

Coral bleaching: one disturbance too many for near-shore reefs of the Great Barrier Reef

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Abstract The dynamic nature of coral communities can make it difficult to judge whether a reef system is resilient to the current disturbance regime. To address this question of resilience for near-shore coral communities of the Great Barrier Reef (Australia) a data set consisting of 350 annual observations of benthic community change was compiled from existing monitoring data. These data spanned the period 1985–2007 and were derived from coral reefs within 20 km of the coast. During years without major disturbance events, cover increase of the Acroporidae was much faster than it was for other coral families; a median of 11% per annum compared to medians of less than 4% for other coral families. Conversely, Acroporidae were more severely affected by cyclones and bleaching events than most other families. A simulation model parameterised with these observations indicated that while recovery rates of hard corals were sufficient to compensate for impacts associated with cyclones and crown-of-thorns starfish, the advent of mass bleaching has led to a significant change in the composition of the community and a rapid decline in hard coral cover. Furthermore, if bleaching events continue to occur with the same frequency and severity as in the recent past, the model predicts that the cover of Acroporidae will continue to decline. Although significant cover of live coral remains on near-shore reefs, and recovery is observed during inter-disturbance periods, it appears that this system will not be resilient to the recent disturbance regime over the long term. Conservation strategies for coral reefs

should focus on both mitigating local factors that act synergistically to increase the susceptibility of Acroporidae to climate change while promoting initiatives that maximise the recovery potential from inevitable disturbances.

Keywords Coral community dynamics · Disturbance · Recovery · Simulation

Introduction

Coral communities exist in a dynamic cycle of disturbance and recovery (Connell 1978). The development and persistence of coral reefs indicates that, historically, settlement and growth rates of corals have been sufficient during inter-disturbance periods for recovery to occur. However, there is growing evidence that well-established coral communities around the globe are in decline, due to the upset of this historical balance, because disturbance severities and frequencies now outstrip recovery potential (e.g., Bellwood et al. 2006; Wilkinson 2008; Bruno and Selig 2007).

At local scales, disturbance to individual coral communities may increase as the effects of direct (e.g., destructive fishing; Jackson et al. 2001) or downstream (e.g., increased sedimentation and pollution; Grigg 1995; McCulloch et al. 2003) anthropogenic activity compound with natural disturbances such as tropical storms (e.g., Gardner et al. 2005) and outbreaks of predators (e.g., Moran 1986). Chronic environmental degradation is likely to exacerbate any increase in acute disturbance by limiting the potential of coral communities to recover; in particular, through the suppression of coral recruitment (reviewed by Fabricius 2005). Potentially overwhelming local influences are issues associated with CO₂-driven climate change. Elevated ocean temperatures have disturbed reefs over unprecedented

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spatial scales in recent years, producing mass bleaching events that occur when corals eject their zooxanthellae as a result of thermal stress (Hoegh-Guldberg 1999; Oliver et al. 2009). In addition to warming of the oceans, higher levels of atmospheric CO₂ will also lead to ocean acidification: a phenomenon that may increase the susceptibility of corals and coral reef organisms to temperature stress, reduce productivity and disrupt the process by which corals produce their calcium carbonate skeletons (Orr et al. 2005; Anthony et al. 2008). These impacts resulting from increased concentration of atmospheric CO₂ are predicted to intensify in the near future (Sheppard 2003; Hoegh-Guldberg et al. 2007; IPCC 2007).

In the face of predicted increases in climate-driven pressures, it has been suggested that the most effective management strategy will be to maximise the resilience of coral communities by mitigating local pressures that reduce the potential for recovery following acute disturbances (e.g., Hughes et al. 2007). It is important, however, to demonstrate the current resilience of coral reefs in order to support, or gauge the necessity of, these management interventions. This is distinct from the prediction of resilience under predicted future disturbance regimes, which involves greater uncertainty, and may lead to debate rather than action.

On the Great Barrier Reef, Australia (GBR), it can be argued that the reefs most at risk to the combined impacts of local and global stressors are those situated in the relatively turbid near-shore waters. Development of adjacent catchments has led to a substantial increase in the flux of fine sediments and nutrients (e.g., McCulloch et al. 2003; Furnas 2003) entering this already marginal habitat for reef growth (Smithers et al. 2006). The reefs in this setting also showed higher levels of bleaching associated with anomalously high water temperatures in 1998 and 2002 compared to reefs further offshore (Berkelmans et al. 2004). To date, there remains considerable disagreement as to whether these reefs are degraded or not. There are many reefs that support high cover of hard corals, while others have few hard corals and disproportionately higher abundance of large fleshy algae (Sweatman et al. 2007). These apparently disparate community conditions can be used to support equally disparate views of coral community status when their dynamic nature is not considered.

Estimating the resilience of coral communities to disturbance is complicated by variation in the severity of disturbance events and the susceptibility of species. For example, susceptibility varies among coral species to crown-of-thorns starfish predation (De'ath and Moran 1998), thermal bleaching (Marshall and Baird 2000; Loya et al. 2001), sedimentation (Stafford-Smith and Ormond

1992), decreased salinity (van Woesik et al. 1995) and storm damage (Woodley et al. 1981). Additionally, estimates of recovery rate or susceptibility to disturbance taken from a single location will almost certainly have insufficient temporal coverage to adequately consider the synergistic interplay of multiple past disturbances and local environmental conditions (Hughes and Connell 1999). Observations made at any one time will reflect point estimates of the status of what are demonstrably dynamic communities, and the impression obtained of reef health will depend on the timing of the observation in relation to the unique disturbance history. Clearly, the intensity and frequency of combined disturbances should be considered when assessing the status of an observed coral community. Similarly, the consideration of status should also include the capacity of a community to recover during periods free from disturbance. This requires a modelling approach that integrates recovery rates and disturbance regimes to generalise from a specific sequence of events to a more general case.

