorea's three sides), a total of 54 transects spread among the 18 sampling locations (ESM Fig. S1). The total length (TL) of each fish observed is estimated, usually to the nearest 1 cm. Total lengths are converted to fork lengths (FL) when necessary using the formula $\text{FL} = a\text{TL} + b$ where a and b represent published species-specific scaling parameters. Fish biomass (g) then is calculated using the formula $w = a\text{FL}^b$, where FL is the fish FL in cm and a and b represent published species-specific scaling parameters (Brooks 2014).

Estimates of the percent cover of corals and other major benthic substrata are derived from censuses of fixed 0.25 m^2 photoquadrats taken annually in April along five 10-m transects located in each reef habitat at each site (eight quadrats are photographed on each of the five transects for a total of 40 quadrats per site) (Edmunds 2014). Additional details concerning sampling protocols can be viewed at http://mcr.lternet.edu/data.

Data analyses

In order to relate changes in the structure of herbivore functional assemblages with changes in the benthic community, we first documented changes in the percent cover of corals, macroalgae, and turf algae on the fore reef, fringing reef, and back reef. Changes in the percent cover of benthic space holders were analyzed separately for each habitat type using linear mixed-effects models (fixed effect = year, random effect = site) with AR 1 correlated errors. For each year, benthic cover was averaged over all quadrats within each site and then logit transformed [$\log(x/(1-x))$] to meet model assumptions. All models revealed significant variation in the cover of coral, turf algae, and macroalgae over the study period. Thus, we used post hoc Tukey's tests to reveal when significant changes in the cover of each benthic space holder occurred.

To assess changes in the functional community of herbivorous fishes, each species was categorized into one of the six functional groups (detritivore, grazer/detritivore, scraper, excavator, browser, or farmer; ESM Table S1). *Acanthurus triostegus*, a very patchily distributed schooling fish, was removed from all analyses because our surveys do not adequately sample this type of highly aggregated and mobile species. In addition, all observed individuals in the family Blenniidae were excluded as a functional group classification could not be identified confidently for these individuals, leaving a total of 49 species retained for analysis. We used linear mixed-effects models to assess whether fish biomass changed through time, and whether these changes were consistent across the different habitats. For each year, biomass was averaged over all three transects within the 18 unique site by habitat combinations and then log-transformed to meet normality and homoscedasticity assumptions. A linear mixed-effects model (fixed effects = habitat, year, and habitat × year; random effect = site) with AR 1 correlated errors tested whether biomass of each functional group differed among habitat types, whether biomass increased or decreased over the study period, and if so, whether those changes were consistent among habitats. To examine whether changes in biomass could be accounted for by changes in abundance, average size (measured as total fish length), or both, we examined the changes in total abundance and mean fish size (TL) for each functional group over the duration of the study period using the same mixed-effects model framework used to evaluate changes in biomass. When mean biomass, abundance, or size of a functional group differed consistently among habitats, we used the Tukey's HSD test to identify which habitats were different. To visualize overall changes in the biomass, abundance, and mean size of herbivorous fishes in each of the six functional groups, we plotted the mean values (±SE) from the period immediately before the disturbances (2006 and 2007) against the mean values (±SE) during the time period after the disturbances (2010–2014).

Non-metric multidimensional scaling (NMDS) enabled visualization of differences in the herbivore functional assemblage among habitats and through time. NMDS uses ranked distances between objects to map objects onto an ordination space to maximize the dissimilarities among objects. Functional group biomass was log-transformed to better differentiate dissimilarities in herbivore functional communities among habitats and through time. A Bray–Curtis similarity matrix was generated among habitats by year. Changes in the functional community assemblage through time were visualized using Kruskal's NMDS of each functional group. NMDS ordination was performed using the monoMDS function implemented by the vegan package (Oksanen et al. 2013) in the R programing language.

