

Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef

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Abstract Changes in the relative abundances of coral taxa during recovery from disturbance may cause shifts in essential ecological processes on coral reefs. Coral cover can return to pre-disturbance levels (coral recovery) without the assemblage returning to its previous composition (i.e., without reassembly). The processes underlying such changes are not well understood due to a scarcity of long-term studies with sufficient taxonomic resolution. We assessed the trajectories and time frames for coral recovery and reassembly of coral communities following disturbances, using modeled trajectories based on data from a broad spatial and temporal monitoring program. We studied coral communities at six reefs that suffered substantial coral loss and subsequently regained at least 50 % of their pre-disturbance coral cover. Five of the six communities regained their coral cover and the rates were remarkably consistent, taking 7–10 years. Four of the six communities reassembled to their pre-disturbance composition in 8–13 years. The coral communities at three of the reefs both regained coral cover and reassembled ten years. The trajectories of two communities suggested that they were unlikely to reassemble and the remaining community did not regain pre-disturbance coral cover. The communities that regained coral cover and reassembled had high relative abundance of tabulate *Acropora* spp. Coral communities of

this composition appear likely to persist in a regime of pulse disturbances at intervals of ten years or more. Communities that failed to either regain coral cover or reassemble were in near-shore locations and had high relative abundance of *Porites* spp. and soft corals. Under current disturbance regimes, these communities are unlikely to re-establish their pre-disturbance community composition.

Keywords Coral recovery · Reassembly · Time frames · Disturbance frequency · Community shift · Great Barrier Reef

Introduction

Variation among coral reef communities in vulnerability to, and recovery from, disturbances has received much attention because of concerns that anthropogenic activities are changing disturbance regimes for coral reefs. For example, human-induced climate change is predicted to increase the frequency and severity of bleaching events and the frequency of high-intensity tropical cyclones (Hoegh-Guldberg et al. 2007; Mendelsohn et al. 2012; IPCC 2013). Consequently, coral reef communities will suffer more frequent pulse disturbances and the intervals for recovery will be reduced (Nystrom et al. 2000).

While research has focused on the many factors that influence recovery rates of coral reef communities, less consideration has been given to the various aspects of recovery itself (Bellwood et al. 2004; Hughes et al. 2010; Graham et al. 2011). Recovery of coral reefs consists of many components. For coral communities, two critical components are coral recovery and reassembly. The return of hard and soft coral cover to pre-disturbance levels,

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hereafter ‘coral recovery,’ is the metric most widely used to assess recovery of coral communities (Hughes et al. 2010; Graham et al. 2011). ‘Reassembly’ is the recovery of coral community composition so that relative abundances of component taxa are similar to pre-disturbance levels. Reassembly ensures that processes and traits that contribute to ecosystem function of a particular coral community are restored (Moberg and Folke 1999; Nystrom et al. 2008). For coral reefs, these processes and traits include framework building (Aronson et al. 2002; Wild et al. 2011), habitat complexity (Graham et al. 2006), diversity of food sources (Pratchett 2005), recruitment (Mumby et al. 2007; McClanahan et al. 2012), and connectivity (Jones et al. 2009). Communities that shift in composition may retain ecological function if the species that are added fulfill the functions of those that are lost. If this is not the case, a shift will result in loss of function and degradation.

Changes in function through shifts in coral communities can occur on millennial time scales. For example, in Belize, reef cores provided evidence of a shift in coral dominance from *Acropora cervicornis* to *Agaricia tenuifolia* that resulted in the loss of the principal reef-building species of the last 3,000 years (Aronson et al. 2002, 2004; Grigg et al. 2002). The accretion of crumbly *A. tenuifolia* skeletons on steep, unstable reef slopes cannot match the rate of reef building based on the upright, interlocking branches of *A. cervicornis*, leaving these coral reefs vulnerable to drowning in the face of rising sea levels caused by climate change. On shorter time scales, coral communities have returned to their pre-disturbance composition in some cases (Benzoni et al. 2006; Burt et al. 2008; Gilmour et al. 2013), while in other cases, the composition has shifted (Berumen and Pratchett 2006; Burt et al. 2008). In Moorea, loss of *Acropora* spp. and replacement by *Pocillopora* spp. and *Porites* spp. resulted in a corresponding change in the community composition of specialized butterflyfishes (Berumen and Pratchett 2006; Adjeroud et al. 2009; Pratchett et al. 2011). The consequences of this shift for the persistence of the reef community remain to be seen, but the altered community can be expected to respond differently to future disturbances.

These examples of both assemblage stability and assemblage shifts provide clear evidence that coral recovery does not necessarily equate to reassembly. However, to date, there has been limited scope for assessing the pathway to this disparity due to the opportunistic approach used in data collection. That is, community composition prior to disturbance has been compared with the composition after the community regains the pre-disturbance level of coral cover (Benzoni et al. 2006; Berumen and Pratchett 2006; Burt et al. 2008). Surveys are usually not frequent enough to track the intervening stages of recovery and reassembly (but see Adjeroud et al. 2009), though recovery trajectories are likely to vary among coral communities.