To date, studies that model the dynamic status of reef communities have typically focused on very small scale but intensive observations aimed at following the demographic processes of small groups of individual colonies (e.g., Hughes and Tanner 2000; Connell et al. 2004; Wakeford et al. 2008). These studies have provided detailed descriptions of the dynamics of these individual reef patches and provided important insights into the relative importance of processes such as recruitment, growth and mortality in coral community persistence. However, the intensity of sampling required to adequately account for spatial and/or temporal variation in demographic parameters has largely precluded the use of similar models to assess the status of communities at larger scales (but see Reigl and Purkis 2009).

This study uses data from multiple visits to a large number of reefs within the turbid coastal waters of the GBR to estimate both the incidence and severity of disturbances and the rate of increase when not disturbed for the various coral community components. This information is used to parameterise a community model. Model simulations allow the assessment of factors controlling the status of reefs in this region and the likely trajectory of these communities to be projected. Importantly, the estimated trajectory of coral communities is based on the observed dynamics of coral communities under experienced conditions and is not a prediction of resilience to predicted future disturbance regimes. It provides a conservative estimate of the response of the reef system to the recent disturbance regime, recognising that the current observed state may be transitory.

Methods

Scope of data

The estimated covers of hard and soft corals used in this study were derived from approximately annual surveys of permanently marked transects on reefs within the Great Barrier Reef Lagoon, between 16°S and 23°S and within 20 km of land (Fig. 1). Importantly, all reefs selected exhibited the development of a reef flat indicating historical reef-building capacity. Sampling was conducted in the same manner for each repeat survey at any particular reef, with cover estimates based on either Line Intercept or Video Point Intercept techniques (Abdo et al. 2003). All data were drawn from Australian Institute of Marine Science (AIMS) databases and were collected by trained personnel from either SeaResearch, AIMS, or persons trained by AIMS.

For each reef sampled, estimates of change in cover of hard coral families (Scleractinia) and total cover of soft coral (Octocorallia) constitute the difference in mean per cent cover from between 5 and 15 transects of either 20 or 50 m in length. Survey depths ranged between 1 and 7 m below datum. At 28 reefs, two depths (2 and 5 m below datum) were surveyed between 2005 and 2007. Given the differences in the communities observed at the two depths, these data were considered independent when estimating rates of change but were only counted once when estimating disturbance frequencies, and disturbance severity was averaged across depths. The total data set included 310 approximately annual estimates of the change in cover of hard and soft coral families spanning the period 1985–2007. Observations of increase in cover made over periods slightly more or less than 12 months were adjusted proportionally to give estimates of annual change, hereafter referred to as rates of change.

Each observation of change in coral cover was categorised as coming from either a disturbance period or a period of undisturbed growth. Observations were assigned to a disturbance category on the basis of the following: (a) showing a decline in overall coral cover and (b) our ability to confidently ascribe the cause of the disturbance (Table 1). Impacts on the coral communities ascribable to floods were limited to just one observation and resulted in a negligible loss of hard coral and soft coral compared to other disturbances and were not considered further.

Minor declines in coral cover that could not be ascribed to a specific disturbance event were designated as “no disturbance” along with all observations of increases in coral cover. The “no disturbance” classification implicitly includes more subtle stressors in the near-shore environment such as outbreaks of disease, predation, competition with other benthic organisms, sedimentation and prolonged

