

Coral reef recovery dynamics in a changing world

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Abstract Coral reef ecosystems are degrading through multiple disturbances that are becoming more frequent and severe. The complexities of this degradation have been studied in detail, but little work has assessed characteristics that allow reefs to bounce back and recover between pulse disturbance events. We quantitatively review recovery rates of coral cover from pulse disturbance events among 48 different reef locations, testing the relative roles of disturbance characteristics, reef characteristics, connectivity and anthropogenic influences. Reefs in the western Pacific Ocean had the fastest recovery, whereas reefs in the geographically isolated eastern Pacific Ocean were slowest to recover, reflecting regional differences in coral composition, fish functional diversity and geographic isolation. Disturbances that opened up large areas of benthic space recovered quickly, potentially because of nonlinear recovery where recruitment rates were high. The type of disturbance had a limited effect on subsequent rates of reef recovery, although recovery was faster following crown-of-thorns starfish outbreaks. This inconsequential role of disturbance type may be in part due to the role of unaltered structural complexity in maintaining key reef processes,

such as recruitment and herbivory. Few studies explicitly recorded potential ecological determinants of recovery, such as recruitment rates, structural complexity of habitat and the functional composition of reef-associated fish. There was some evidence of slower recovery rates within protected areas compared with other management systems and fished areas, which may reflect the higher initial coral cover in protected areas rather than reflecting a management effect. A better understanding of the driving role of processes, structural complexity and diversity on recovery may enable more appropriate management actions that support coral-dominated ecosystems in our changing climate.

Keywords Resilience · Ecosystem function · Diversity · Marine protected areas · Coral bleaching · Coral reef ecology

Introduction

Anthropogenic stressors are becoming the dominant drivers of community structure in marine ecosystems (Polunin 2008). Coral reefs are particularly sensitive to many disturbances, such as those resulting from climate change (Hoegh-Guldberg et al. 2007). Thermally induced coral bleaching has already contributed to significant reductions in live coral cover at regional scales (e.g., Gardner et al. 2003; Bruno and Selig 2007; Graham et al. 2008). Other disturbances, such as crown-of-thorns starfish (COTS) outbreaks and destructive fishing techniques, are also greatly depleting coral cover on many reefs (Moran 1986; McClanahan et al. 1999). There is now detailed knowledge of how different disturbances influence coral reef benthic communities (Hughes and Connell 1999; Fabricius 2005;

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McClanahan et al. 2007; Pratchett et al. 2009) and the ramifications of these benthic changes to other components of the ecosystem, such as fish (Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2008). However, there are critical gaps in our knowledge of how reefs can bounce back and recover from disturbances and retain a coral-dominated state in the face of multiple disturbances (Hughes et al. 2010; Wilson et al. 2010). It is clear that coral reefs that maintain their structure and function can recover from large-scale disturbances (Halford et al. 2004; Sheppard et al. 2008). Furthermore, although disturbances are increasing in frequency, coral bleaching of the scale and intensity of the 1998 El Niño event (Hoegh-Guldberg 1999) has not been repeated in the 12 years that have since passed. This is enough time for reefs to recover, and many are doing so (Baker et al. 2008).

Disturbances to ecosystems can be thought of as either chronic or acute (Connell et al. 1997). Chronic disturbances to coral reefs, such as sedimentation and nutrient input from catchment land-use practices are slow to change and exert continuous pressure on the system (McCulloch et al. 2003; Fabricius 2005). In many cases, an acute disturbance, for example a disease epidemic or a coral bleaching event, can flip the system into a new domain of attraction, where reinforcing feedback mechanisms can prevent coral recovery (Hughes 1994; Scheffer et al. 2001; Mumby et al. 2007; Hughes et al. 2010). However, in some cases, recovery does occur between acute disturbance events and there is a need to understand which factors promote such recovery dynamics to keep coral-dominated reefs persisting in a changing world.

Potential predictors of recovery can be broadly split into five groups: disturbance characteristics, reef characteristics, reef connectivity, ecological characteristics and anthropogenic influences. For example, disturbances that remove coral, but leave the skeleton intact, such as coral bleaching, may be expected to maintain ecological processes and facilitate recovery more rapidly than disturbances that remove coral and reduce 3-dimensional structure, such as storms (Colgan 1987). High connectivity is known to be important for replenishing marine organisms, such that more isolated reefs would be expected to show slower recovery (Ayre and Hughes 2004; Graham et al. 2006; Jones et al. 2009). Ecological characteristics, such as grazing and scraping by herbivorous fish and urchins and high levels of functional diversity, are thought to promote functioning ecosystems that will rebound more rapidly from disturbances (Mumby et al. 2007; Burkepile and Hay 2008). Reefs close to high human population centres may be expected to show slower recovery due to the likelihood of increased terrestrial inputs and exploitation (Sandin et al. 2008). Finally, management interventions may be expected to influence recovery rates; however, there is little