The Long-Term Monitoring Program (LTMP) at the Australian Institute of Marine Science (AIMS) has documented multi-decadal changes in coral cover and community composition on reefs spanning 12° of latitude on the Great Barrier Reef (GBR). Such broad spatial and temporal sampling provides an opportunity to assess variation in the temporal trajectories for coral recovery and reassembly among GBR coral communities recovering from disturbance. In this study, we use models to examine trajectories and estimate time frames of coral recovery and reassembly. We used modeled estimates to assess the likelihood that coral communities would reassemble or that communities would shift. Specifically, we address the following questions: (1) What are the time frames and trajectories for coral recovery and reassembly? (2) How does this vary among individual reefs? (3) Do pre-existing differences in community composition alter recovery outcomes? We discuss recovery outcomes for these communities in relation to currently observed disturbance intervals and also consider how outcomes may change if disturbance intervals become shorter.

Materials and methods

Data collection

Coral cover and composition of the benthic community were documented annually from 1993 until 2005, and biennially thereafter. Coral recovery and reassembly following disturbance were assessed for coral communities that met the following criteria: (1) loss of $\geq 33\%$ of initial coral cover due to a known disturbance, (2) occurrence of $\geq 50\%$ recovery of lost coral cover, (3) at least 1 year of data from prior to the disturbance, (4) the community was described at high taxonomic resolution ($>90\%$ of hard corals were classified to genus), and (5) surveys continued for at least six years after the disturbance. Ten of sixteen reef communities that met Criteria 1, 3, and 4 did not meet Criterion 2. In six of these ten cases, the disturbance was relatively recent and so recovery periods were not yet long enough to meet Criterion 5. Ultimately, this yielded six reef communities (Thetford Reef, Reef 19138, Horseshoe Reef, Green Island, Fitzroy Island, and Low Isles) across a range of inshore and mid-shelf locations spread over 1,000 km and 6° of latitude.

Benthic communities were sampled using digital still images taken along five permanent 50-m transects in each of three sites per reef ($n = 15$ transects). Sites were situated in a standard habitat: reef slope on the north-east flank of each reef. Fifty images were taken at approximately 1-m intervals along each transect, and 40 were selected at random for analysis. Five points, arranged in a quincunx

pattern, were projected onto each image ($n = 200$ points per transect), and the benthic organisms beneath each point were identified to the highest taxonomic resolution possible. These figures were then converted to percent cover. In this study, ‘coral recovery’ is based on increases in cover of all hard and soft coral taxa summed, while reassembly is based on composition of coral communities, with hard corals identified to genus (*Acropora* spp., *Porites* spp., and *Montipora* spp. are further sub-divided to growth forms) and soft corals as one category.

Statistical analyses

The coral assemblage in the year immediately prior to the disturbance was taken as the reference point. At five of the six locations, coral cover was high prior to disturbance and in a state of slow growth, indicating that the community had not experienced recent pulse disturbance. The exception was Green Island, where coral cover has remained relatively low since at least the *Acanthaster planci* outbreak in the 1960s (Baxter 1990). In addition, the Bray–Curtis similarity among communities in pre-disturbance years indicated that their composition was relatively stable at each reef.

Coral recovery was taken to be the increase in coral cover relative to the amount lost during the disturbance. For example, if coral cover declined from 50 to 10 % (e.g., 40 % coral cover was lost) following disturbance and 20 % was re-established during recovery, coral recovery would be 50 %. In the absence of any disturbance (both pulse and chronic of all magnitudes), we expected that coral cover would return at least to the pre-disturbance level, if not higher. Thus, we anticipated 100 % coral recovery.

To assess changes in composition of coral communities during recovery, cover of coral taxa was averaged across 15 transects for each reef in each year and then transformed to relative abundance so that the sum of all coral components was 100 %. A Bray–Curtis similarity matrix for each reef was produced in PRIMER (Clarke and Warwick 2001) to compare pre-disturbance coral communities with those in each year of recovery. The recovery period was defined as the sequence of years with no coral loss attributable to documented disturbances. The temporal changes in similarity during recovery were used to assess reassembly. Even stable communities will show some year-to-year variation in composition due to colony growth, undetected disturbances, and sampling error. In order to account for this, we calculated a ‘reassembly benchmark’ as the average Bray–Curtis similarity between coral communities from year-to-year in the years prior to disturbance. The reassembly benchmark was 85 % (± 1.4 % SE, $n = 13$), with a range of 77.5–92.4 %.

Data for all reefs were combined to examine the generality of the relationship between coral recovery and reassembly. Percent coral recovery was normalized via square root transformation (back-transformed values are presented on all figures). Models including linear, asymptotic, sigmoidal, exponential, and second order polynomial were fitted to the data as were numerically appropriate using lme and nlme in R (R Core Team 2013; Electronic Supplementary Material, ESM, Table 1). All candidate models incorporated a first order autoregressive correlation structure to account for the accumulative nature of the coral recovery variable. A random effect of ‘reef’ was also included. The best-fit model was selected using Akaike’s information criterion (AIC; Akaike 1973; ESM Table 1) as well as likelihood ratio tests. Specifically, a linear model was selected if it had the lowest AIC or if there was no evidence that it fitted the data less well than the model with the lowest AIC. Ninety-five percent confidence intervals (CIs) based on expected deviations from the selected model were also calculated. The model and CIs were fitted to the data and provided an estimate of the level of reassembly when 100 % coral recovery had occurred. We checked the fit of the final model using the proportion of the variance that was explained (R^2 , Anderson-Sprecher 1994).

