

Ecological consequences of major hydrodynamic disturbances on coral reefs

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A recent tsunami^{1,2} and an apparent increase in the frequency of severe tropical storms^{3–5} underscore the need to understand and predict the ecological consequences of major hydrodynamic disturbances⁶. Reef corals provide the habitat structure that sustains the high biodiversity of tropical reefs⁷, and thus provide the foundation for the ecosystem goods and services that are critical to many tropical societies^{6,8}. Here we integrate predictions from oceanographic models⁹ with engineering theory, to predict the dislodgement of benthic reef corals during hydrodynamic disturbances. This generalizes earlier work^{10,11}, by incorporating colonies of any shape and by explicitly examining the effects of hydrodynamic gradients on coral assemblage structure. A field test shows that this model accurately predicts changes in the mechanical vulnerability of coral colonies, and thus their size and shape, with distance from the reef crest. This work provides a general framework for understanding and predicting the effects of hydrodynamic disturbances on coral reef communities; such disturbances have a major role in determining species zonation^{12,13} and coexistence¹⁴ on coral reefs, and are critical determinants of how coral assemblages will respond to changes in the frequency and intensity of tropical storms associated with a changing climate^{3–5,15}.

A framework to predict whole-colony dislodgement of corals caused by hydrodynamic force requires three elements^{16,17}: (1) engineering theory for translating levels of ambient water motion into internal mechanical stress within the coral; (2) measures of the maximum stress that colonies can withstand before breakage (that is, material strength); and (3) estimates of the probability that the maximum tolerable stress is exceeded where colonies live on the reef. For corals, internal tensile stress at the base and periphery of a colony—produced by hydrodynamic drag force (see Supplementary Information)—limits mechanical integrity in the vast majority of cases¹⁸. Because reef substrate is substantially weaker than coral skeleton (particularly for morphologies prone to hydrodynamic dislodgement), the capacity to resist dislodgement by a hydrodynamic force is generally limited by the tensile strength of the reef substrate¹⁸. Therefore, if the basal tensile stress produced by a hydrodynamic event exceeds the substrate strength, dislodgement is expected. Using cantilever beam theory, and approximating the basal cross-sectional area of a colony as an ellipse, we can derive a dimensionless expression for the threshold mechanical vulnerability of colonies:

$$\frac{\sigma_s}{U^2 \rho_w} \leq \frac{16}{d_{\parallel}^2 d_{\perp} \pi} \int_0^h y w(y) dy \quad (1)$$

(see Methods for derivation). U is horizontal water velocity, σ_s is the tensile strength of the substrate, ρ_w is water density, d_{\parallel} is the width of the base of the colony parallel to water flow, d_{\perp} is the width of the

base perpendicular to water flow, y is distance above the substrate, and h is the height of the colony. $w(y)$ is the projected width (that is, excluding interstitial space between branches) of the colony perpendicular to water flow as a function of distance y above the substrate. The left side of the inequality is a dimensionless quantity describing the mechanical threshold imposed by the environment, which we term the Dislodgement Mechanical Threshold (*DMT*). The right side is a dimensionless quantity describing the colony's mechanical vulnerability, which we term the Colony Shape Factor (*CSF*). Dislodgement occurs when a colony's *CSF* exceeds the *DMT* imposed by a hydrodynamic event.

To test the model, we measured *CSF* for 1158 colonies from three coral species on an exposed coral reef at Lizard Island in the northern region of the Great Barrier Reef (see Methods). These species (*Acropora hyacinthus*, *Acropora gemmifera* and *Acropora palifera*) occur broadly along hydrodynamic gradients, and they have very different colony shapes. Thus, they are likely to exhibit substantial differences in *CSF*, and consequently to be ideal for testing a model of structural stability in reef corals. Using an existing 37-yr hindcast of hourly horizontal water velocity generated by waves over the study reef at 4-m increments⁹, and an existing *in situ* measurement of the average tensile strength of reef substrate for the study site¹⁸ ($\sigma_s = 0.2 \text{ MN m}^{-2}$) we used expression (1) to compare the mechanical threshold (*DMT*) imposed by the maximum hydrodynamic event during the year before the field test with the *CSFs* of colonies on the reef. This predicted threshold is highly consistent with field data on the distribution of *CSF* in our study species: *CSFs* are at or below the threshold for all species (Fig. 1). Indeed, *A. hyacinthus* provides exceptionally strong support for the model: the predicted *DMT* threshold corresponds extremely well with the maximum observed *CSF* values, closely following the gradient in maximum *CSF* with distance from the reef crest (solid line, Fig. 1a).