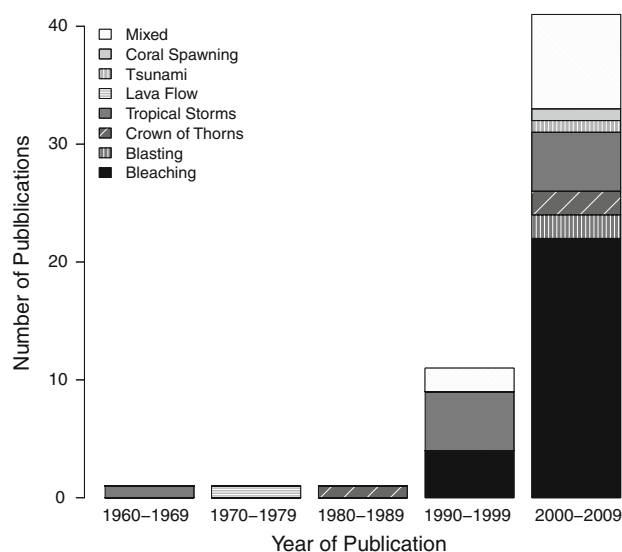


Fig. 1 Number of peer-reviewed publications documenting coral reef recovery from differing acute disturbance events from 1960 to 2009

consensus about the role of marine protected areas, with examples of both positive and neutral effects on recovery rates compared to fished areas (Graham et al. 2008; McClanahan 2008; Mumby and Harborne 2010).

This paper quantitatively assesses the literature on recovering coral reef ecosystems from acute disturbance events and assesses which characteristics promote faster recovery rates. There has been exponential growth in the number of studies documenting recovery of reefs from disturbances over the last 50 years, with nearly a fourfold increase in studies within the last decade (Fig. 1). The dominant disturbances assessed have shifted from tropical storms to coral bleaching and mixed disturbance events (Fig. 1). Despite this rapid increase in published primary literature, the subject has not been reviewed since 1997 (Connell 1997), aside from a study reviewing recovery specifically from coral bleaching events (Baker et al. 2008). We focus specifically on recovery literature from acute disturbances, because recovery trajectories are masked if assessing the entire literature on changes in coral cover, and there have been a number of very detailed analyses of declines in coral cover in the Caribbean and across the Indo-Pacific (Gardner et al. 2003; Bruno and Selig 2007; Schutte et al. 2010). We are interested in understanding factors that drive inter-reef variations in recovery trajectories.

Methods

Study selection

Searches of the ISI Web of Science (1972–2009), Google Scholar and the reference lists of returned publications

provided 55 studies describing recovery on coral reefs subsequent to an acute disturbance (Fig. 1). Twenty-two of these publications, detailing data from 48 different sites, were selected for the meta-analysis based on the following criteria: (i) percentage live hard coral cover data were provided, (ii) the initial drop in coral cover as a result of the disturbance exceeded 10%. Studies recording lower initial mortality were excluded as small disturbances may have negligible impact on hard coral cover (e.g., Edmunds 2002). Furthermore, inter-annual variation in coral cover can be ~5% prior to a disturbance (e.g., Halford et al. 2004). A 10% decline reflects a sudden change in benthic cover in response to a pulse disturbance, (iii) sites were monitored for at least 3 years post-disturbance, (iv) post-disturbance coral cover levels increased after the disturbance and (v) data were not included in a subsequent publication used in the meta-analysis. Where coral cover was recorded as 0%, it was rounded up to 0.1 for the purpose of the analyses. Each site considered as separate by the studies' authors were analysed separately.

Meta-analysis

To quantitatively investigate the magnitude of change after an acute disturbance, we calculated the annual rate of change in absolute coral cover (C_{Rp}) (Coté et al. 2006):

$$C_{Rp} = (C_{END} - C_{START})/d$$

where C_{START} is the per cent coral cover immediately after the disturbance, C_{END} is the peak per cent coral cover reported in the monitoring period after the disturbance and d is the time in years between recordings of C_{START} and C_{END} . This metric provides a transparent, directly interpretable measure of coral recovery. Confidence intervals were calculated in Matlab using bias-corrected bootstrapping (bootci function, 4,999 samples). All confidence intervals depart from zero, as studies were specifically selected where recovery from acute disturbances had occurred.

We were able to extract information on four groups of potential drivers of coral recovery to examine heterogeneity of recovery rates among sites: disturbance characteristics, reef characteristics, reef connectivity and anthropogenic influences. Disturbance characteristics included type of disturbance (e.g., coral bleaching and tropical storm) and post-disturbance coral cover, while reef characteristics included reef type (e.g., atoll, fringing) and reef zone (e.g., flat and slope). For reef connectivity, 'distance to nearest reef' and 'number of neighbouring reefs' within a 50-km radius (chosen based on peak probability of connectivity values in Cowen et al. 2006) were calculated from Google Earth, and sites were assigned to one of four geographical areas (Caribbean, western Pacific, eastern Pacific and

Indian Ocean). The western Pacific region included sites within the Indo-Australian Archipelago. Anthropogenic influences included human population density and management. Coastal population density estimates for all sites were obtained from the Socioeconomic Data and Applications Centre's 'Global Populations of the World 2000' gridded population map (SEDAC 2005). Data on population densities in the Lakshadweep islands were sourced from the 2001 Census of India (Directorate of Census Operations 2001). If management status of a site was not clear within a study, data on regulation of fishing and extraction were sourced from the MPA Global Database (Wood 2007).

