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Climate-mediated mechanical changes to post-disturbance coral assemblages

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Increasingly severe storms and weaker carbonate materials associated with more acidic oceans will increase the vulnerability of reef corals to mechanical damage. Mechanistic predictions based on measurements of colony mechanical vulnerability and future climate scenarios demonstrate dramatic shifts in assemblage structure following hydrodynamic disturbances, including switches in species' dominance on the reef and thus potential for post-disturbance recovery. Larger colonies are more resistant to factors such as disease and competition for space, and complex morphologies support more associated reef species. Future reefs are thus expected to have lower colony abundances and be dominated by small and morphologically simple, yet mechanically robust species, which will in turn support lower levels of whole-reef biodiversity than do present-day reefs.

Keywords: reef corals; hydrodynamic disturbance; assemblage structure; seawater acidification

1. INTRODUCTION

Scleractinian reef corals build physical structures that provide essential ecosystem functions for reef communities, including substrate for settlement, protection from predators and shelter from disturbances. Growing most successfully in shallow tropical waters, coral colonies are continually exposed to hydrodynamic forces produced by surface waves (Done 1983) and intermittently bombarded by severe tropical storms (Madin *et al.* 2006). Gradients in wave exposure are known to play a major role in determining species zonation (Rosen 1975) and coexistence patterns (Connell 1978). In large part, this occurs because corals exhibit an enormous variety of morphological strategies with differing mechanical performance (Jackson 1979; Madin 2005). For instance, a trade-off exists where morphologies that grow vertically (and thus are better able to compete for space and/or maximize light and food interception) typically face an increased risk of dislodgement by hydrodynamic force. Given that vertically growing species provide disproportionately more habitat for associated reef organisms (Luckhurst & Luckhurst 1978; Almany 2004), their survival during hydrodynamic disturbances and subsequent recovery are essential to sustain whole-reef biodiversity.

Some climate models project that tropical storms and the corresponding wave climates will become more intense with time (Emmanuel 2005; IPCC 2007). Moreover, acidification of seawater due to increased atmospheric CO_2 is expected to weaken reef carbonate materials (Kleypas *et al.* 1999; Hoegh-Guldberg *et al.* 2007). Changes in factors that affect the mechanical vulnerability of coral colonies will alter the relative success of different morphological strategies during disturbances, resulting in assemblage-level ecological shifts. To forecast such shifts, it is necessary to first understand how individual colonies within coral assemblages respond to hydrodynamic force (Denny 1995). An existing mathematical model predicts colony dislodgement based on coral colony morphology and environmental conditions (Madin & Connolly 2006). A colony is predicted to become dislodged from the reef when the 'colony shape factor' (CSF, a dimensionless index of mechanical vulnerability based on the distribution of colony shape above the substrate and basal attachment area) exceeds the mechanical threshold imposed by the environment (determined by wave-induced water velocity and the strength of the reef substrate to which colonies attach). Rearranging the model's equation gives the maximum water velocity a colony can withstand before dislodgement (U_{thresh})

$$U_{\text{thresh}} = \sqrt{\frac{\sigma_s}{\rho_w \text{CSF}}},$$

where σ_s is the tensile strength of the substrate (the limiting strength when growing on carbonate reefs; Madin 2005) and ρ_w is the water density (approx. $1030\ \text{kg m}^{-3}$ for seawater). A colony is predicted to be dislodged when the maximum water velocity generated by passing waves exceeds U_{thresh}.

In this study, we model post-disturbance assemblage structure as a function of disturbance intensity, using the existing empirical measurements of CSF for three common coral species at Lizard Island, the Great Barrier Reef (figure 1*a*). The species exhibit a broad range of colony shapes, from mechanically robust *Acropora palifera* (low CSF) to mechanically vulnerable *Acropora gemmifera* (intermediate CSF) and to *Acropora hyacinthus*, which grows into delicate, competitively dominant morphologies (high CSF). Maximal water velocities generated by different disturbance intensities (presented as wave height, wind speed and storm category) have previously been modelled for the study site (Madin *et al.* 2006). In addition, we contrast two reef substrate strength scenarios: present day (based on empirical data) and under more acidic conditions where we halve reef strength as a conservative estimate of future change (detailed below). The results provide a mechanistic view of how an existing coral assemblage might respond to future disturbance events.