Results

Benthic dynamics

Coral cover declined precipitously on the fore reef from an island-wide mean of ~40 % in 2007 to ~3 % in 2011 (post hoc Tukey's test, $P < 0.001$), before quickly increasing to more than 15 % by 2014 (post hoc Tukey's test, $P < 0.001$) (Fig. 1). Concomitant with coral decline, there was a sharp increase in the cover of turf algae, with turf algae increasing from ~60 % in 2005 to ~90 % by 2010 (post hoc Tukey's test, $P < 0.01$). Macroalgae also initially increased on the fore reef between 2007 and 2008 (post hoc Tukey's test, $P < 0.01$), but has subsequently

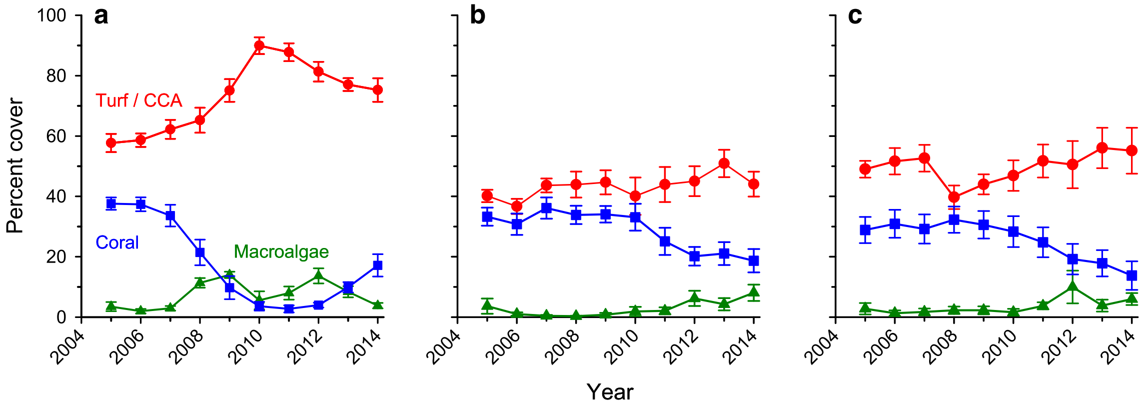

Fig. 1 Dynamics (mean ± SE) of coral (*blue symbols*), turf algae/crustose coralline algae (*red*), and macroalgae (*green*) on the **a** fore reef, **b** back reef, and **c** fringing reef of Moorea from 2005 to 2014 ($N = 6$ sites in each habitat type)

oscillated around 10 % (Fig. 1). As corals recovered, the cover of turf algae declined from a peak of 90 % in 2010 to 75 % in 2014 (post hoc Tukey's test, $P < 0.01$). In contrast to the sharp decline and recovery of coral observed on the fore reef, coral cover on the back reef and fringing reef was relatively stable through 2010 (Fig. 1). However, beginning in 2010, the lagoon habitats began a period of gradual coral decline, with significant declines (relative to peak coral cover) observed by 2011 on the back reef and 2012 on the fringing reef (post hoc Tukey's test, $P < 0.05$ for both comparisons). While decline in coral cover on the fore reef was clearly caused by the COTS outbreak (Adam et al. 2011; Kayal et al. 2012), densities of COTS have consistently been more than an order of magnitude lower within the lagoons of Moorea compared with the peak densities observed on the fore reef (Adam et al. 2011; Brooks 2015b). Thus, coral decline within the lagoons may not have been caused solely by COTS, although the cause(s) remain unknown. Similar to the fore reef, there was a trend for both turf algae and macroalgae to increase somewhat following coral decline (Fig. 1). Nonetheless, the average cover of macroalgae has remained below ~10 % at the lagoon study sites throughout the duration of this study (Fig. 1).

Spatial and temporal patterns of herbivore biomass, abundance, and body size

A total of 54 herbivore species were observed from 2006 to 2014 in the three habitats of Moorea; however, one or two species accounted for the majority of biomass in most functional groups (ESM Table S1). The total biomass of herbivores (excluding poorly sampled species; see "Methods") differed greatly among the habitats ($F_{2,151} = 24.81$, $P < 0.0001$; Fig. 2). Post hoc Tukey's tests indicated that the mean biomass over the entire time period was significantly higher on the fore reef (27.9 g m^{-2}) than on the fringing reef (13.2 g m^{-2}), and the back reef (17.3 g m^{-2}). In addition, biomass was significantly higher on the back reef compared with the fringing reef ($P < 0.01$ for all comparisons). Despite large differences in total herbivore biomass among habitats, biomass increased in all habitats over the study period ($F_{1,151} = 68.00$, $P < 0.0001$) with no evidence for differential responses in different habitat types (year × habitat interaction: $F_{2,151} = 1.57$, $P = 0.211$; Fig. 2).