Attempts were made to extract information on ecological characteristics thought to be important for coral recovery. These included coral diversity and per cent cover of different life-forms, structural complexity, fish diversity, density and biomass, including densities of different functional groups and algal cover. However, the majority of studies monitoring coral recovery did not record this information, and the few studies that did, do not provide sufficient data to include these variables. High spatial and temporal variability in most of these variables preclude including data on these variables from other sources.

Collinearity between the numeric variables was tested by plotting pairwise relationships of the covariates. Correlations were further investigated by calculating the Spearman rho correlation coefficient. A large negative correlation was found between distance to nearest reef and number of neighbouring reefs, $r_s(46) = -0.83$, $P < 0.001$; therefore, number of neighbouring reefs were omitted from the analyses. For nominal variables, we looked for a lack of overlap between variables as evidence of correlation. No further collinearity was found.

Categorical regression

We used Categorical regression (CATREG) using the SPSS Categories package v.18 to assess the relative importance of the potential drivers of coral recovery. CATREG allows linear multiple regression of nonlinear relationships between nominal, ordinal and continuous variables via optimal scaling (Gifi 1990) and is robust where a high number of variables are of interest in relation to sample size (Meulman et al. 2009). Optimal scaling is the transformation of categorical variables to produce numerical values or 'quantifications'. Transformations may be nonlinear or linear depending on the restrictions of the scaling level chosen, and occur concurrently with the calculation of the regression coefficients to produce the maximum coefficient of determination, R^2 (Hartmann et al. 2009).

Table 1 Details of studies used to assess differences in coral recovery rates from acute disturbances

Location	Disturbance	Total number of years studied ^a	Years since disturbance	No. of sites	Mean post-disturbance coral cover (%)	Mean peak-year coral cover (%)	Source
Belize	Bleaching	3	4	3	14.2	22.3	Robbart et al. (2004)
Lakshadweep, India	Bleaching	3	5	4	7.0	18.7	Arthur et al. (2006)
Pulau Pari Islands, Indonesia	Bleaching	7	5	2	2.9	15.0	Brown and Suharsono (1990)
Pulau Tiga, Indonesia	Blasting	5	5	1	15.9	57.2	Fox and Caldwell (2006)
Palau	Bleaching	3	6	3	12.8	23.0	Golbuu et al. (2007)
Trunk Reef, GBR, Australia	Bleaching	8	6	1	3.2	6.5	Pratchett et al. (2008)
Scott Reef System, Australia	Bleaching	11	7	1	11.0	19.5	Smith et al. (2008)
Northern Atolls, Chagos	Bleaching	5	8	4	16.3	30.0	Sheppard et al. (2008)
Southern Seychelles	Bleaching	3–7	8	8	20.6	27.9	Buckley et al. (2008); Stobart et al. (2002, 2005)
Alphonse Atoll, Seychelles	Bleaching	9	9	1	10.3	22.6	Hagan and Spencer (2008)
St. John, US Virgin Islands	Tropical storm	11	9	1	32.5	35.9	Edmunds (2002)
St. Leu, Reunion Island	Tropical storm	7	11	1	7.2	36.0	Naim et al. (2000)
Central GBR, Australia	Crown-of-thorns	14	12	3	7.4	68.6	Halford et al. (2004) ^b
Tanguisson Reef, Guam	Crown-of-thorns	11	12	3	7.4	48.6	Colgan (1987)
GBR, Australia	Mixed	12	12	2	11.1	63.8	Emslie et al. (2008)
Hawai'i, USA	Tropical storm	20	13	1	10.5	15.0	Dollar and Tribble (1993)
Cano Island, Costa Rica	Mixed	15	14	1	11.2	12.9	Guzman and Cortés (2001)
Iriomote Island, Japan	Crown-of-thorns	10	15	1	0.1	100.0	Sano (2000)
Tiahura Reef, Moorea	Bleaching	15	15	1	24.9	51.2	Adjeroud et al. (2009)
Cocos Island, Costa Rica	Bleaching	15	19	2	3.2	21.2	Guzman and Cortés (2007)
O'ahu, Hawai'i, USA	Tropical storm	24	24	1	19.9	22.7	Coles and Brown (2007)
Heron Island, GBR, Australia	Tropical storm	30	25	3	16.8	57.9	Connell et al. (1997)

^a Where total number of years is shorter than years since disturbance, sampling began after the disturbance and severity of disturbance was reported in the paper from another data source

^b Data sourced from Williams (unpublished)

The variables were scaled with ranking discretisation to minimise the influence of outliers on the regression. Standardised residuals were plotted against quantifications for predictor variables to ensure optimal scaling; however, to minimise overfitting of the model and maximise the predictive utility for other data sets, the data were resampled using tenfold cross-validation (Meulman 2003).