To examine temporal trajectories for both coral recovery and reassembly, models with 95 % CIs were fitted to each variable through recovery time as described previously (ESM Table 1). Time frames for coral recovery and reassembly to reach their respective benchmarks were estimated from the models. For reassembly, the best-fit model was extrapolated to reach the benchmark of 85 % and the time frame was estimated from the forward projection. Coral recovery was rescaled so that zero recovery was aligned with the lowest observed Bray–Curtis similarity value, and 100 % coral recovery was aligned with the reassembly benchmark of 85 %. This meant that percent coral recovery and percent reassembly were shown on equivalent scales. The final fit of each model was also assessed as the proportion of the total variance explained (via deviance) by the model (R^2 , Anderson-Sprecher 1994).

To examine the variation in coral recovery and reassembly trajectories among reefs, the model selection process was repeated for each reef separately (ESM Table 1). However, in this case, gls and gnls in R (R Core Team 2013) were used and first order autoregressive correlation structures were incorporated in final models only when inferential comparisons (AIC, log-likelihood ratio tests) indicated improved fit. Time frames for coral recovery and reassembly were estimated from the best-fit model. When benchmarks for coral recovery (100 %) or reassembly (85 %) had not been reached over the course of surveys, best-fit models were extrapolated to reach them and time frames were estimated from the forward projection. R^2

Table 1 Summary of disturbance and recovery attributes for six reefs that met the selection criteria for recovering coral communities

Location	Sector shelf position	Disturbance type	Pre-disturbance coral cover (%)	Proportion of coral loss (%)	Recovery years	Coral recovery relative to loss (%)
Thetford Reef	Cairns mid-shelf	<i>A. planci</i>	53	69	8	105
Reef 19138	Whitsundays mid-shelf	Cyclone	44	60	10	121
Horseshoe Reef	Swains mid-shelf	<i>A. planci</i>	57	74	8	90
Green Island	Cairns inshore	<i>A. planci</i>	21	56	9	147
Fitzroy Island	Cairns inshore	Bleaching/ <i>A. planci</i>	56	60	11	87
Low Isles	Cairns inshore	<i>A. planci</i> /cyclone	50	68	9	88

provided an estimate of the fit of final models. For simplicity, coral recovery and reassembly outcomes for each reef community are discussed based on the line of best fit, though we acknowledge high uncertainty surrounding future projections, as indicated by CIs, when appropriate.

We used Kruskal's non-metric multi-dimensional scaling (nMDS) in PRIMER (Clarke and Warwick 2001) to examine the within- and among-reef variation between coral communities in the pre-disturbance year and in the final year of the recovery period. A SIMPER analysis (PRIMER; Clarke and Warwick 2001) was used to assess the contribution of each coral taxon to the variation observed. Coral taxa that contributed to at least 10 % of the variation between any assemblage pair or had a correlation of ≥ 0.75 were displayed on the nMDS ordination.

Results

Disturbance and recovery for six GBR coral communities

Pre-disturbance coral cover varied among the six reefs: Green Island Reef had a relatively low pre-disturbance cover of 21 %, while the other communities ranged from 44 to 57 % (Table 1). Disturbance histories varied considerably among the communities (Table 1). Reef 19138 was impacted by Cyclone Justin in 1997. Thetford Reef, Horseshoe Reef, and the reef at Green Island suffered *A. planci* outbreaks in the late 1990s and early 2000s. Reefs at Fitzroy Island and Low Isles suffered multiple disturbances in the 1990s including bleaching, cyclone damage, and *A. planci* outbreaks. The proportion of initial coral cover that was lost ranged from 56 to 74 % and coral recovery ranged from 87 to 147 % (Table 1). Recovery at each reef was surveyed for 8–11 years.

The relationship between coral recovery and reassembly

For the combined data, there was a positive linear relationship between coral recovery (square root transformed)

and reassembly of coral communities ($R^2 = 0.64$; Fig. 1; ESM Table 1). Coral recovery occurred more rapidly than reassembly: where 100 % coral recovery occurred, com-

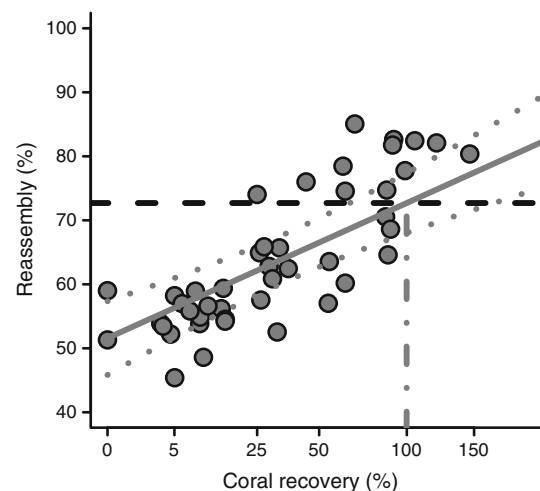


Fig. 1 Relationship between coral recovery (square root transformed) and reassembly (Bray–Curtis similarity) for combined data from the six recovering communities, with a best-fit linear model (solid line) and 95 % CIs (gray-dotted lines). The level of reassembly when coral recovery reaches 100 % (vertical gray line) is marked by the black horizontal dashed line

munity reassembly had reached 73 % (± 5 % CI; Fig. 1), 12 % short of the benchmark.