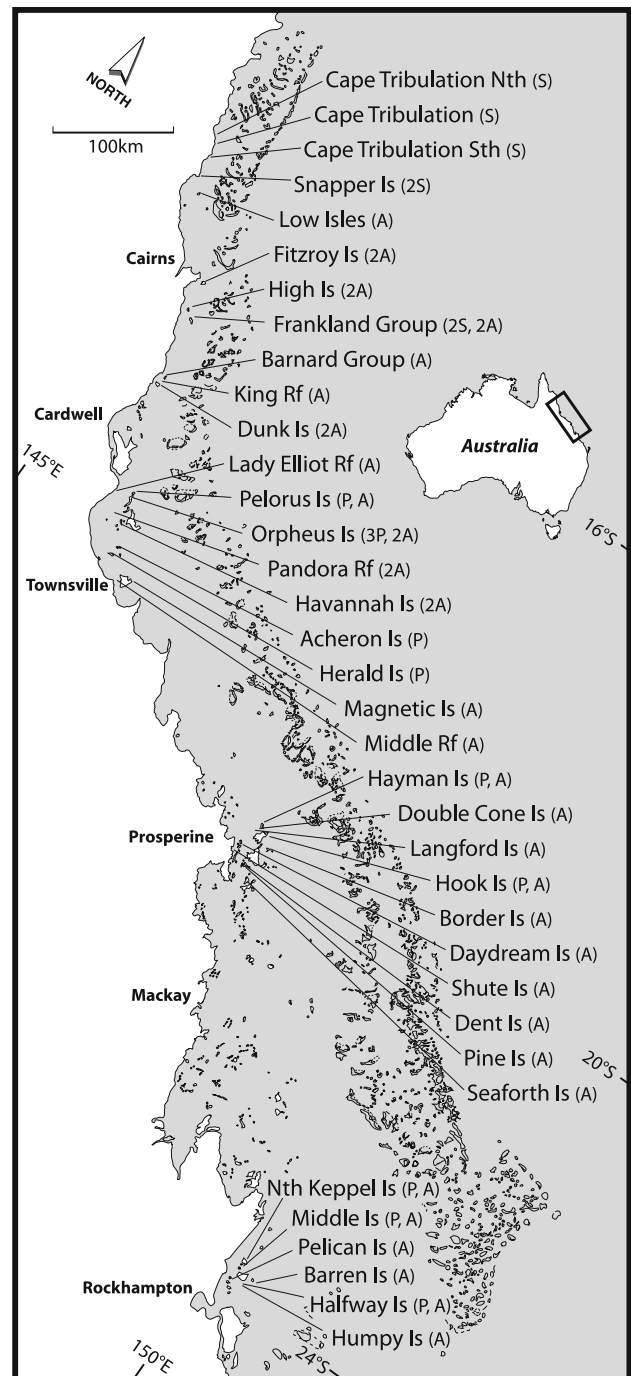


Fig. 1 Location of reefs from which estimates of change were derived. The monitoring provider for each reef and the number of distinct locations monitored follow the reef names and are as follows: A for the Australian Institute of Marine Science, P for the then Queensland Parks and Wildlife Service and S for SeaResearch. Where more than one broad habitat was sampled at a given reef, the number of habitats sampled precedes the abbreviation for monitoring provider. Where more than one monitoring provider is indicated, either habitats or period of observation are distinct

periods of high turbidity that combined may suppress growth and survivorship and hence the realised increase in cover. Sampling error about repeated cover estimates will

Table 1 Decision rules for the designation of disturbances

Disturbance	Criteria
Cyclone	Knowledge that a cyclone passed within close proximity of a reef combined with the observation of obvious physical disturbance to the coral community during the subsequent survey
Crown-of-thorns starfish	Observation of COTS at a reef during a period of observed decline
Bleaching	Observed declines in coral cover over a period during which bleaching was either observed or its likelihood high as determined from coral thermal bleaching risk maps (Berkelmans et al. 2004)
Flood	Decline in coral cover over a period during which a flood plume was known to extend to a reef

also result in some observations of minor decline especially if coral cover is relatively unchanged.

Modelling and simulation

To gain an improved understanding of the dynamic status of this reef system, the survey data were used to parameterise a density-dependent growth model of benthic cover, allowing the long-term consequences of the current disturbance regime to be simulated. It was impractical to build a model with, and estimate separate parameters for, each coral family, and so families were aggregated according to similar rates of cover increase and response to disturbance. This resulted in the aggregation of the hard coral community into two groups, the family Acroporidae (Scleractinia) and the sum of all other hard coral families (see “Results”). A third group, soft corals, represents the aggregated cover of all Octocorallia families, as taxonomic resolution for this order was low for many observations.

The dynamics of these coral groups were modelled as linked, discrete-time, density-dependent processes, treating cover (in per cent) as population sizes. The presence of cover of one group inhibits the growth rate of itself and the other two groups symmetrically as if the groups compete with each other (and themselves) through space pre-emption. No limits were placed on the maximum percentage cover attainable by individual coral groups, i.e., each can attain a cover of 100% in the absence of competitors. Specifically, a multi-species form of the Gompertz growth equation was used (Dennis and Taper 1994; Ives et al. 2003), modified such that the equilibrium size of all populations combined was 100, the maximum total per cent cover attainable.

The resulting growth equations were:

$$\ln Acr_t = r_{Acr} + \ln Acr_{t-1} + (-r_{Acr}/\ln K) \times \ln(Acr_{t-1} + OthC_{t-1} + SC_{t-1}) + \varepsilon \quad (1)$$

$$\ln OthC_t = r_{OthC} + \ln OthC_{t-1} + (-r_{OthC}/\ln K) \times \ln(Acr_{t-1} + OthC_{t-1} + SC_{t-1}) + \varepsilon \quad (2)$$

$$\ln SC_t = r_{SC} + \ln SC_{t-1} + (-r_{SC}/\ln K) \times \ln(Acr_{t-1} + OthC_{t-1} + SC_{t-1}) + \varepsilon \quad (3)$$

where Acr_t , $OthC_t$ and SC_t are the cover at time t of Acroporidae, other hard coral and soft coral, respectively, r_{Acr} is the rate of increase in per cent cover of Acroporidae (hereafter referred to as growth rate), K is the equilibrium community size (100 here), and ε is the random error term that accounts for low-level or background levels of disturbance that appear in the data as minor losses of coral cover to which it was impossible to attribute a cause.

An important point to note is that the dynamics of reef-associated macroalgae were not explicitly modelled. The cover of algae was highly variable at most temporal and spatial scales and reasonable estimates of annual rates of change could not be derived. However, the influence of algae on the trajectories of coral communities was implicit in the model, as all observations of recovery from disturbance of the coral communities include limitations imposed by competitors such as macroalgae.

Disturbances were modelled by first determining by random draw, for a given year, whether an event occurred, and then drawing a random deviate from a fitted distribution of disturbance severities to determine the level of impact of that event. The annual probability for the occurrence of each disturbance category was estimated as the proportion of the total number of reef-years in which an event of that category impacted a reef.

As it was not possible to normalise the distributions of disturbance impact severities, it was convenient to estimate the growth rate parameters and the disturbance severity distributions separately in a two-stage process. First, growth rates of Acroporidae, other hard coral and soft coral were estimated by fitting Eqs. 1–3 to data for reef-years in which no major disturbance event occurred. These estimated growth rates were then used to predict expected change in cover for years where disturbance did occur but assuming there had been no disturbance. Skewed-normal distributions were then fit to the differences between expected and observed changes in cover for disturbance years (estimates of disturbance severity) for each disturbance category.