Along with R^2 , β coefficients and partial F values, CATREG also reports: (1) quantifications—allowing interpretation of the relative impact of different categories within each variable where quantifications of similar size indicate which categories influence the response variable in a similar manner (Meulman et al. 2009), (2) part r values—indicating the effect of the predictor variables on the effect size once the effects of other variables have been removed

from the predictor variables (Cohen and Cohen 1975) and (3) importance values—summing to 1 and representing the relative importance of each predictor variable in the model (Pratt 1987).

Non-independence of data

To assess the impact of incorporating data from multiple sites from one study, the grand mean effect size (all sites) was compared with a) the mean effect size when omitting data from the Southern Seychelles study (Buckley et al. 2008; Stobart et al. 2002, 2005), which provided the largest number of sites and b) the mean effect size when only one randomly selected site from each study was included. The mean effect size using one selected site from each study

was calculated using 4,999 iterations of the randomised selection. There was no difference in the mean annual rate of change between the above groupings (Electronic Supplemental Material, ESM Fig. S1), suggesting all sites could be used in the analyses.

A second possible bias is introduced by using studies which incorporate different survey methods (Côté et al. 2005). However, the relatively crude measure of total coral cover used here is robust to differences in methods used to measure it (Carleton and Done 1995; Wilson et al. 2007).

Use of alternative and weighted effect size metric

Coral reef meta-analyses often weight the effect size metric by the natural log of total survey area (m^2) per location, in order to give greater weight to more substantial surveys (Mosquera et al. 2000). To assess the effect of weighting our annual rate of change metric (ESM), the categorical regression analysis was repeated using weighted effect sizes. We also calculated a geometric rate of change effect size metric (ESM) which allows for non-linear changes in coral cover through time (Côté et al. 2005), and ran categorical regression analyses on both unweighted and weighted data.

Results

A grand mean annual rate of change in absolute coral cover of 3.56% (95% CI = 2.89–4.43) was calculated for the 48 sites. The variability represents a range in effect size (C_{Rp}) of 0.13–12.49%. The mean length of time that studies examined post-disturbance coral cover was 11.1 years (Table 1). The changes in terms of absolute cover of benthos were positively influenced by time since disturbance ($r^2 = 0.23$, $P < 0.01$). However, C_{Rp} was not influenced by time since disturbance, and high variability indicates other factors were influencing annual recovery rates. Further investigation of these differences used the standardised effect size metric (C_{Rp}) and CATREG.

Fifty-eight per cent of the variance in annual rate of change in coral cover was explained by the CATREG model incorporating all eight predictor variables ($r^2 = 0.581$, $F = 2.958$, $P = 0.005$). Importance values (Pratt's measure) emphasise the relative importance of geographical region, (0.31), exploitation (0.31) and post-disturbance coral cover (0.22); these variables accounting for 84% of importance in the regression model (Table 2).

Disturbance characteristics

Post-disturbance coral cover accounts for 9% of the variance in annual rate of change in coral cover (C_{Rp}). Sites

with a post-disturbance coral cover of $\leq 5\%$ exhibited variable rates of recovery ($C_{Rp} = 4.00\%$, 95% CI = 2.54–6.24; Table 2; Fig. 2a). However, sites with a post-disturbance coral cover of 6–10% exhibited an annual increase in coral cover of 4.90% (95% CI = 4.19–5.85), compared to sites with higher post-disturbance coral cover, for example sites with post-disturbance coral cover of 31%+ only exhibited an annual increase of 2.01% (95% CI = 0.93–4.05).

The type of disturbance did not significantly influence annual rate of change in coral cover in the CATREG (Table 2; Fig. 2b); however, impacts caused by COTS resulted in higher mean annual rates of recovery ($C_{Rp} = 5.77\%$, 95% CI = 4.13–9.13) than those experienced by sites impacted by either bleaching or tropical storms ($C_{Rp} = 3.09\%$, 95% CI = 2.37–4.02 and $C_{Rp} = 2.29\%$, 95% CI = 1.07–3.87, respectively). Sites affected by a mix of disturbance types showed a wide range of annual change in coral cover ($C_{Rp} = 5.44\%$, 95% CI = 0.13–7.48).

Reef characteristics

Categories of the predictor variable Reef Zone were combined, where additional levels did not provide extra information to the model. Reef type and reef zone did not significantly influence post-disturbance recovery of coral cover (Table 2, Fig. 3).

Reef connectivity

Geographic region explains 10% of the variance in effect size. Sites located in the eastern Pacific experienced the lowest annual geometric rate of change in coral cover ($C_{Rp} = 0.93\%$, 95% CI = 0.45–1.62), whereas sites located in the western Pacific exhibited the greatest positive change in coral cover ($C_{Rp} = 4.70\%$, 95% CI = 3.62–6.05) (Fig. 4a). The Caribbean sites overlapped with all other geographic locations, whereas the Indian Ocean sites showed faster recovery rates ($C_{Rp} = 3.28\%$, 95% CI = 2.35–4.58) than the eastern Pacific (Fig. 4a). Distance to nearest reef, and therefore the correlated number of neighbouring reefs, did not explain significant variance in effect size (Fig. 4b).