Both scrapers and excavators had greater biomass on the fore reef compared with either lagoon habitat (post hoc Tukey's tests; $P = 0.05$ for scrapers for the comparison between the fore reef and back reef; all other comparisons $P < 0.0001$). The greater biomass of both groups on the fore reef resulted from their greater mean size on the fore reef compared with the back reef and fringing reef (post hoc Tukey's test, $P < 0.0001$ for all comparisons). Despite large differences in size structure among habitat types, scrapers and excavators responded similarly in all habitats (year × habitat interaction, $P > 0.05$ for both groups), with overall biomass increasing nearly sevenfold for scrapers ($F_{1,151} = 104.1$, $P < 0.0001$) and threefold for excavators between 2006 and 2014 ($F_{1,151} = 80.1$, $P < 0.0001$; Fig. 3a; Table 1; ESM Fig. S2). Increases in biomass of scrapers and excavators were driven by increases in abundance, with scrapers increasing about sevenfold ($F_{1,151} = 165.68$, $P < 0.0001$) and excavators by nearly threefold in abundance ($F_{1,151} = 71.06$, $P < 0.0001$; Fig. 3b; ESM Table S2).

Detritivores had similar levels of biomass in all habitat types ($F_{1,151} = 1.93$, $P = 0.15$), while grazers/detritivores had higher biomass on the fore reef compared with the back reef and fringing reef habitats (post hoc Tukey's tests, $P < 0.0001$ for both comparisons). Grazers/detritivores tended to be smaller on the fore reef (post hoc Tukey's tests, $P < 0.0001$ for both comparisons), but were more abundant

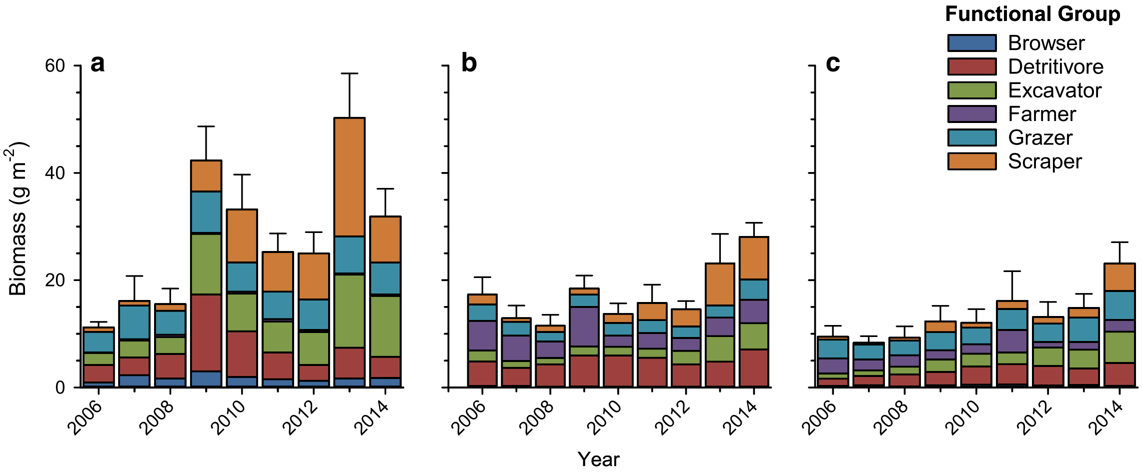

Fig. 2 Stacked *bar* chart showing the dynamics (mean ± SE) of total herbivore biomass and the contribution of each herbivore functional group on the **a** fore reef, **b** back reef, and **c** fringing reef of Moorea ($N = 6$ sites in each habitat type; 'Grazer' key label = grazer/detritivore functional group)

than in the back reef and fringing reef habitats (post hoc Tukey's tests, $P < 0.0001$ for both comparisons). Overall biomass increased ~64 % for detritivores ($F_{1,151} = 11.71$, $P = 0.0008$) and ~14 % for grazers/detritivores ($F_{1,151} = 11.20$, $P = 0.001$) between 2006 and 2014 (Fig. 3a; Table 1; ESM Fig. S2). While detritivores tended to increase in abundance ($F_{1,151} = 4.39$, $P = 0.038$), the increase in biomass of both detritivores and grazers/detritivores was driven largely by an increase in average size of individuals ($F_{1,151} = 56.03$, $P < 0.0001$, and $F_{1,151} = 7.95, P < 0.005$) in all habitat types (time x habitat interaction, $P > 0.8$ for both groups; Fig. 3; ESM Table S2). In contrast to other herbivores, the biomass of browsers and farmers was relatively constant over the study period ($P > 0.5$ for both groups; Fig. 3a; Table 1; ESM Fig. S2).