The differences among species in the extent to which they approach the predicted threshold (for example, *A. hyacinthus* abutting the threshold, but *A. palifera* remaining well below it) are also consistent with the model. This is apparent from differences among species in how colonies change shape with increasing size (Fig. 2). For *A. hyacinthus*, *CSF* increases with increasing colony size (Spearman's $\rho = 0.733$, $P < 0.001$, $n = 496$), so that colonies grow into increasing categories of vulnerability (Fig. 2a). For *A. gemmifera*, colonies beyond ~25 m of the reef crest approach the threshold more closely than colonies within 25 m of the crest (Fig. 1b). This pattern is caused by differences in how colonies of this species change shape as they grow. Towards the reef back, *A. gemmifera* adopt a tabular growth form, and become less stable as they grow (Fig. 2b, solid points; Spearman's $\rho = 0.491$, $P < 0.001$, $n = 311$). Consequently, like *A. hyacinthus*, the largest colonies approach the threshold. In contrast, near the crest, adults adopt a more digitate growth form, so they

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retain low CSF values with increasing size (Fig. 2b, open points; Spearman's $\rho = 0.227$, $P = 0.003$, $n = 176$), and do not approach the threshold shown in Fig. 1. Finally, *A. palifera* exhibits pronounced increases in attachment area relative to projected area as a colony grows, which actually causes CSFs in this species to decrease as colony size increases (Spearman's $\rho = -0.258$, $P < 0.001$, $n = 175$; Fig. 2c). Consequently, like the digitate form of *A. gemmifera*, they never approach the threshold.

Using the largest hydrodynamic event captured in the 37-yr database (tropical cyclone Rona, a category 3 on the Saffir-Simpson scale, which passed 200 km to the South in 1999), we have also projected a plausible mechanical threshold produced by a 'moderate' cyclone (dashed line, Fig. 1). Our predictions indicate that many larger colonies from the *A. hyacinthus* and *A. gemmifera* populations would have been dislodged, but other large colonies would have remained, owing to spatial differences in maximal water velocity over the reef, as well as variation in how CSF changes with size for colonies that adopt different growth forms (Fig. 2, red points). The difference between the Rona and the 2002 thresholds also helps to explain why a large number of *A. hyacinthus* colonies approach the 2002 threshold so closely. Specifically, published estimates of colony growth for *A. hyacinthus* colonies, and increases in CSF with increasing colony size (Fig. 2a), indicate that *A. hyacinthus* colonies could readily double their CSFs within 1–2 yr, an increase comparable in magnitude to the difference between the two thresholds shown in Fig. 1a (see Supplementary Information for calculation). Thus, one would expect the largest *A. hyacinthus* colonies to grow beyond (and be removed

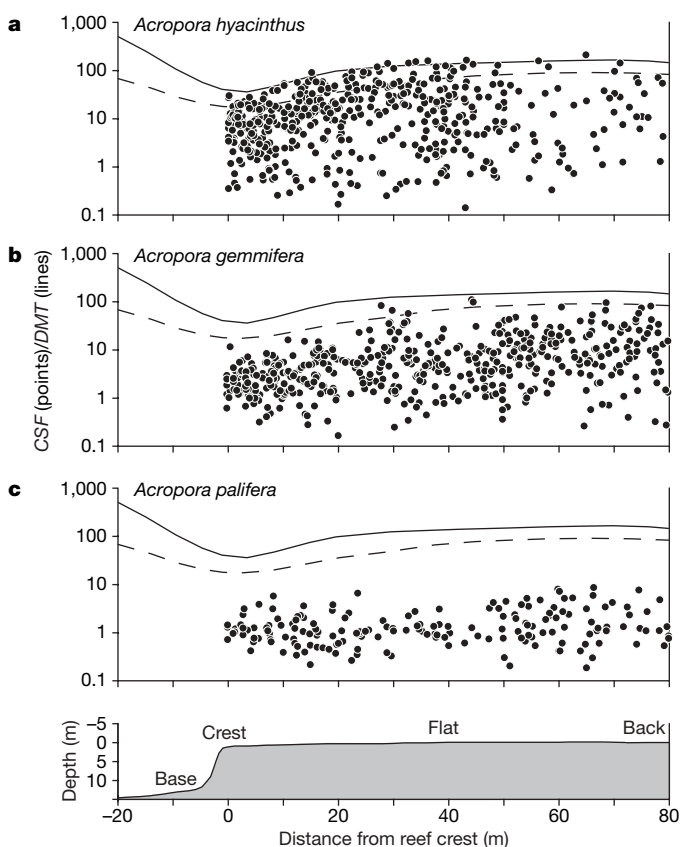


Figure 1 | Colony CSF as a function of colony distance from the reef crest. **a**, *A. hyacinthus*; **b**, *A. gemmifera*; **c**, *A. palifera*. Calculated CSFs are represented as points. The prediction of the DMT expected to have been imposed by the largest hydrodynamic event in the year before the field test (September 2002; see text for details) is represented by a solid line. The dashed line is the predicted DMT for Cyclone Rona (February 1999)—the most significant hydrodynamic event captured in the 37-yr oceanographic hindcast of the test site (see text for details). The reef depth profile is shown in the bottom panel.