Anthropogenic influences

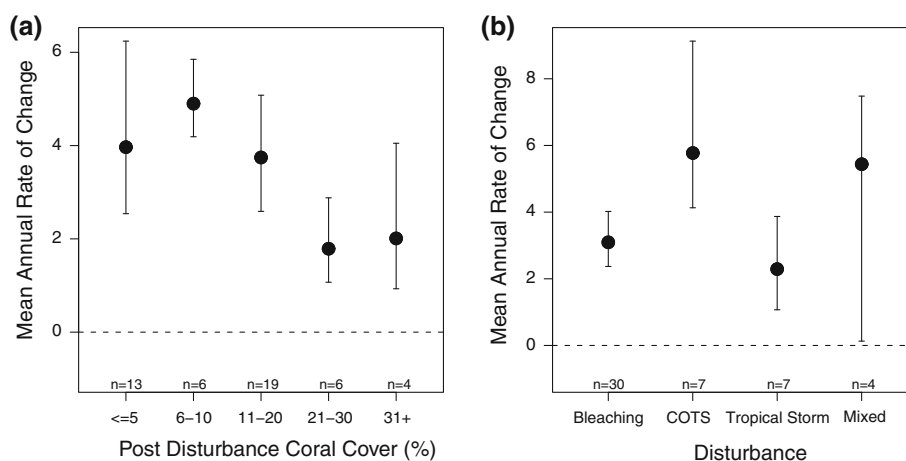
Management status of the reef explained 12% of the variance in annual rate of change in coral cover (Table 2, Fig. 5a). Evaluation of quantifications and the mean effect sizes shows open, mixed and gear restriction levels of management influenced annual rate of change in coral cover in a similar manner ($C_{Rp} = 4.04$, 4.09 and 3.97%,

Table 2 Results of a categorical regression analysis, quantifying the role of a range of variables in explaining different rates of coral recovery from acute disturbance events

Factor	Quantification	$\beta \pm$ S.E.	d.f.	<i>F</i>	<i>P</i> *	Part <i>r</i>	Importance
Disturbance characteristics							
Post-disturbance coral cover	**	-0.325 ± 0.16	4	3.97	0.010	-0.31	0.22
Type of disturbance		0.109 ± 0.15	1	0.50	0.485	0.09	0.03
Reef characteristics							
Reef type		0.150 ± 0.14	1	1.15	0.291	0.13	0.02
Reef zone		0.258 ± 0.17	1	2.43	0.129	0.22	0.02
Reef connectivity							
Geographic region		0.366 ± 0.19	3	3.68	0.022	0.33	0.31
1. Eastern Pacific	-2.08						
2. Caribbean	-0.70						
3. Indian Ocean	-0.23						
4. Western Pacific	0.98						
Distance to nearest reef		-0.063 ± 0.20	1	0.10	0.749	-0.06	0.04
Anthropogenic influences							
Management status		-0.392 ± 0.14	3	7.65	0.001	-0.35	0.31
1. Open	-0.65						
2. Mixed	-0.22						
3. Gear restrictions	0.39						
4. Protected	2.22						
Human population density (km ⁻²)		0.186 ± 0.14	1	1.81	0.188	0.16	0.05

* Significant results in bold

** Ordinal transformation with ranking discretisation used

Fig. 2 Mean annual rate of change in per cent coral recovery with respect to disturbance characteristics: (a) Post-disturbance coral cover (%) and (b) Type of disturbance (*n* = number of sites; error bars = 95% bootstrapped CI)

respectively), whereas protected sites experienced reduced rates of recovery ($C_{RP} = 0.80$, 95% CI = 0.49–1.16). Human population density did not influence rate of change in coral cover.

Model robustness

Outliers have a disproportionate effect on the results of a categorical regression. Plots of standardised residuals displayed against predictor variable quantifications showed

that all residuals were distributed randomly and within two standard deviations of zero indicating optimal scaling (Meulman et al. 2009).

Alternative effect size metrics

Although the magnitude of effect differed between the weighted and the unweighted measures of annual rate of change, the general patterns were consistent (ESM). We therefore present the unweighted effect sizes measure here

Fig. 3 Mean annual rate of change in per cent coral cover recovery with respect to reef characteristics: (a) Reef type and (b) Reef zone (n = number of sites; error bars = 95% bootstrapped CI)