Observations of change were not used where initial cover was less than 1% because below this level, the limit of sampling sensitivity is approached. During simulation, impact severities for given events were drawn from the fitted distribution for the Acroporidae, and then the fitted quantile functions for the other two groups used to look up the equivalent severities for an event of that probability. In this way, the relative severities of given events were correlated across coral groups while their absolute severities reflected their differing susceptibilities.

Equations 1–3 were fit as a nonlinear mixed effects models with the R package NLME (Pinheiro et al. 2008) using random effects for the growth rate parameters (random intercepts) at reefs nested into latitudinal regions to improve the accuracy of the estimates by accounting for repeated measurements at individual reefs and the unequal numbers of observations at different reefs and in different latitudinal regions. Residual plots were examined and a small number of outlying observations removed before estimating growth rates. Skew-normal distributions were fit to deviations from the expected change in cover during years where a disturbance event occurred by maximum likelihood using the R package “sn” (Azzalini 2009).

The simulation model, coded in the R language (R Team 2008), was run 1,000 times for each of the following scenarios: (a) 100 years with a disturbance regime equivalent to the observed cyclone and COTS frequency and severity but with no mass bleaching events; (b) completion of scenario (a) after which bleaching events were added at the observed frequency and severity and the state of the benthic community recorded after 10 further years; (c), (d) and (e) scenario (b) but 20, 50 and 100 years with bleaching passed before recording the state of the benthic community. In each simulation, cover of each of the three benthic groups started at 20%. This value approximates the average initial cover of Acroporidae (24%), other hard corals (16%) and soft coral (15%) at reefs visited prior to a major bleaching event in 1998. As projections for cover under the various disturbance scenarios follow 100 years of modelled dynamics including only cyclone and COTS disturbance, the outcomes are insensitive to the exact starting covers.

Results

Observed disturbances and community responses

Over the period 1985–2007, 88 of the 310 observations of change in coral cover on near-shore reefs could be categorised as including a disturbance event. Coral bleaching was the most common category of disturbance, accounting for 60% of the identified disturbance events and 59% of the cover of hard corals lost over all disturbances. Cyclones

were also relatively frequent, accounting for 31% of disturbance events and 32% of hard coral loss. Soft corals were more susceptible to cyclones than bleaching events with 69% of the total soft coral cover lost during disturbance events attributable to cyclones compared with 30% attributable to bleaching. Crown-of-thorns starfish were less frequently encountered and were implicated in declines at just six reefs and accounted for 8% of the hard coral cover lost. Soft corals were not adversely impacted by crown-of-thorns starfish.

Considering just the two most prevalent disturbance categories, bleaching and cyclones, it is clear that the spatial foot print of the disturbance varied both between disturbance categories and also between individual events. For each of the eight cyclones, disturbance was limited to reefs within a band spanning not more than one degree of latitude. There were no cyclone impacts recorded on the more southern reefs (Fig. 2). At a finer scale, impacts of cyclones varied substantially over distances of just a few kilometres, dependant on the aspect of the reef relative to the path of the storm. For example, cyclone Larry passed to the north of Dunk Island resulting in an 81% reduction in coral cover at 2 m depth on the northern side of the island, while at the same depth on the southern side, only 2% of the coral cover was lost. The typically constrained scale of

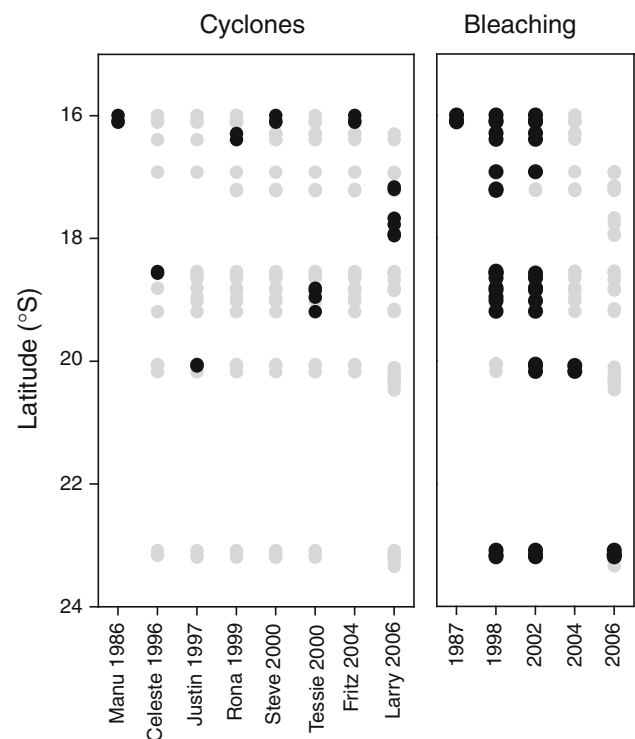


Fig. 2 Spatio-temporal location of cyclone (*left*) and bleaching (*right*) events. Each point represents a reef sampled at a particular latitude and time. Grey symbols indicate no impact to coral communities, while black symbols indicate impacted reefs

disturbance observed for cyclones was in contrast to two of the five bleaching events. Both the 1998 and 2002 events affected most reefs over the full 7 degrees of latitude included in this study except for reefs in the Whitsunday region (around 20°S) in 1998 (Fig. 2). In 1987, only three reefs (around 16°S) were sampled, and so the spatial extent of this bleaching event is unknown. Anecdotal evidence, however, suggest that this event was also widespread. In contrast, bleaching in 2004 and 2006 was confined to the more southern reefs (>19°S and 20°S, respectively) but damage was widespread within this region. Five of the six reefs impacted by crown-of-thorns were located between 16°S and 17.3°S and during the period 1998–2000. The only other observation of crown-of-thorns impact was at Hayman Island (20°S) in 1994.