Trajectories and time frames of coral recovery and reassembly

In general, both coral recovery (square root transformed) and reassembly followed linear trajectories (Fig. 2). One hundred percent coral recovery occurred after 9 years, while 85 % reassembly occurred over 3 years later (Fig. 2; Table 2). The time frames for coral recovery among the six communities were remarkably similar. With the exception of Fitzroy Island, full coral recovery was expected to occur

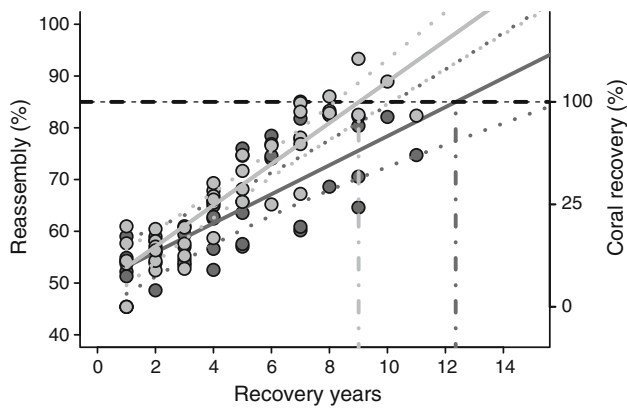


Fig. 2 Reassembly (left y-axis; black points) and coral recovery (square root transformed; right y-axis; gray points) through time (number of recovery years) for the combined data, with best-fit models (solid lines of corresponding color) and 95 % CIs (dotted lines of corresponding color). Eighty-five percentage of reassembly and 100 % coral recovery are simultaneously represented by a single horizontal black-dashed line. The number of recovery years for 85 % reassembly and 100 % coral recovery are marked by vertical dashed lines of corresponding color

within the narrow range of 7.3–9.4 years (Table 2). Green Island and Thetford Reef had the fastest coral recovery, with pre-disturbance cover returning after 7.3 and 7.7 recovery years, respectively (Table 2). However, their coral recovery trajectories (square root transformed) were variable; coral recovery approached an asymptote at Thetford Reef but was linear at Green Island (Fig. 3a, d). At Reef 19138, coral recovery progressed linearly and reached 100 % after 8.9 years (Fig. 3b; Table 2). At Horseshoe Reef, coral recovery reached 100 % after 8.8 years, following a sigmoid trajectory (Fig. 3c; Table 2). Coral recovery was notably slow at Low Isles for the first 4 years, but the rate increased over time (Fig. 3f)

and was expected to be complete after 9.4 years (Table 2). A plateau at 87 % coral recovery was predicted for the Fitzroy Island community, suggesting that the pre-disturbance level of coral cover would not be reached (Fig. 3e). However, this was uncertain, with the upper CI indicating that pre-disturbance coral cover could be restored as soon as 7.9 years (Table 2).

Reassembly occurred during recovery at all reefs, meaning that similarity to the pre-disturbance community always increased, rather than remaining constant or decreasing. Reassembly had a linear trajectory at Thetford Reef, Reef 19138, and Green Island Reef (Fig. 3a, b, d). These three communities had the most rapid reassembly trajectories, reaching the 85 % benchmark after 7.8, 9.3, and 10.1 years, respectively (Table 2). The trajectory for Horseshoe Reef was sigmoid, with rapid reassembly from the 2nd to the 6th recovery years, but minimal reassembly beyond that (Fig. 3c). The coral community at Horseshoe Reef was the only one predicted not to reach the reassembly benchmark of 85 % by the model. Rather, a plateau was reached at 70 % reassembly. However, the wide 95 % CIs show the uncertainty in this prediction (Fig. 3c). Reassembly accelerated through time at Fitzroy Island, with minimal reassembly in the first four years (Fig. 3e, f). For Fitzroy Island, the best model indicated that the 85 % benchmark would be reached after 12.3 years (Table 2). At Low Isles, minimal reassembly over the entire recovery period resulted in great uncertainty surrounding future projections, giving little credence to the model trajectory and time frames (Fig. 3f). Nevertheless, the best-fit reassembly trajectory was linear and 85 % reassembly was predicted to take 30.7 years, with a best case scenario of 21.9 years (95 % CI; Table 2).