2. MATERIAL AND METHODS

To explore the changes in assemblage structure associated with different disturbance intensities, we used the existing estimates of mechanical vulnerability (CSF) and size (planar area) for 1158

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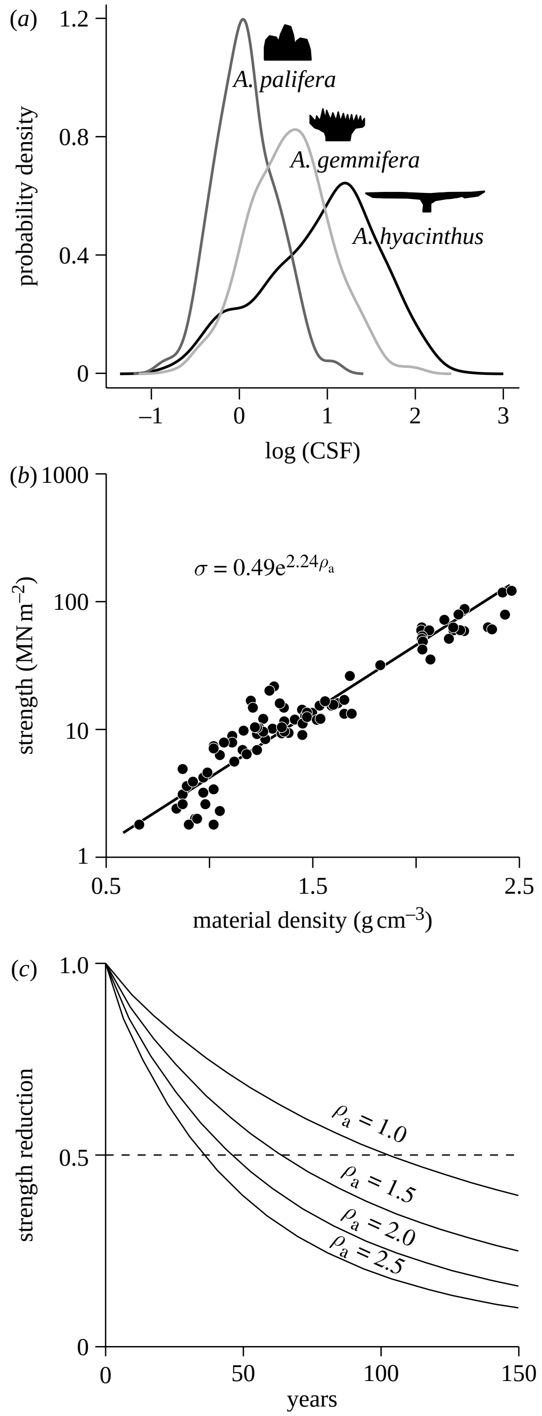

Figure 1. (*a*) Probability densities of log-transformed colony CSF levels illustrating the different distributions of mechanical vulnerability for the three study species. Smaller colonies of all species tend to have low CSF levels, and increases in CSF depend on species-specific morphological changes with growth. (*b*) Synthesis of coral skeleton density and compressive strength of coral skeleton samples ($n=91$) from three studies investigating a range of coral species and morphologies (see Chamberlain 1978; Scott & Risk 1988; Madin 2004). (*c*) Projected loss in the strength of coral skeleton with four different material densities (ρ_a) assuming that density decreases at 0.36% yr^{-1} (Cooper *et al.* 2008).

colonies on the exposed southeast reef at Lizard Island (Madin & Connolly 2006). To run the model, the colonies were randomly assigned substrate strengths (see below), and the proportion of colonies dislodged by a given wave height was calculated according to the inequality: $U_{\text{wave}} \geq U_{\text{thresh}}$. U_{wave} can be estimated using linear wave theory and scales linearly with wind speed at the fetch-limited study site (Madin *et al.* 2006). The randomization was repeated 10^6 times per wave height to estimate the distribution of survivorship, from which medians and 95% confidence intervals were calculated for a given velocity.