Spatial structure and dynamics of herbivore functional assemblages

The first NMDS axis revealed clear separation of herbivore functional assemblages among the three habitat types (Fig. 4a). The fore reef was distinguished from the back reef and fringing reef habitats by a greater biomass of browsers and grazers/detritivores, while the back reef was distinguished from the other two habitats by having a greater biomass of farmers (Fig. 4b). The second NMDS axis accounted for temporal changes that occurred following the disturbances and showed that the herbivore assemblages changed in a consistent way in all habitats following the disturbances, with all habitats moving toward communities with increased proportional representation of scrapers and excavators.

Discussion

The herbivorous fish community on Moorea suppressed the proliferation of macroalgae on the fore reef for the initial 5 yr following a COTS outbreak and major cyclone that drove the cover of live coral to near zero (Adam et al. 2011). By preventing widespread establishment of macroalgae, herbivorous fishes can maintain a state suitable for recolonization by coral propagules. Indeed, coral recruitment in Moorea has been very high on the fore reef, and this has enabled significant coral recovery since 2010 (Fig. 1; Edmunds 2014). Bellwood et al. (2004) suggested that scrapers and excavators are the main two functional groups of herbivores that prevent the establishment of macroalgae by removing algal propagules and young macrophytes while scraping reef surfaces; in Moorea, these were the two groups that increased most substantially following the disturbances. Two other functional groups—grazers/detritivores and detritivores—are thought to play a less prominent role in preventing the establishment of macroalgae by consuming turf algae and associated early developmental stages of macroalgae (Williams and Polunin 2001; Diaz-Pulido and McCook 2002; Cheal et al. 2010; Pratchett et al. 2011b). Interestingly, while grazers/detritivores and detritivores accounted for a large fraction of biomass of the assemblage throughout the time period, and both increased significantly following the recent perturbations, they did not increase to the same degree as scrapers and excavators. Thus, biomass of herbivore functional groups believed to be of greatest importance following a landscape-scale loss of coral responded quickly enough over a sufficiently large area to maintain fore reef surfaces around Moorea in a state suitable for recolonization of coral.

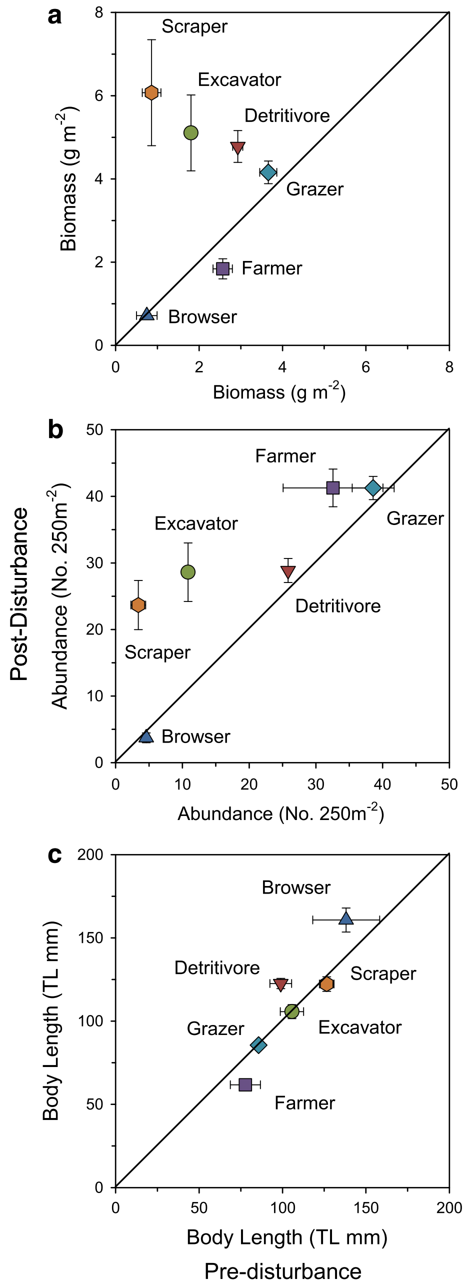

Fig. 3 Mean (±SE) **a** biomass, **b** abundance, and **c** total length (mm) for the pre-disturbance ($N = 2$) and post-disturbance ($N = 5$) time periods on an island-wide scale for each functional group (color coded as in Fig. 2; 'Grazer' = grazer/detritivore functional group)