Among the four communities that both regained coral cover and reassembled, reassembly either occurred at the

Table 2 Time frames for 100 % coral recovery and 85 % reassembly predicted by the best-fit model (± 95 % CIs) for the combined data and for individual reefs

Location	Coral recovery model	Predicted 100 % coral recovery time (yr)	R^2	Reassembly model	Predicted 85 % reassembly time (yr)	R^2	Lag in reassembly following coral recovery (yr)
All reefs	Linear*	9.0 (8.2, 10.1)	0.84	Linear*	12.4 (10.2, 16.0)	0.62	3.4
Thetford Reef	Asymptote	7.7 (7.3, 8.3)	0.99	Linear	7.8 (7.1, 8.6)	0.96	0.1
Reef 19138	Linear	8.9 (8, 10.3)	0.91	Linear	9.3 (8.0, 11.9)	0.83	0.4
Horseshoe Reef	Sigmoid*	8.8 (8.6, 9.0)	0.99	Sigmoid	∞ (10.2, ∞)	0.92	∞
Green Island	Linear	7.3 (6.4, 8.7)	0.91	Linear	10.1 (8.7, 12.6)	0.90	2.8
Fitzroy Island	Sigmoid	∞ (7.9, ∞)	0.94	2nd order polynomial*	12.3 (11.9, 12.9)	0.96	N/A
Low Isles	2nd order polynomial	9.4 (8.8, 10.6)	0.95	Linear	30.7 (21.9, 57.3)	0.76	21.3

Slowest and fastest times for coral recovery and reassembly are highlighted in bold

* The model incorporated autoregressive correlation structure

∞ That, the best-fit model or confidence interval did not reach the target. R^2 indicates the fit of the model based on the proportion of variance explained. Lag times in reassembly are calculated using estimates extracted from the best-fit line of the model only

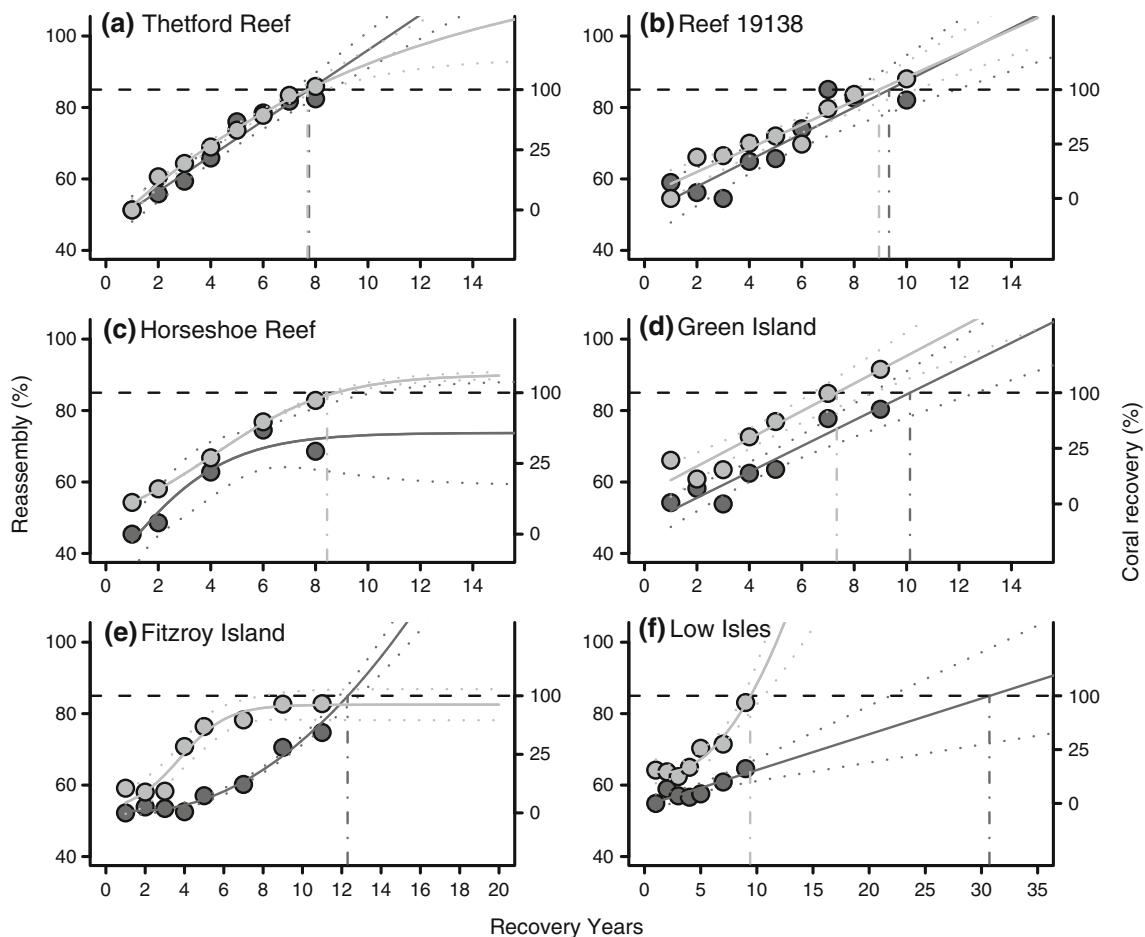


Fig. 3 Reassembly (left y-axis; black points) and coral recovery (square root transformed; right y-axis; gray points) through time (number of recovery years) are shown for each location separately, with best-fit models (solid lines of corresponding color) and 95 % CIs (dotted lines of corresponding color). Eighty-five percentage of

reassembly and 100 % coral recovery are simultaneously represented by the horizontal black-dashed line. The number of recovery years for 85 % reassembly and 100 % coral recovery are marked by vertical dashed lines of corresponding color

same time as, or following, coral recovery (Table 2). Reassembly occurred almost simultaneously with coral recovery at Thetford Reef and Reef 19138, but lagged behind coral recovery by almost 3 years at Green Island (Table 2). By far the greatest disparity between coral recovery and reassembly occurred at Low Isles, with reassembly lagging 21.3 years behind coral recovery (Table 2), though this projection was very uncertain.