For the hard coral community, there were clear differences in susceptibility between families. The distributions of observed proportional change in cover of hard coral families during identified disturbance events (Fig. 3a, b) showed clear differences in susceptibility between families, along with variation in the severity of the impacts themselves. The family Acroporidae is clearly highly susceptible to bleaching and cyclones as well as COTS predation (data not presented in Fig. 3 due to too few observations for most families). Of the total coral cover lost over all disturbances, 81% was of the family Acroporidae. This was disproportionate to the occurrence of Acroporidae in pre-disturbance communities in which it accounted for 59% of

the hard coral cover. The family Pocilloporidae was also highly susceptible to bleaching but not so much to cyclones (Fig. 3a cf. b). The family Pocilloporidae, however, is a relatively minor component of the coral communities on near-shore reefs. Although highly susceptible, losses of Pocilloporidae during bleaching events accounted for only 4% of the total cover lost. For many families, net increases in cover were observed during some disturbance years (Fig. 3a, b). In such instances, growth of corals following disturbance may have compensated for any loss in cover, or a perceived increase occurred as a result of removal of overshadowing corals revealing previously obscured corals to sampling. Overall, the families Dendrophylliidae, Oculinidae and Pectiniidae seem least impacted by bleaching, and the family Merulinidae least impacted by cyclones (Fig. 3a, b).

During periods of no disturbance, the cover of the family Acroporidae increased at a median rate of 11% per year (Fig. 3c). This was substantially higher than median increases in cover of 2–3% for Agariciidae, Faviidae and Poritidae, and negligible median increases or even declines for the remaining families.

The combination of a high susceptibility to disturbance, along with a high rate of increase in cover relative to other hard coral families during periods of no disturbance, suggested that the Acroporidae be explicitly modelled as a separate group. The rarity of several other Scleractinian families precluded modelling all families separately and

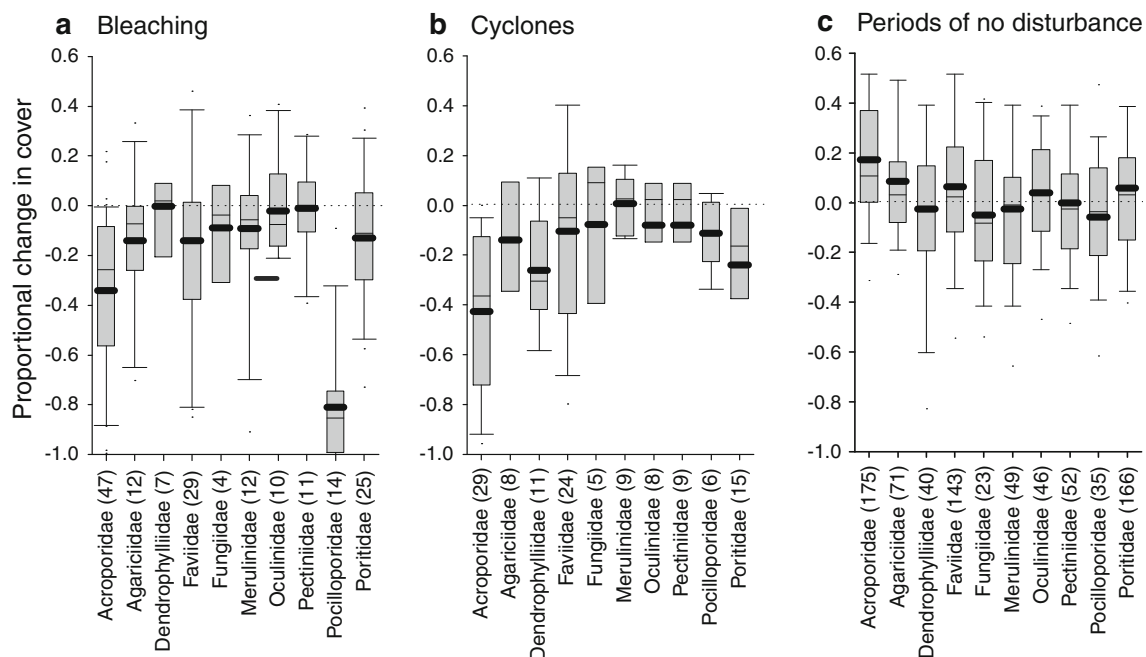


Fig. 3 Distributions of annual estimates of proportional change in cover for hard coral families associated with: **a** coral bleaching events, **b** cyclones, **c** disturbance free periods. Proportional changes were estimated only for those years in which initial cover was >1%.

Numbers in brackets associated with each family on the x axes indicate the number of observations that met this criterion. Boxes indicate the mean (heavy line), median (light line), 25th–75th percentiles (box) and 10th and 90th percentiles (whiskers)

this, along with the fact that none of the more common (e.g., Poritidae or Faviidae) families showed obviously differing rates of increase (Fig. 3c) or susceptibility to disturbance (Fig. 3a, b), suggested the pooling of observations across all families other than Acroporidae. Despite their elevated susceptibility to disturbance events, the Pocilloporidae were likewise grouped with other families on the basis of their similar growth (increase) rates. The cover of Pocilloporidae was typically very low (<1%) on the reefs in this study, and grouping estimates with either Acroporidae or other families did not substantially alter estimates of model parameters.