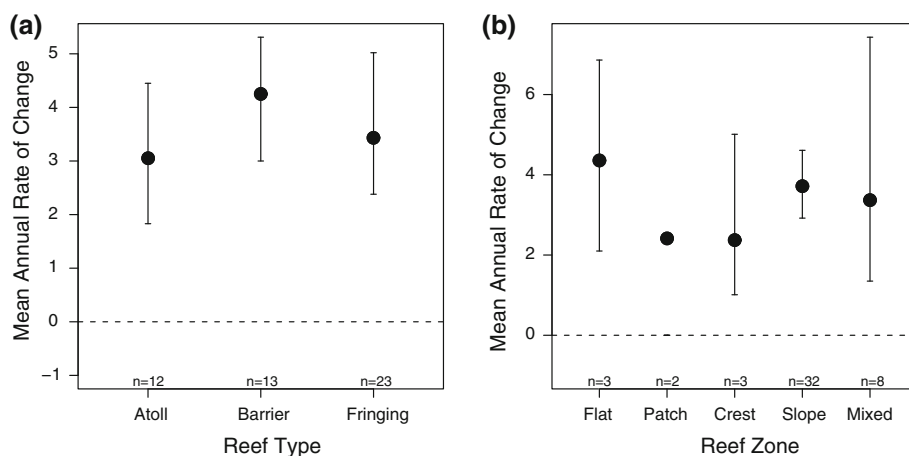
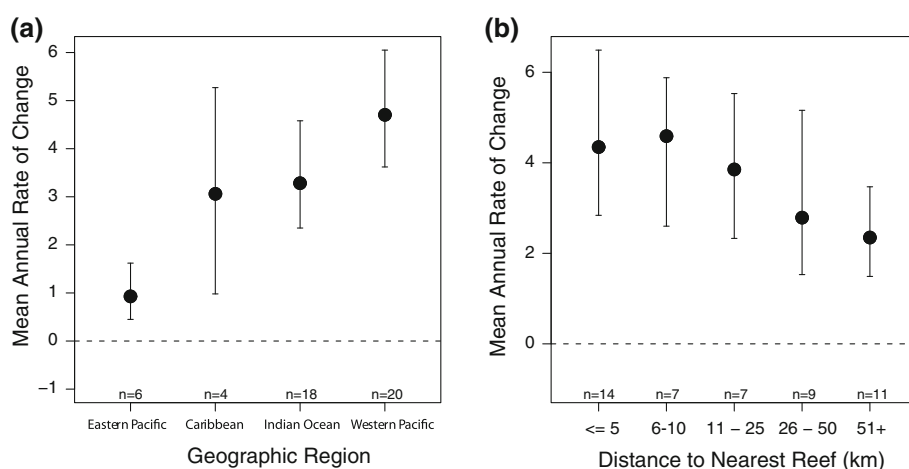


Fig. 4 Mean annual rate of change in per cent coral cover recovery with respect to reef connectivity: (a) Geographic region and (b) Distance to nearest reef (km) (n = number of sites; error bars = 95% bootstrapped CI)



as they are more intuitive to interpret. The results using the geometric rate of change effect size metric are broadly similar to those found for the annual rate of change in absolute coral cover effect size used, although the effects of human population density and type of disturbance were stronger and the effect of management was weaker (ESM).

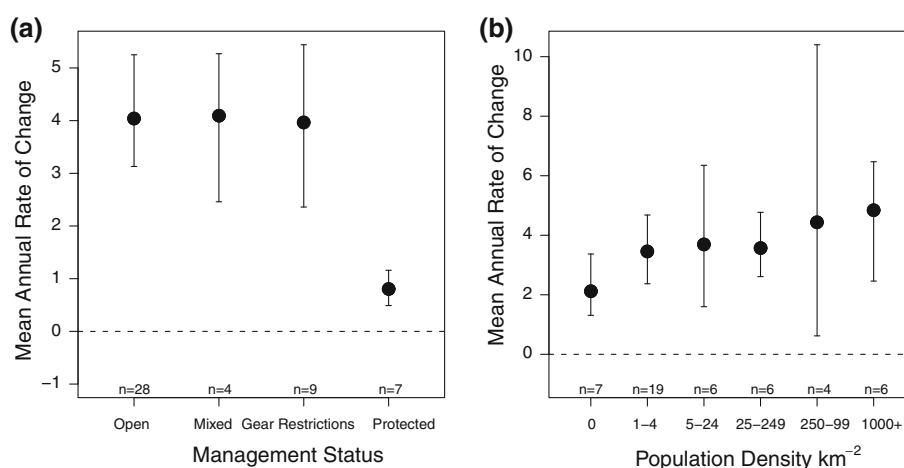
Discussion

We found that of those reefs that have been recovering from acute disturbances, the greatest predictors of rate of recovery were geographic region, management status and severity of disturbance. These findings are important in furthering our knowledge of how reefs can recover between acute disturbance events and indicate that some of the perceived impediments to recovery, such as the severity of disturbances, are not necessarily as strong as expected. It must be noted, however, that many of the potential predictors of reef recovery, such as herbivore biomass (Mumby et al. 2006; Hughes et al. 2007), fish functional

diversity (Burkepile and Hay 2008; Nyström et al. 2008) and habitat structural complexity (Colgan 1987; Emslie et al. 2008) were not documented in the majority of studies and thus could not be evaluated in this review.

Recovery might be expected to be slower after severe disturbances that kill most coral as repopulating the area is dependant on new recruits, rather than growth, division and budding of existing corals (Connell et al. 1997). However, we found evidence that recovery was greater after disturbances that reduced coral cover to <10% of benthic cover (but not <5%) and was slowest after disturbances that only reduced coral cover to >20%. There are two potential reasons why this pattern may emerge. Firstly, we have specifically assessed studies that documented recovering reefs, and thus reefs that are resilient. This suggests that recovery processes, such as ample coral recruits to occupy free space (Hughes and Tanner 2000), are likely to be present. In this situation, occupation of new space may be rapid, and disturbances that have opened up more benthic space have greater recovery potential. Secondly, recovery dynamics of coral cover are likely to be nonlinear, such

Fig. 5 Mean annual rate of change in per cent coral cover recovery with respect to anthropogenic influences: (a) Management status and (b) Human population density (number km⁻²) (*n* = number of sites; error bars = 95% bootstrapped CI)



that recovery from extreme coral loss (<5% post-disturbance cover) and small losses may be slower, with most rapid recovery at medium to high levels of coral loss (Emslie et al. 2008).