Variation in coral assemblages between pre-disturbance and recovery years

In the last recovery year, communities at Thetford Reef and Reef 19138 resembled the pre-disturbance communities most closely, with Bray–Curtis similarities of 82.3 and 82.2 %, respectively (ESM Table 2). Minor differences at Thetford Reef included lower relative abundance of branching *Acropora* spp. and *Isopora* spp. and increased

relative abundance of tabulate *Acropora* spp. and *Pocillopora* spp. (Fig. 4; ESM Table 2). At Reef 19138, the community in the last recovery year had less branching *Acropora* spp. and more tabulate *Acropora* spp. than the pre-disturbance community (Fig. 4; ESM Table 2). At Green Island, in the last recovery year, the community had a Bray–Curtis similarity of 80.14 % to the pre-disturbance community (ESM Table 2). The minor changes in this coral community included lower relative abundance of soft corals and a greater proportion of massive *Porites* spp. (Fig. 4; ESM Table 2). Similarity between the pre-disturbance community and the community in the last recovery year at Fitzroy Island was 74.5 % (ESM Table 2). Differences in this case could be attributed to loss of branching *Acropora* spp. and replacement by encrusting *Porites* spp. and soft coral (Fig. 4; ESM Table 2). Coral communities in the last recovery year at Horseshoe Reef and Low Isles were least similar to their pre-disturbance communities,

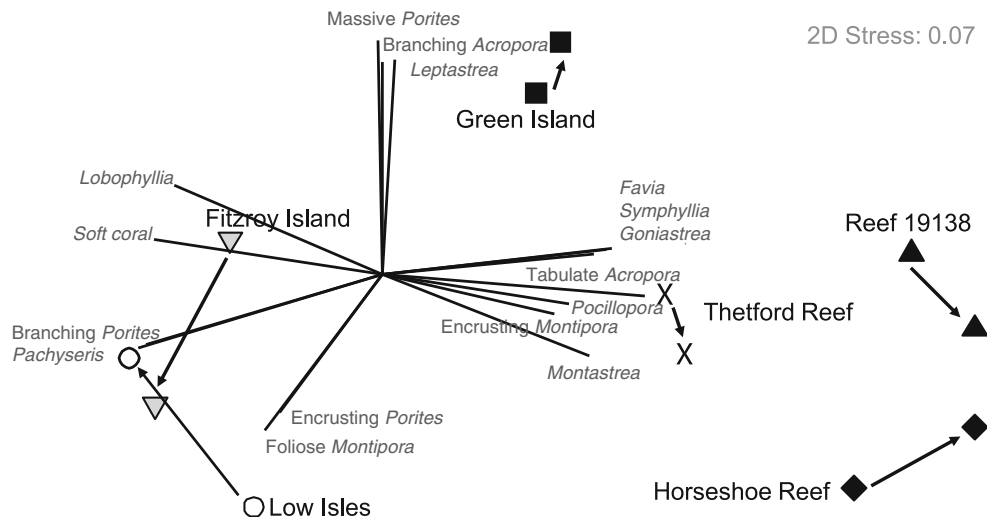


Fig. 4 Kruskal's non-metric multi-dimensional scaling (nMDS) demonstrating shifts in coral assemblages before and after disturbance. Locations are underlined and labeled at the pre-disturbance assemblage. Arrows show the direction of change from the pre-

disturbance assemblage to the recovering assemblage. Coral taxa that contributed to at least 10 % of the variation observed among any assemblage pair or had a correlation of ≥ 0.75 according to a SIMPER analysis are displayed

with Bray–Curtis similarities of 68.4 and 64.2 %, respectively (ESM Table 2). At Horseshoe Reef, the proportion of foliose *Montipora* spp. declined, while the proportion of tabulate *Acropora* spp. increased (Fig. 4; ESM Table 2). At Low Isles, relative abundance of foliose *Montipora* spp. decreased and dominance by soft coral and encrusting *Porites* spp. increased (Fig. 4; ESM Table 2).

Strong cross-shelf and latitudinal gradients were evident among pre-disturbance communities, and these were maintained following disturbance (Fig. 4). However, loss of branching *Acropora* spp. at Reef 19138 and *Montipora* spp. at Horseshoe Reef, and their subsequent replacement by tabulate *Acropora* spp. caused the initial differences between the pre-disturbance communities at these two locations to be substantially reduced as communities reassembled (Fig. 4). Similarly, loss of branching *Acropora* spp. at Fitzroy Island and *Montipora* spp. at Low Isles, and their subsequent replacement by *Porites* spp. and soft corals caused these communities to converge during recovery (Fig. 4).