Estimated community parameters

Growth rates for Acroporidae, other hard corals and soft corals were estimated as 0.933, 0.349 and 0.282, respectively. These equate to proportional increases in cover of 16.9, 6.03 and 4.83% per year when total cover of all corals was 46.2%—the average total cover observed on near-shore reefs. The parameterised growth model allowed estimation of the impact severity of observed disturbance events as the difference between the observed cover change and that predicted given no disturbance event. For each benthic group and disturbance combination, the resulting estimates and fitted skewed-normal distributions are presented in Fig. 4. From these distributions, there are clear differences in susceptibility between the three benthic groups to the three disturbance categories. The distributions for other hard corals for example are concentrated towards low impacts compared to the distributions for Acroporidae that show a flatter distribution encompassing a higher proportion of more severe impacts. The lack of impact to soft corals as a result of crown-of-thorns is also clear. Wide distributions encompassing both positive and negative impacts of bleaching and cyclones for soft corals remain largely unexplained though may indicate rapid post-disturbance colonisation of available space in some instances or variable susceptibility to these disturbances among taxa, remembering that soft coral families were not consistently differentiated in the data set.

Simulation output

A model was created to simulate the long-term consequences of the estimated disturbance distributions given the growth rates observed over the period 1987–2007 (Fig. 5). The first simulation, in which only cyclones and crown-of-thorns disturb reefs, suggests that in the absence of bleaching, the median cover of the family Acroporidae would be 24%, and the median for all hard corals combined 45%. This is considerably higher than the last observed median covers of Acroporidae (6%) and all hard coral

combined (19%). The inclusion of bleaching as an additional disturbance progressively decreased the cover of Acroporidae and, to a lesser degree, the pooled cover of other hard coral families in the model run over 10–100 years. The longer that bleaching is part of the disturbance regime, the greater the reduction in cover, especially of Acroporidae. The cover of other hard corals and soft coral was less affected by bleaching but did not compensate for the loss of Acroporidae cover. Comparing the model output to the median of the covers last observed at each survey reef indicates that the cover of both Acroporidae and the pooled other hard coral families was similar to our simulated community state exposed to a disturbance regime that included cyclones, COTS for 120 years and coral bleaching for a period of 20 years (Fig. 5). This implies that the model well represented the actual dynamics of coral communities on near-shore GBR reefs.

Discussion

Modelling observed growth and disturbance dynamics of coral communities on reefs within 20 km of the Great Barrier Reef coast indicates a system in decline. **The observed rate of increase in cover during disturbance free periods was adequate to compensate for losses caused by tropical cyclones and crown-of-thorns starfish predation.** However, the inclusion of thermal bleaching disturbances at the frequency and severity observed over the last two decades resulted in a rapid decline in coral cover. This decline was primarily driven by changes in cover of the historically dominant Acroporidae; the pooled cover of other hard coral families and also soft corals remained relatively constant under the recently observed disturbance regime. While this might imply that non-Acroporid hard corals and soft corals are more resilient to disturbance, growth of existing colonies rather than recruitment of new individuals can be the main process of recovery of after disturbance events (Mumby et al. 2007; Wakeford et al. 2008) meaning that a community may appear resilient due to growth of existing colonies but be destined for decline upon the eventual mortality of large individuals (Hughes and Tanner 2000). Certainly, on many near-shore GBR reefs, cover for many of the non-Acroporid families consists predominantly of relatively few but large colonies (Sweatman et al. 2007). It is plausible that these colonies represent relics that settled and grew under different conditions to those now experienced and may not be replaced if they suffered whole colony mortality.

There are several reasons why our estimates of coral decline may be conservative. **First, our model does not explicitly include recruitment that is assumed to be constant and unaffected by a changing disturbance regime or**