by) annual thresholds in most years, and thus for these thresholds to correspond closely with the maximum observed CSF for this species, as in Fig. 1a. In contrast, the slower growing and less mechanically vulnerable *A. gemmifera* would probably take many times longer, on average, for comparable increases in CSF to occur (see Supplementary Information for calculation). Thus, even though tabular forms of *A. gemmifera* become more vulnerable as they grow, one would expect fewer colonies to reach the threshold for dislodgment in any given year, relative to *A. hyacinthus*, as Fig. 1 suggests.

Calibrating a model of structural stability for corals makes possible the estimation of colony dislodgement rates from time series of hydrodynamic disturbances. Specifically, maximum water velocities on reefs are wave-driven, and waves within the GBR lagoon are predominantly wind-generated and thus implicitly related to regional meteorological conditions⁹. Therefore, we should be able to approximate rare hydrodynamic disturbances and resulting colony dislodgement as a Poisson process¹⁹. To test this, we used the 37-yr database of water velocities and fitted exponential distributions to the frequency distributions of the waiting times in years between the rare wave events that would theoretically dislodge a colony of a given CSF. This analysis confirms that an exponential distribution closely approximates the distribution of waiting times (see Supplementary Information), and it allows us to calculate (from the fitted rate parameter of the exponential distribution, μ) estimates of annual

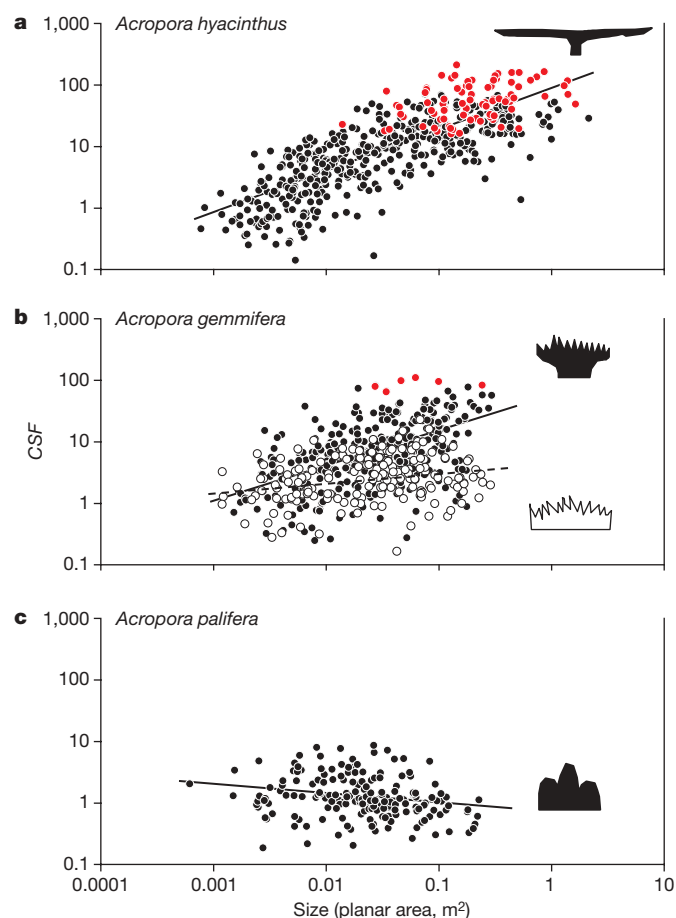


Figure 2 | Colony CSF as a function of colony size for three morphologically different coral reef species. **a**, *A. hyacinthus*; **b**, *A. gemmifera*; **c**, *A. palifera*. Least-squares regression lines are shown to illustrate trends with size. Silhouettes are examples of projected shapes for larger colonies. For *A. gemmifera*, open points indicate colonies living between the reef crest and 25 m, and solid points indicate colonies living beyond 25 m of the crest. Dashed and solid regression lines, respectively, indicate differences in how these colonies change shape with increasing size. Red points indicate the colonies above the estimated DMT in Fig. 1 for Cyclone Rona.