Discussion

This study of recovery at six GBR locations found that coral communities did reassemble after disturbance, taking at least eight years, and generally following the return of coral cover to pre-disturbance levels by more than three years. Coral recovery mostly occurred within a decade but the reassembly benchmark was reached concurrently with coral recovery at only two locations (Thetford Reef and Reef 19138). Only one other

community (Green Island) both regained coral cover and reassembled within the limits of the model projection (20 years), leaving three communities that fell short of either the coral recovery or the reassembly benchmark. At Horseshoe Reef and Low Isles, reassembly to 85 % was not expected within 20 years. Conversely, at Fitzroy Island, reassembly to the benchmark was predicted, but without full coral recovery. This disparity demonstrates that coral recovery does not equate to community reassembly, highlighting the complex nature of recovery processes and hence the limitations of coral cover as an index of community recovery.

These coral recovery time frames of 7–10 years are among the most rapid rates reported for coral reefs (Halford et al. 2004; Baker et al. 2008; Adjeroud et al. 2009). These time frames seem typical for western Pacific reefs, while recovery time frames in other regions are generally longer (Graham et al. 2011). In the eastern Pacific, time frames for coral recovery following bleaching often exceeded 20 years (Wellington and Glynn 2007). The return of coral cover is commonly used to assess recovery for coral reef communities and, on this basis, five of the six reefs examined here were expected to recover. However, there is a general consensus that coral cover insufficiently represents ecological condition (Bellwood et al. 2004; Price et al. 2007; Sheppard et al. 2008; Hughes et al. 2010; McClanahan et al. 2011). The use of coral cover to describe recovery of reefs can mask changes in community composition, which may mean altered vulnerability and different responses to stressors. Reassembly is, therefore, a critical aspect of coral community recovery and should be part of any such assessments.

In recent decades, GBR reefs have experienced disturbances that reduce coral cover to the extent seen on our study reefs at 11-year intervals on average (Osborne et al. 2011). In general, tabulate *Acropora* spp. communities on our study reefs recovered coral cover and reassembled in this time frame, indicating a capacity to persist under such a disturbance regime. Conversely, near-shore coral communities with high abundance of *Porites* spp. and soft corals and low abundance of *Acropora* spp. needed longer intervals between large disturbances to avoid shifts in the coral community composition.

A community that reassembles before the next disturbance but fails to regain pre-disturbance coral cover could have suffered further disturbance that disrupted recovery or could be experiencing ongoing stress that is keeping coral mortality in balance with growth. The recovery at Fitzroy Island potentially fits this profile after a 13-year window for reassembly. Coral recovery at Fitzroy Island was apparently not impaired by another pulse disturbance, but coral cover reached a plateau below pre-disturbance levels after nine recovery years. Ongoing stressors that might prevent further increases in coral cover include low-density *A. planci* populations, low occurrence of coral disease or high water temperatures. Where disturbances or chronic stress are preventing coral cover growth, high coral cover could eventually be attained if space is colonized by coral species that are more resistant to disturbances and stress. This might occur over decades if the stress-tolerant species are slow growing.

Live coral cover provides food, shelter, and recruitment habitat for many reef fishes (Jones et al. 2004) that in turn perform functions essential for the health of coral reef communities, such as controlling macro-algae abundance (Bellwood et al. 2004). Reef fish abundance, species richness, and diversity are generally positively correlated with coral cover (Jones et al. 2004; Wilson et al. 2006). For reef fish communities, lowered coral cover could be accompanied by reduced functional redundancy or loss of function through low numbers (Cheal et al. 2010, 2013). Such changes in fish communities are generally linked to a reduced capacity for coral reef communities to recover after disturbances (reduced resilience; Nystrom 2006; Cheal et al. 2013). The loss of coral cover, though, will not always correspond linearly with change in the structure of reef fish communities. In Moorea, French Polynesia, the structure of the reef fish community was similar across a range of ~5–50 % coral cover, but there was an apparent tipping point at 5 % coral cover that corresponded with dramatic changes in the structure of the reef fish community (Holbrook et al. 2008).

Communities that regain coral cover but do not reassemble following disturbance risk shifts to an alternative assemblage with altered ecosystem processes and function.

The communities at Low Isles and Horseshoe Reef fit this profile. The consequences of a community shift depend on the qualitative nature of the change. Previously described community shifts after disturbances have focused on loss and replacement of *Acropora* spp. (Aronson et al. 2004; Berumen and Pratchett 2006). However, among the community shifts described in this study, there were no shifts away from *Acropora* spp.; rather, the community shifts at Horseshoe Reef and Low Isles involved substantial loss of *Montipora* spp. At Horseshoe Reef, loss of *Montipora* spp. was compensated by increased relative abundance of the already dominant tabulate *Acropora* spp. At Low Isles, a large proportion of *Montipora* spp. was replaced in the recovering community by an increase in the proportion of the already dominant *Porites* spp. and soft corals. Neither such shifts have previously been described.