For our present-day strength scenario, substrate strengths were assigned to colonies from a density distribution based on empirical measurements taken at the study reef (lognormal mean 5.3 log (N m^{-2}), s.d. 0.35; Madin 2005). We were unable to find predictions for future reef substrate weakening due to acidification. However, the reef substrate is composed primarily of high-magnesium calcite (Macintyre & Marshall 1988), a less stable form of calcium carbonate than the aragonitic skeleton of living corals. Therefore, we used the estimates of coral skeleton weakening via acidification as a conservative approximation for the reef substrate. A recent study found that a 21% reduction in calcification rate in the scleractinian coral genus *Porites* led to a 6% reduction in skeletal density over a 16-year period, or an apparently modest 0.36% reduction per year (Cooper *et al.* 2008). However, small reductions in density result in dramatic weakening of carbonate materials (Wainwright *et al.* 1982). Indeed, a synthesis of paired coral skeleton density (ρ_a)/compressive strength (σ) measurements from three studies (Chamberlain 1978; Scott & Risk 1988; Madin 2004) elucidated an exponential relationship for coral skeleton (figure 1*b*). Porosity values in Chamberlain (1978) and Scott & Risk (1988) were converted into density values using $\rho_a = 2.94 \times (1 - porosity)$ because the maximum density of aragonite is approximately 2.94 g cm^{-3} (Hughes 1987). Compressive strength of carbonate materials is typically an order of magnitude greater than tensile strength, but both scale similarly with density (Madin 2004). Therefore, assuming similar rates of future density decrease as found by Cooper *et al.* (2008), projections show coral strength halving within the next 50–100 years (figure 1*c*) depending on species' characteristic skeletal density and ignoring other nonlinear considerations such as solubility thresholds (Hoegh-Guldberg *et al.* 2007). We therefore halved the present-day substrate strength measurements as a conservative illustration of future reef conditions (again, because reef substrate diagenetic processes are expected to be more vulnerable to acidification than coral skeleton synthesis).

3. RESULTS AND DISCUSSION

Dramatic species-specific differences exist in the expected numbers of colonies remaining in the post-disturbance assemblage following larger disturbance events for the present-day strength scenario (figure 2*a*, solid curves). For instance, a direct hit by a category 1 cyclone (S1) is expected to dislodge almost 50% of the existing *A. hyacinthus* population, but only 5% of the *A. palifera* population. These trends are driven by the way in which species characteristically distribute colony shape above the substrate as they grow (Madin & Connolly 2006), whereby top-heavy colonies with smaller attachment areas are much more prone to hydrodynamic dislodgement than colonies with wide bases and low profiles. For instance, the table-shaped morphology of *A. hyacinthus* is particularly good at 'overtopping' (growing up and over) and outcompeting neighbours (Baird & Hughes 2000) and provides more habitat structure for reef organisms; however, it is disproportionally affected by hydrodynamic force. Consequently, this population is expected to display dramatic decreases in colony size following relatively small disturbance events (figure 2*b*), resulting in increases in relative dominance (abundance and cover) of the other two species (figure 2*c*,*d*).

Owing to the hierarchy in mechanical vulnerability among these species, each is expected to dominate the post-disturbance assemblage at some point over the disturbance continuum (figure 2*d*). Larger colonies of *A. gemmifera* are more vulnerable to hydrodynamic force than *A. palifera* due to their