Our analyses suggest little difference in coral recovery rates between “biological” and “physical” disturbances. Biological disturbances are those that cause a loss of the coral tissue, but leave the skeleton and therefore, the structural complexity of the reef intact, such as coral bleaching events, disease and crown-of-thorns starfish (Wilson et al. 2006). Physical disturbances (for example tropical storm damage and destructive fishing methods, e.g., dynamite blasting) cause a loss of coral cover and structural complexity (Wilson et al. 2006). However, recovery was faster following COTS outbreaks. The maintenance of reef structure following COTS outbreaks may maintain the diversity, abundance and size structure of herbivorous fish stocks (Graham et al. 2007), thus facilitating herbivory on macroalgae (McClanahan 1999). It is therefore possible that critical reef processes that are maintained where reef structure remains may promote faster recovery from disturbances. For example, Colgan (1987) concluded that the rapid recovery of reefs in Guam from a COTS outbreak was due to the fact that the COTS did not destroy the structural integrity of the reef framework. However, it should also be noted that coral bleaching and COTS outbreaks can be spatially extensive disturbances, whereas tropical storms are often very patchy in nature, leaving a myriad of areas undamaged that may facilitate recovery of the seascape (Bythell et al. 2000; Halford et al. 2004). Also, in many cases, although the dead reef structure may be suitable for coral recruitment, it can be unstable and must be removed prior to recovery of the reef (Bellwood et al. 2004). Our results indicate that recovery from COTS outbreaks may be more rapid than some other disturbances, but these effects need to be teased apart with more empirical research.

We found no evidence of dissimilar recovery rates among different reef types or reef zones. Reef zones typically have differing baseline coral cover, with greater cover on reef crests and slopes than reef flats (Connell et al. 1997). This variability may be greater than the variability in recovery from disturbances, which on resilient reefs likely tracks a similar trajectory among zones back to the baseline for that zone. We expected fringing reefs to show slower recovery potential than atolls and barrier reefs, because fringing reefs are often associated with more terrestrial influence. The lack of difference suggests all reef types have a similar capacity to recover if conditions are favourable, and that other factors, such as type and severity of disturbance, play a greater role in dictating recovery.

Coral recovery was slowest in the eastern Pacific and fastest in the western Pacific, with the Indian Ocean also showing faster recovery than the eastern Pacific. There are known substantial differences in functional diversity of corals and fish among these regions, which is highest in the western Pacific, intermediate in the Indian Ocean and lowest in the Caribbean and eastern Pacific (Bellwood et al. 2004; Allen 2008). Higher diversity is thought to promote functioning of ecosystems and their capacity to recover from disturbances (Hooper et al. 2005). A paucity of fast-growing *Acropora* corals in the eastern Pacific may also limit the rate of recovery (Guzman and Cortés 2007; Baker et al. 2008). A further impediment to the eastern Pacific reefs is geographical isolation; separated by the east Pacific filter bridge, a 5,000–8,000-km-wide area of open ocean between the eastern Pacific reefs and those of the western Pacific. The region is thus largely reliant on self-seeding among the fairly species depauperate reefs (Heck and McCoy 1978; Glynn and Ault 2000). Connell (1997) found no examples of recovering reefs in the Caribbean. Thirteen years later, we have only found examples of 4 sites (in 2 studies) recovering from an acute disturbance in the

Caribbean, compared to 18 in the Indian Ocean and 20 in the Pacific. This suggests the capacity for Caribbean reefs to recover from disturbances is still extremely retarded.

We found no evidence of small-scale connectivity, measured as distance to nearest reef and number of neighbouring reefs, influencing recovery potential of reefs. Brooding corals obviously do not disperse very far, but spawning corals can disperse among reefs at a scale of 10s of km (Jones et al. 2009). However, the maximum distances of 50 km+ that we include in our analyses are likely to have a limited amount of ecologically significant settlement from external source populations (Jones et al. 2009). Isolated reefs may be expected to have slower recovery if local broodstocks of corals and other organisms are depleted (Ayre and Hughes 2004; Cowen et al. 2006; Graham et al. 2006). However, given that rates of local recruitment can be high, some semi-isolated reefs with fewer chronic stresses can experience rapid recovery from acute disturbances if enough broodstock is available locally for replenishment (Connell 1997; Graham et al. 2008; Sheppard et al. 2008; Smith et al. 2008; Halford and Caley 2009). It should be noted, however, that due to the geographical scale of our study, the metrics of connectivity used are relatively coarse. Furthermore, connectivity can be driven by many processes, and so distance may not always capture variation among locations affectively. As more comprehensive connectivity models emerge for a greater number of locations (e.g., using biophysical models—Cowen et al. 2006), the role of connectivity in recovery dynamics can be better incorporated into analyses.