Table 1 ANOVA table for mixed-effects models testing whether the mean biomass of each functional group varied among habitats and years

Source	Num DF	Den DF	*F* value	*P* value
Browser biomass				
Year	1	151	0	0.9909
Habitat	2	151	46.27	<0.0001
Year × Habitat	2	151	0.14	0.8697
Detritivore biomass				
Year	1	151	11.71	0.0008
Habitat	2	151	1.93	0.1485
Year × Habitat	2	151	1.25	0.2888
Excavator biomass				
Year	1	151	80.07	<0.0001
Habitat	2	151	36.88	<0.0001
Year × Habitat	2	151	0.95	0.3897
Farmer biomass				
Year	1	151	0.34	0.5623
Habitat	2	151	34.64	<0.0001
Year × Habitat	2	151	0.49	0.6131
Grazer/detritivore biomass				
Year	1	151	11.2	0.001
Habitat	2	151	46.92	<0.0001
Year × Habitat	2	151	0.94	0.3918
Scraper biomass				
Year	1	151	104.13	<0.0001
Habitat	2	151	13.87	<0.0001
Year × Habitat	2	151	2.62	0.0759

While large increases in the abundance and/or biomass of herbivorous fishes have been observed in other systems following large coral mortality events (e.g., Garpe et al. 2006; Hawkins et al. 2006; Gilmour et al. 2013), the magnitude of the increases we observed in Moorea is striking. For both scrapers and excavators, increases in biomass were driven almost entirely by large increases in the abundance of a single dominant species (excavators: *Chlorurus sordidus*; scrapers: *Scarus psittacus*), suggesting massive population-level responses. There is both behavioral and body condition evidence for one of these species (*Chlorurus sordidus*) that strongly suggests it is food-limited in Moorea (Tootell and Steele 2015). Both species were abundant before the disturbance and are among the fastest growing and earliest to mature of any members of their functional groups. In addition to conferring greater resilience to fishing (Taylor et al. 2014), the tendency of a fish to grow fast and reproduce early likely enables these species to respond quickly to favorable environmental conditions, such as increased food supply that could result in increased growth, survivorship, and reproductive output. Inspection of size frequency distributions indicates that population increases of *C. sordidus* and *S. psittacus* may have been driven in part by increased recruitment, with recruitment of both species increasing over the course of the study, especially in 2012 and 2013 (ESM Figs. S3, S4, S5, S6). While it is unknown what fraction of larvae produced by *C. sordidus* and *S. psittacus* are retained in Moorea, there is evidence for another reef fish that at least