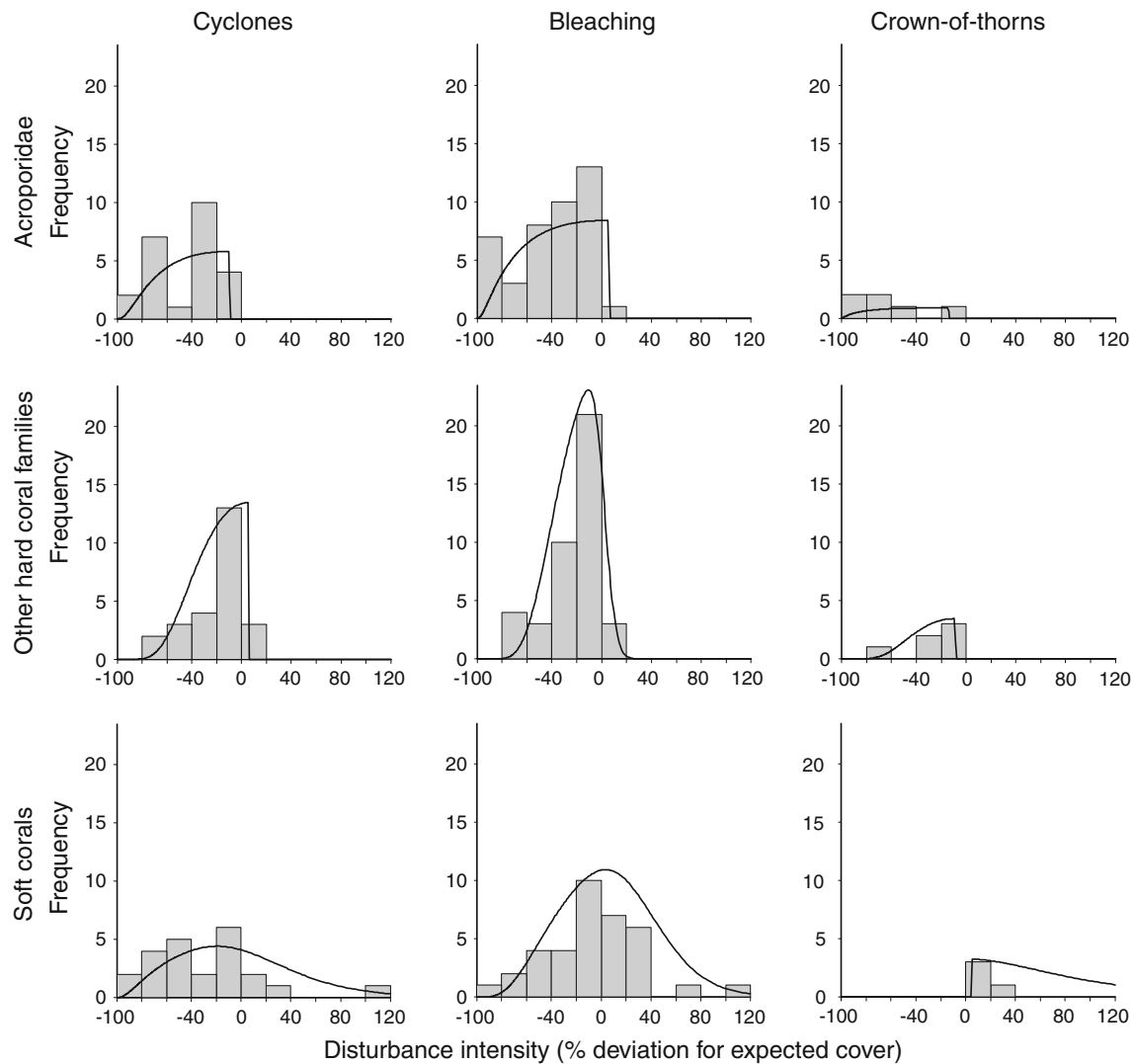


Fig. 4 Distribution of intensity of impact of major disturbance events for three benthic groups expressed as percentage deviation from the cover expected if no major event occurred. Bars indicate observed

deviations; solid lines show fitted beta-distribution probability density functions used to generate random disturbance intensities for the simulation model

declining cover. It is implausible that larval supply or survival would increase under the current or future disturbance regimes that include mass bleaching events—recruitment is more likely to decline as broodstocks dwindle. **Second** reason is that **there is a clear difference between the impacts of cyclones and bleaching with ramifications for recovery. While cyclones can cause whole colony mortality, it is more typical that recovery rapidly proceeds from remaining fragments of tissue** (Highsmith 1982). Also, there are often local refugia not affected during cyclonic events due to the directional nature of the storm driven seas (Harmelin-Vivien 1994, this study). This is different than the impact of bleaching where reductions in cover are often the result of complete mortality of susceptible colonies (Baird and Marshall 2002) and local refugia may not occur as temperature anomalies can affect

large areas (see Fig. 2), especially in shallow and turbid areas where refugia in deeper waters do not exist. There is also the possibility of a severe reduction in larval supply following bleaching events if broodstock is regionally suppressed through widespread mortality (e.g., Smith et al. 2008) or compromised fecundity of surviving colonies (McClanahan et al. 2009). Our model does not explicitly include suppression of recovery rates; however, a number of estimates were derived from the Townsville region where bleaching in 1998 severely reduced the cover of Acroporidae on most reefs, and as a result, any broodstock limitation to growth rates will be at least partially represented in our estimates. If Acroporidae communities continue to follow the predicted declines, the associated reductions in broodstock would lead to a reduction in the recovery rate and accelerated rate of Acroporidae decline.

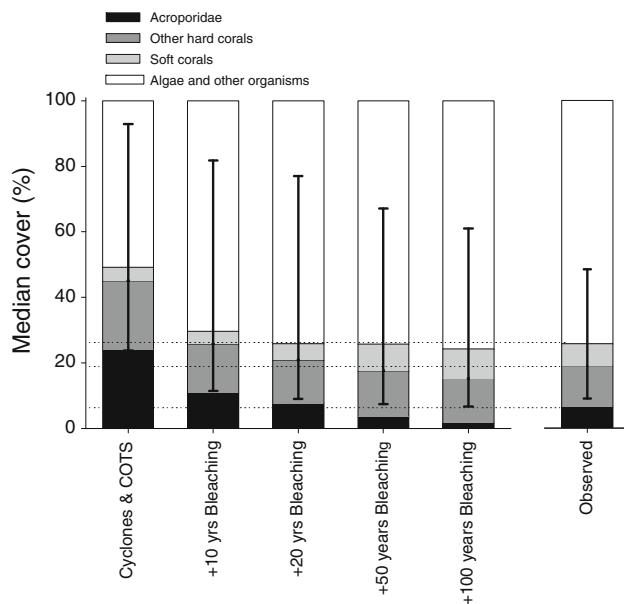


Fig. 5 Predicted and observed covers of major benthic groups. Stacks present the median cover for each benthic group. Error bars encompass the 10th–90th percentiles for total hard coral cover (sum of Acroporidae and other hard corals). From left to right, stacks present simulation estimates with increasing exposure to bleaching disturbances. In each case, populations are exposed to 100 years of cyclones and crown-of-thorns predation plus the additional duration of bleaching as indicated on the x-axis. The final stack shows the median observed covers from the final surveys made at reefs in this data set; these data points are predominantly from between 2004 and 2007