Coral recovery rates were slower in our analysis within fully protected areas, compared to areas with gear restrictions, mixed management or open access. In undisturbed states, protected areas can promote higher cover of corals (Selig and Bruno 2010) that are more susceptible to disturbances such as coral bleaching (Graham et al. 2008; Darling et al. 2010). Indeed, several studies have shown greater declines in coral cover in protected areas compared to adjacent fished sites due to higher starting coral cover in protected areas, with resultant post-disturbance coral cover very similar between the protected and fished sites (Graham et al. 2008; McClanahan 2008; Darling et al. 2010). Although our analysis suggests slower recovery in protected areas compared to areas under alternative management, this result must be interpreted with some caution as we were unable to standardise by region, levels of enforcement/compliance or quantify ecological processes. A recent study from the Caribbean indicated faster coral recovery rates within a protected area compared to fished areas (Mumby and Harborne 2010). Processes promoting faster coral recovery rates in protected areas can take many years to develop (Selig and Bruno 2010) and may be

severely disrupted following acute disturbances. Clearly, as protected areas are often small, fully controlled empirical studies assessing their role in promoting coral recovery from acute disturbances are difficult, and disturbances are becoming ever more frequent, there is a need to consider complementary management actions that build the resilience of fished areas. These may include specific gear restrictions that reduce pressure on key herbivorous fish stocks (Cinner et al. 2009) and an increase in the scale of policy decisions taking into account environmental, ecological and social considerations (Hicks et al. 2009; McClanahan et al. 2009).

There was a weak, non-significant increase in recovery rates with increasing human population densities, which was significant if using an area weighted effect size metric or the geometric rate of change. The influence of humans on reef ecosystems is not always as intuitive as one may expect. For example, Pollnac et al. (2010) found that the success of no-take marine protected areas in the Indian Ocean was positively associated with increasing population density. It is important to remember that we have specifically reviewed the literature of reefs that are recovering, and there are likely to be many examples of reefs that are not recovering in close proximity to large human population centres (Baker et al. 2008).

There is a conspicuous absence of many key variables expected to influence coral recovery from almost all of the studies reviewed. Notable absences include structural complexity of the habitat, water quality, and the diversity, abundance and biomass of key groups of fish. Many of these variables have been proposed as key drivers of coral reef recovery and have been identified as crucial knowledge gaps in coral reef science (Wilson et al. 2010). For example, structural complexity was shown to be important for the recovery of fish assemblages on the Great Barrier Reef (Emslie et al. 2008) and has been suggested as important for coral recovery in both Guam and the eastern Pacific (Colgan 1987; Guzman and Cortés 2007). Erosion of the reef structure to a smooth pavement can result in few crevices for newly settled recruits to survive (Connell et al. 1997) and mobile rubble banks can kill new recruits and young corals, thus retarding recovery (Victor 2008). Fish are thought to be extremely important in recovery dynamics (Andres and Witman 1995; Bellwood et al. 2004). Indeed, the abundance and biomass of herbivorous fishes on a reef are important to control benthic algae and allow recovery of corals (Mumby and Harborne 2010), and high levels of functional diversity and feeding complementarity of key groups of fish are thought to provide the best chances of a functioning ecosystem (Bellwood et al. 2004; Burkepile and Hay 2008; Palumbi et al. 2008). Although we were able to distinguish recovery rates with the variables currently available, a greater number of

studies assessing coral recovery dynamics need to include assessment of the reef structure and associated fauna that may, in part, explain patterns of recovery.

The focus on coral cover used here reflects that the majority of studies assessing recovery of reefs from disturbance use this metric. However, coral cover as a metric can miss the complexities of recovery in some instances (Hughes et al. 2010). For example, a different assemblage of coral taxa may dominate a reef following disturbance and recovery (e.g., Berumen and Pratchett 2006; McClanahan et al. 2007). In other cases, a similar composition of dominant reef inhabitants may return (e.g., Brown and Suharsono 1990; Guzman and Cortés 2007; Sheppard et al. 2008). Such complexities of reef recovery can have huge implications for the future resilience of the system or the diversity of other components of the ecosystem (Nyström et al. 2008; Pratchett et al. 2008) and should not be overlooked. The size structure of the coral assemblage is also proving important. If maintenance or recovery of remnants of live tissue from large corals contributes most of the post-disturbance coral cover, it may mask a lack of key processes, such as recruitment of new corals (Hughes and Tanner 2000; Done et al. 2010).

We have included all the quantitative studies of coral recovery from acute disturbances from which we could extract suitable data, ranging from the western Indian Ocean, to the eastern Pacific and the Caribbean. We have incorporated as many potential variables in the analysis to explain differences in recovery rate as were available. However, there is currently a paucity of information on key ecosystem processes, such as herbivory and recruitment, and other factors, such as structural complexity and functional diversity, to enable a more holistic analysis. To understand the resilience of coral reefs to increasing acute disturbance events, and how recovery can be bolstered through changes in management and governance structures, there is a need to redress the focus on assessing coral cover, and incorporate more complex measures of reef processes and dynamics into ecological studies and monitoring programs.

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