The importance of *Acropora* spp. to the health of coral reef ecosystems has been well established. *Acropora* spp. dominate coral assemblages (Wallace 1999) and are major contributors to reef building (Aronson et al. 2002; Bellwood et al. 2004), and the provision of food (Pratchett 2005) and shelter (Munday 2004; Wilson et al. 2006; Alvarez-Filip et al. 2009; Bonin 2012) for reef dwellers, especially reef fishes. However, *Acropora* spp. are highly susceptible to disturbances including bleaching (Marshall and Baird 2000), storms (Halford et al. 2004; Fabricius et al. 2008), disease (Willis et al. 2004), and are the preferred food of *A. planci* (De'ath and Moran 1998). Consequently, extensive, low diversity stands of *Acropora* spp. are vulnerable to extirpation when impacted by these disturbances. For example, in Belize, the combination of *Acropora* spp. dominance, low diversity within the genus and dependence on asexual fragmentation for propagation, resulted in the dramatic loss of coral cover and poor recovery of *Acropora* when these species succumbed to white band disease (Aronson and Precht 2001). Responses of corals to disturbance are linked to their life history traits, which can vary among species within a genus. A diversity of responses to disturbance among corals that overlap in their functional capacity can facilitate persistence of coral dominance on reefs over multiple cycles of disturbance and recovery. While some species are lost due to disturbance, other surviving species that fulfill the same functional roles can maintain ecosystem function long enough for recovery and reorganization of the community to occur (Nystrom 2006). Further investigation into the species composition of the tabulate *Acropora* assemblage at Horseshoe Reef, and the degree of response diversity among these species, may improve our understanding of the recovery potential of this coral community following various types of disturbance.

Diversity of life history traits is apparent within the *Montipora* genus (Darling et al. 2012). Many *Montipora* spp. share the competitive life history traits of *Acropora*

spp., while other species have a ‘generalist’ life history strategy and thrive in habitats where the more competitive *Acropora* spp. and *Montipora* spp. are limited by environmental stresses (Grime 1977; Darling et al. 2012; Grime and Pierce 2012). *Montipora* spp. are major contributors to coral cover and reef building on coral reefs worldwide (Montaggioni 2005; Darling et al. 2012), yet little is known of other potential contributions of *Montipora* spp. to the healthy functioning of coral reef ecosystems. Expanding our focus beyond *Acropora* spp. to also understand the functional capacities of other coral species is critical for determining the implications of the loss of any particular coral group.

The life history characteristics of many *Porites* spp. and soft corals make them relatively stress tolerant (Darling et al. 2012). There are various pathways that could lead to a community shift toward these stress-tolerant forms at Low Isles. Low-density populations of *A. planci*, diseases or high temperatures may frequently kill susceptible corals preventing an increase in their cover, while less susceptible corals continue to grow. *Montipora* spp. are a highly preferred food of *A. planci* after *Acropora* spp., while *Porites* spp. are their least preferred food (De’ath and Moran 1998; Pratchett 2007). Also, a change in nutrient, light, or sedimentation levels associated with freshwater runoff from land may impede the recruitment and survival of corals at near-shore locations (Fabricius 2005), with some species affected more than others.

If pulse disturbance intervals are no shorter than ten years and environmental conditions do not dramatically change, at least three communities in this study indicate potential to repeatedly regain coral cover and reassemble, and therefore persist. If pulse disturbance frequency increased to seven years, all of the coral communities in this study would be at risk of community shifts, with various potential outcomes for coral cover. Community shifts toward stress-tolerant species can increase the resistance of a coral community to disturbances, so that coral cover can reach high levels in spite of frequent pulse disturbances and chronic stressors. However, the ability of even stress-tolerant corals to resist or recover is limited (Cote and Darling 2010). For example, *A. planci* will consume other types of coral, including *Porites* spp., when abundance of *Acropora* spp. is low (De’ath and Moran 1998). Assemblages of slow-growing *Porites* corals can take decades to centuries to recover to the pre-disturbance population size structure even when background mortality and disturbance frequency are low (Done 1988).

All six study reefs showed recovery periods of 11 years or less either because of recurring disturbance or the time frame of the study. Studies of succession in coral communities following disturbance indicate that reshuffling of relative species abundances would continue without further

increase in coral cover, given a more extensive recovery period (Tanner et al. 1994; Hughes and Connell 1999). Species turnover and architectural development in coral communities may change over longer disturbance intervals.

In summary, coral assemblages dominated by tabulate *Acropora* spp. can regain coral cover and reassemble rapidly. This characteristic gives greater potential for persistence in the long-term given current disturbance frequencies, provided a variety of species from that genus are present. In contrast, fundamental changes to coral community composition on reefs at Fitzroy Island and Low Isles seem likely given current threats to coral reefs. Interestingly, the communities at these locations were on trajectories for reassembly, but the time frames needed were much longer than for simple coral recovery. If disturbance frequency increases, the six communities in this study are at high risk of community shifts and/or losing coral cover, with implications for their vulnerability to disturbance and recovery potential.

These simple models are based on recovery of GBR coral communities in a present day disturbance regime. They demonstrate that temporal changes in community composition are a critical aspect of recovery. This is not to say that recovery assessments end at coral recovery and reassembly. Assessments of coral community recovery should also incorporate colony size, complexity, and recruitment data collected at various spatial scales and over long temporal scales. A comprehensive understanding of recovery processes is essential for establishing models that can meaningfully predict outcomes for coral communities under a variety of disturbance regimes.

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