Third reason is that the dynamics of potential space competitors, such as macroalgae, were not explicitly modelled, and so any limitations imposed on the recovery of coral communities (as reviewed by Birrell et al. 2008) remain static. It is likely that at least some of the coral-free space projected by the model would be colonised by macroalgae or another non-coral organism, resulting in an increased limitation to coral recovery rate. Finally, the model estimates the trajectory of coral cover based on the status of reefs over the observation period and the projections assume no change in disturbance regime. This may well be conservative as the severity and frequency of bleaching events and intensity of tropical storms are widely expected to increase given climate change projections (IPCC 2007). In addition to expected increases in the current suite of impacts to coral communities, it is largely acknowledged that increasing atmospheric CO₂ concentrations will lead to ocean acidification that will in turn reduce the ability of marine organisms, including corals, to lay down their carbonate skeleton (Orr et al. 2005). Reduced skeletal strength will further increase corals' susceptibility to the likely increased levels of physical disturbance associated with intensifying storms (Madin et al. 2008). It is thus highly unlikely that any increase in disturbance will be

compensated for by an increase in the rate of recovery as recovery will rely more and more on larval recruitment, while potential brood-stocks decline.

Direct impact of floods in our data set is likely under-represented as the majority of sites are at least 2 m below datum, which is deeper than the typical penetration of low salinity in flood plumes (Devlin et al. 2001). Cover communities on reef crests and flats would be more severely impacted than those on reef slopes (see van Woerik 1991).

Indirect impact of run-off including chronically high levels of nutrients and turbidity are implicitly accounted for in the model as they represent the environmental setting from which all estimates of growth rate and disturbance severity are derived.

This analysis strongly implicates mortality associated with climatically linked bleaching events as a key factor contributing to the decline of coral communities in the near-shore environment of the Great Barrier Reef. There are several factors that may predispose reefs in this setting to be susceptible to a changing climate. Wooldridge (2009) argues that the susceptibility of corals to bleaching is linked to the availability of dissolved inorganic nitrogen DIN whereby increased availability of DIN promotes the maintenance of detrimentally high rates of zooxanthellae photosynthesis during periods of thermal stress. The environmental setting is also likely to have a profound influence on the recovery potential of coral communities.

Reef accretion on near-shore GBR reefs has been very low for ~5,000 years due to a lack of available suitable substratum (Smithers et al. 2006). The combination of a slight drop in sea level that precludes corals from colonising old reef flats and the prevalence of high turbidity and/or soft sediments that preclude coral communities from deeper water restricts coral communities to the narrow reef slope. As a result, populations of corals are regionally small making potential broodstock particularly susceptible to large scale disturbances. Any reduction in local fecundity is further compounded by regional water quality issues such as suspended sediments and dissolved nutrients that synergistically reduce fertilisation and disrupt embryo development (Humphrey et al. 2008). Any resulting reduction in supply of competent larvae will further compound pressures associated with the silty substrates and algal communities typical of these reefs that may reduce the survival of coral recruits (reviewed by Fabricius 2005).

Current management strategy in the face of global climate change is to bolster the resilience of communities to inevitable disturbance events by mitigation of factors considered to exacerbate climatic pressures (e.g., Nyström and Folke 2001; Hughes et al. 2003; Marshall and Schuttenberg 2006). Improving or sustaining regional water quality is justified, based on the links between nutrient availability and susceptibility to bleaching or recovery

outlined above. A second approach is the use of marine protected areas (MPAs) to limit ancillary impacts on coral communities identified as having natural resistance to bleaching (West et al. 2006). Such natural resistance is often associated with local hydrodynamics that promote mixing or greater depth, both of which can reduce exposure to prolonged elevated temperatures. Given the generally well-mixed waters (Luick et al. 2007) and limited depth range of coral communities in the near-shore GBR, it is unclear as to the utility of such an approach in this particular setting. That said, protection of broodstock from other disturbances such as anchor damage may prove important in areas where coral populations are locally small. Strategies such as the transplantation of cultured corals or coral fragments (e.g., Edwards and Clark 1999) or the translocation of cultured wild-caught larvae (Heyward et al. 2002) might also be considered in conjunction with the use of MPAs where the aim is to augment the recovery of breeding populations into well-situated MPAs.

For the bioregion studied here, we provide clear evidence that the advent of bleaching has increased mortality of Acroporidae to levels beyond those that can be compensated for by their observed recovery potential. This is particularly worrisome given the likelihood that these projections are conservative: based as they are on levels of disturbance observed in the recent past with no compensation for either increased severity or frequency of disturbance or feedback between reducing populations and recovery potential. These results are consistent with those of other recent works that predict both shifts in community composition and reductions in cover as a result of altered disturbance regimes (e.g., Reigl and Purkis 2009; Madin et al. 2008). It seems clear that the decline is due to susceptibility of the Acroporidae to bleaching and the ensuing lag in recovery due to reduced broodstock availability. Acroporidae are an ecologically important component of coral communities offering unique habitat complexity and food resources for other reef biota (e.g., Emslie et al. 2008; Pratchett 2007). If this component of near-shore coral communities is to be maintained, it is imperative that local management strategies aimed at reducing the susceptibility of existing corals to thermally induced mortality, enhancing recovery potential by direct protection of broodstock and mitigation of factors limiting survival of recruiting corals be continued and enhanced where possible.

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