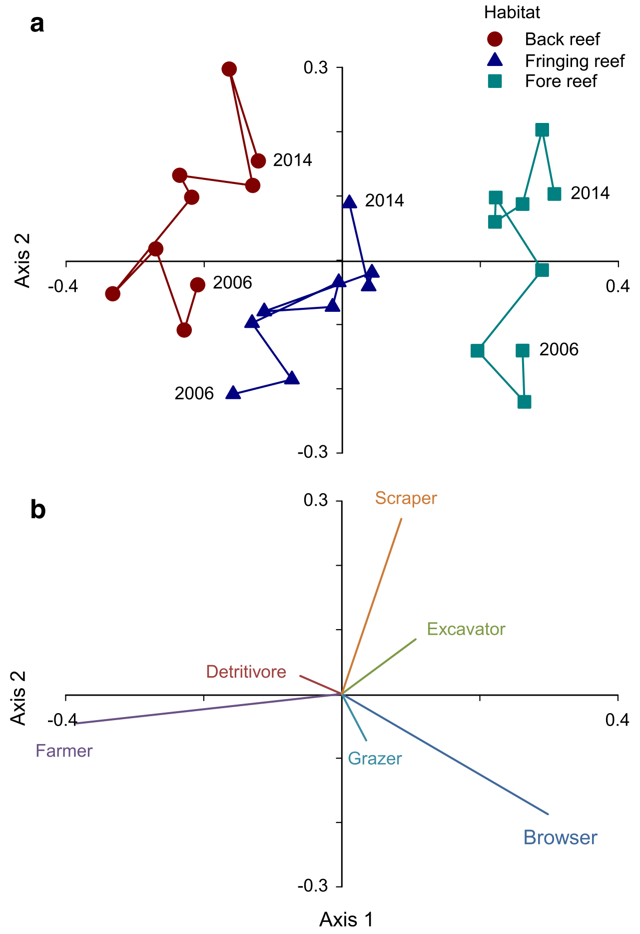

Fig. 4 Non-metric multidimensional scaling (NMDS) plots of Bray–Curtis dissimilarities on log-transformed biomass of herbivore functional groups. **a** Site ordinations showing the changes in herbivore functional communities through time on the fringing reef (*blue triangles*), back reef (*red circles*), and fore reef (*turquoise squares*) habitats. **b** Species loadings plot showing the relative contribution of the different functional groups to the site ordinations (color coded as in Fig. 2; 'Grazer' = grazer/detritivore functional group). Stress = 0.07

~30 % of the recruits arriving in Moorea were produced locally (Beldade et al. 2012). Further, Beldade and colleagues (2012) found that larger fish contributed disproportionately to self-recruitment, likely due to maternal effects on larval quality. Thus, if a significant fraction of the larvae produced by *C. sordidus* and *S. psittacus* are locally retained, it is possible that population increases resulted in part from increased recruitment resulting from increased reproductive output. An alternative explanation for the increase in biomass of scrapers and excavators compared with other functional groups could be reduced fishing pressure on these groups after the disturbance. However, we believe this is unlikely as these herbivores are highly valued as food and are a main staple of the lagoon fishery of Moorea (Madi Moussa 2010).

The biomass of detritivores was also dominated by a single species (*Ctenochaetus striatus*). However, unlike scrapers and excavators, increases in the biomass of detritivores were driven largely by increases in mean size rather than abundance (ESM Fig. S7). *Ctenochaetus striatus* appears to be much longer-lived and likely reaches maturity at an older age than *Chlorurus sordidus* and *S. psittacus* (Choat and Robertson 2001; Ochavillo et al. 2011), traits that could result in a slower numerical response. Unlike scrapers, excavators, and detritivores, increases in the biomass of grazers/detritivores were not due primarily to changes in the abundance and/or size structure of a single dominant species, but were related instead to changes in the relative abundances of different species. For example, small-bodied *Acanthurus nigrofuscus* (mean size across all habitats and years = 85 mm) declined in relative abundance during the study period, while larger-bodied *A. olivaceus* (mean size across all habitats and years = 153 mm) increased. Thus, both life history traits of dominant species and the potential for differential responses within a functional group are likely to influence how herbivore functional groups respond to disturbances.

By virtue of their ability to consume mature foliose algae, browsers become a critically important functional group for resilience when other herbivores cannot completely prevent macroalgae from becoming established (Bellwood et al. 2004; Green and Bellwood 2009). The biomass of browsers did not change on Moorea over the course of the study, perhaps because foliose macroalgae remained largely suppressed by other herbivorous fish following the sudden, massive death of coral to COTS and Cyclone Oli (Fig. 1; Adam et al. 2011). Alternatively, the biomass of browsers present before the disturbances may have been sufficient to consume any increase in the production of macroalgae afterward, with any resulting increases in biomass of these fishes being small and undetectable. Finally, many browsers in Moorea (and elsewhere) have life history traits that make them especially vulnerable to fishing (Nash et al. 2013; Edwards et al. 2014). Since many browsers in Moorea are preferentially fished, it is possible that fishing pressure on browsers is high enough to prevent any potential response to increased food availability.

The presence of suitable substrata for recruitment of coral is a necessary but not sufficient condition for the return of coral following a large-scale disturbance. Return to a coral state requires coral propagules to recolonize the reef and a sufficient number of those recruits to survive and grow. So, in addition to influencing resilience by affecting the availability of substrata suitable for coral recruits, herbivorous fishes can further affect the return rate of coral by influencing growth and survivorship of coral recruits.