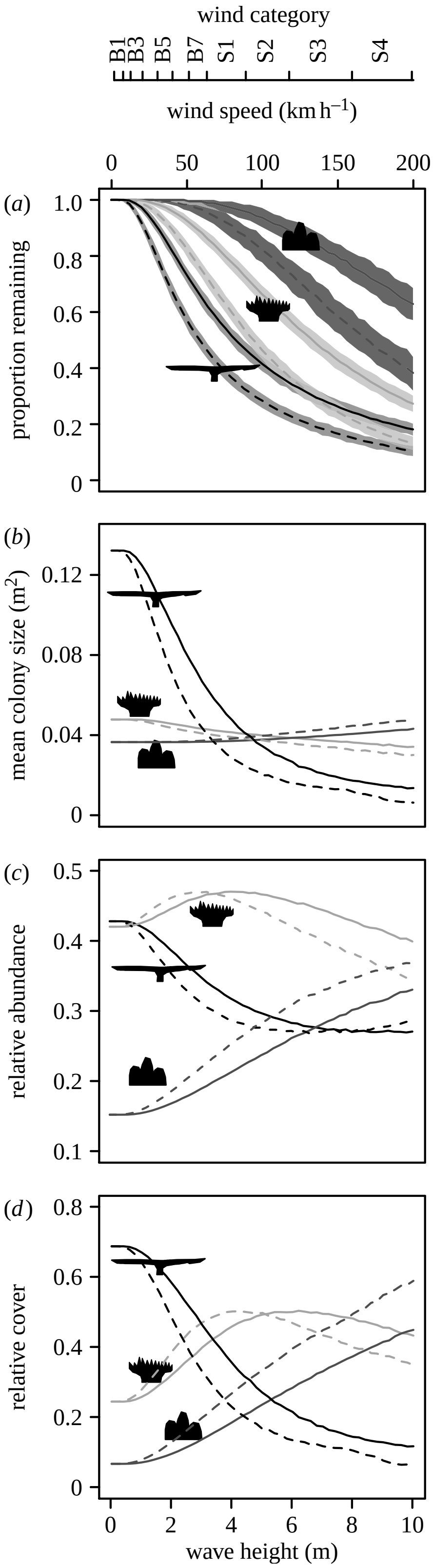

Figure 2. Forecasted ecological changes in post-disturbance coral assemblages. Solid curves represent assemblage changes based on the present-day substrate strength; dashed curves represent halving of strength due to ocean acidification. (*a*) The proportion of colonies expected to remain as a function of wave height, wind speed and wind category (Beaufort [B] and Saffir-Simpson [S] scales); grey bands indicate 95% confidence intervals, which are not presented in (*b*–*d*) for clarity. (*b*–*d*) Mean colony size, relative abundance and relative cover of colonies remaining in post-disturbance assemblage, respectively.

narrower bases relative to their vertical mass distribution. Therefore, at greater disturbance intensities, the *A. gemmifera* population declines along a similar trajectory to that of the *A. hyacinthus* population. The mean colony size of *A. palifera* colonies actually tends to increase following larger disturbances, because larger colonies tend to have wider bases and lower profiles and are therefore more likely to survive. Reducing substrate strength by half, i.e. simulating acidification conditions 50–100 years into the future, exacerbated changes in assemblage structure by causing assemblage trends to shift (leftwards) to lower disturbance intensities than are predicted under the present-day conditions (figure 2, dashed lines). Consequently, populations are expected to lose up to 20% more colonies than under the present-day strength conditions (figure 2*a*), and switches in the dominance hierarchy happen at much lower disturbance intensities (figure 2*d*). These shifting trends will give mechanically adapted species a substantial advantage in the post-disturbance assemblages. Furthermore, the shifts caused by acidification will be compounded by predicted changes in the future storm intensity regimes.

Relative per cent cover, relative abundance and colony size are critical for the recovery of both colonies and populations following disturbances. For example, larger colonies tend to be more resistant to physical abrasion and disease, have greater competitive and reproductive potential, and command greater proportions of limited substrate space (Jackson 1979; Hughes 1984). Increases in available space and smaller (competitively weaker) colonies facilitate growth of other benthic reef-dwelling species, including fast-growing algae and soft corals, which can preclude coral population recovery (McCook *et al.* 2001). Moreover, the number of associated species supported by a colony scales with both colony size and morphological complexity (Luckhurst & Luckhurst 1978). For example, many reef fishes require spatial heterogeneity for their nursery habitats (Almany 2004), including juvenile parrotfish, a functional group that is important for freeing surfaces from algae for coral settlement (Mumby 2006). The post-disturbance dominance of mechanically robust, morphologically simple, coral species is expected to lead to decreased whole-reef diversity and functional redundancy with cascading ecosystem effects.

These mechanistic expectations, which are based on the physical constraints imposed by the environment, elucidate the fundamental boundaries within which other important factors operate to structure communities (e.g. herbivory, competition, bleaching, disease). An important next step will be to expand upon this work to include demographic rates (i.e. recruitment, growth, background mortality) so as to track coral population growth and post-disturbance recovery in relation to different climate change scenarios. Understanding physical constraints and their effects on coral assemblage structure in the context of pressing environmental factors (acidification and hydrodynamic disturbance regimes) provides a useful basis for assessing reef vulnerability.

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