Territorial farmerfishes can enhance growth and survival rates of coral by protecting recruits that settle into their defended turf farms from corallivores and herbivores (White and O'Donnell 2010); however, the biomass of this functional group of herbivores did not change appreciably following the disturbances. By contrast with farmerfishes, scraper and excavator species, which increased substantially in abundance and biomass following the disturbances, can weaken as well as strengthen resilience of the coral state. Aside from their positive effects via suppression of macroalgae, scraping and excavating herbivores potentially can enhance the suitability of substrate for coral recruitment by exposing reef matrix (Green and Bellwood 2009). However, their function as bioeroders and corallivores can result in scrapers and excavators directly reducing growth and survivorship of corals via coral predation and indirectly by increasing recruit mortality by eroding the stability of reef substrate (e.g., Penin et al. 2010; Mumby et al. 2015). Despite these potential negative effects, and our observations of frequent predation on coral recruits by scraping and excavating grazers, coral cover has increased rapidly on the fore reef, suggesting that the positive impacts of these herbivores on coral recruitment may outweigh any potential negative impacts of corallivory on the growth and survivorship of coral recruits (as has also been suggested in other systems, e.g., see Mumby 2009).

At the island scale, there was considerable variation in the responses of different herbivore functional groups following the widespread death of coral on the fore reef. The greatest biomass responses were by functional groups that provide the first line of defense against domination by foliose algae, specifically the groups that are most effective at suppressing the establishment of macroalgae, and most notably scrapers whose collective biomass increased by an average of sevenfold in the 5 yr following the initial disturbances. This is precisely the response expected to confer greatest resilience to the sudden availability of a massive amount of substrata that potentially can be colonized by foliose algae. However, there may be heterogeneity in the strength of resilience properties among the habitat zones of Moorea due in part to spatial differences in the structure and responses of the herbivore functional groups. Interestingly, our results showed that despite considerable variation in the structure of the functional assemblage among the three major habitat zones of Moorea, responses of the assemblages on the fringing reef, back reef, and fore reef all were similar, moving toward a community where scrapers and excavators had proportionately greater representation. Inspection of time series plots indicates that biomass of scrapers and excavators was increasing in all habitats following the loss of coral cover on the fore reef; however, the largest increases in biomass in the lagoon habitats appear to have occurred since 2011, as turf algae and macroalgae have begun to increase, suggesting that fish in these habitats are responding at least in part to changes in local resource availability. Nonetheless, there are clearly strong connections among habitat types. For example, the lagoon serves as a nursery habitat for the dominant scraper and excavator species before they migrate to the fore reef later in life (Adam et al. 2011). In addition, a previous analysis of the entire herbivore assemblage found the timing of the herbivore response was congruent around the island despite differences in the timing of coral decline at different sites (Adam et al. 2014). Both patterns strongly suggest the importance of island-scale processes (such as large-scale recruitment events potentially resulting from significant self-recruitment) in mediating the herbivore response to local disturbances. While much work remains to understand the precise mechanisms operating, this study points to the importance of both local and island-scale processes in influencing the spatial structure and dynamics of herbivore assemblages following disturbances.

The fore reef has experienced multiple large-scale disturbances over the past four decades and historically has returned rapidly (~1 decade time scale) to a coral-dominated community state (Adjeroud et al. 2009; Pratchett et al. 2011a; Adam et al. 2011, 2014). Following past disturbances, some lagoon habitats on Moorea transitioned to a community dominated by foliose macroalgae that persisted for years (Done et al. 1991), whereas seaweeds have historically remained rare on the fore reef (Adjeroud et al. 2009). There are many differences between the lagoon and fore reef that can contribute to the difference in resilience, including human-influenced drivers that alter bottom-up (e.g., greater nutrient enrichment in the lagoon) and top-down (e.g., more intense fishing of herbivores in the lagoon) forcing. Our study suggests the overall lower abundance and biomass of functionally important herbivores may be a contributor. While spatial differences in the structure of the herbivore assemblages (e.g., fore reef supports greater biomass of key herbivore functional groups) could contribute to the greater resilience of the fore reef relative to the lagoon, our study also indicates that the herbivore assemblages responded similarly in the two habitats. Exploring responses of functional groups revealed that herbivores that play fundamentally different roles in reef ecosystems responded in substantially different ways to major disturbances. In our case, the functional groups that have been identified as conferring the greatest resilience to a coral-dominated state by suppressing establishment of macroalgae increased the most. Future work is needed to better understand the demographic mechanisms underlying the biomass responses, as well as the properties of systems that enable herbivores to respond to sudden, widespread increases in food following perturbations that kill coral over landscape scales.

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