colony dislodgement caused by wave-induced disturbances on a reef platform, for colonies of any size and shape (Fig. 3). Specifically, if μ is the rate of occurrence of wave events whose threshold exceeds some colony's *CSF*, then the corresponding annual probability of dislodgement is $1 - e^{-\mu}$ (ref. 20). Colonies with high *CSF* (that is, mechanically vulnerable colonies) are dislodged by smaller waves that propagate further over the reef, and thus their mortality risk decreases gradually with distance from the crest. Indeed, for particularly vulnerable forms, such as those with a *CSF* of 250 or 500, annual mortality risk is approximately constant over much of the reef platform. In contrast, colonies with low *CSF* are dislodged by only very severe events. Because those events are associated with large waves, and because large waves break and attenuate rapidly^{9,21}, mortality risk for low *CSF* colonies drops off very rapidly with distance behind the reef crest.

Understanding how coral assemblages respond to hydrodynamic disturbances is essential for explaining zonation on present-day coral reefs, as well as for projecting how coral reef communities will change

in response to predicted increases in the frequency and intensity of tropical storms^{3–5}. A major obstacle to achieving both objectives has been our inability to estimate the effects of major disturbances on the mortality rates of different coral species. Whole-colony dislodgement occurs during episodic and very rare events. Consequently, direct estimates of mortality during such events can come from only the very few existing long-term monitoring studies that record abundances at the species level²² and our ability to extrapolate from these studies is constrained, because logistical considerations limit them to relatively small sample sizes and spatial scales. Our study offers a solution to this longstanding problem: by calculating the *CSF* of key reef coral species, the strength of the substrate to which they attach, and the attenuation of waves across reef platforms, we can predict the changes in size structure and species composition of coral assemblages caused by recent and future hydrodynamic disturbances. Such a framework is essential for understanding the dynamics of coral assemblages over space and time^{12–14}. This understanding can, in turn, facilitate informed policy and management decisions that aim to protect the world's coral reefs^{15,23}.

METHODS

Cantilever beam theory. For a given horizontal water velocity, the drag force F acting on an attached colony is directly proportional to the colony's area, A , projected onto a plane perpendicular to the direction of water flow¹⁶:

$$F = \left(\frac{\rho_w C_d}{2} \right) U^2 A \quad (2)$$

(see Supplementary Information). U is water velocity, ρ_w is water density (approximately 1025 kg m^{-3} for seawater) and C_d is the drag coefficient (approximately 1.0 for corals; see Supplementary Information). There is neither sufficient distance nor time as an orbital wave passes for a significant vertical velocity gradient to form at the scale of a colony (see Supplementary Information). Therefore, we assume that water motion acts similarly on all regions of a colony's projected area, in which case the maximum bending moment M is:

$$M = \frac{\rho_w U^2}{2} \int_{y=0}^h y w(y) dy \quad (3)$$

where h is colony height, y is vertical distance from the substrate, $w(y)$ is the projected width (that is, excluding interstitial space) of the colony perpendicular to water flow as a function of height y above the substrate.

The maximal tensile stress, σ_t , produced by bending a coral colony is given by²⁴:

$$\sigma_t = \frac{M d_{||}}{2 I_{xx}} \quad (4)$$

where M is the bending moment, $d_{||}$ is the width of the base of the colony parallel to water flow, and I_{xx} is the second moment of area for the colony about the substrate. Assuming the cross-sectional area at the colony base is approximately elliptical, the second moment of area is²⁴:

$$I_{xx} = \frac{\pi d_{||}^3 d_{\perp}}{64} \quad (5)$$

d_{\perp} is the width of the base perpendicular to water flow. Combining equations (4) and 5 yields:

$$\sigma_t = \frac{32 M}{\pi d_{||}^2 d_{\perp}} \quad (6)$$

Substituting equation (3) for M in equation (6), then rearranging, we obtain:

$$\sigma_t = \frac{16 \rho_w}{\pi d_{||}^2 d_{\perp}} U^2 \int_{y=0}^h y w(y) dy \quad (7)$$

Dislodgement occurs when this quantity equals or exceeds the tensile strength of the reef substrate, σ_s . Setting up this inequality, and rearranging, yields expression (1) in the main text.

Field test. The field test was conducted at Lizard Island in the northern Great Barrier Reef (GBR) lagoon, Australia. The study site, the southeastern reef, is typical of exposed reef platforms in this region; it is composed of steep reef slopes, shallow exposed crests and extensive reef flats. Three species of scleractinian reef

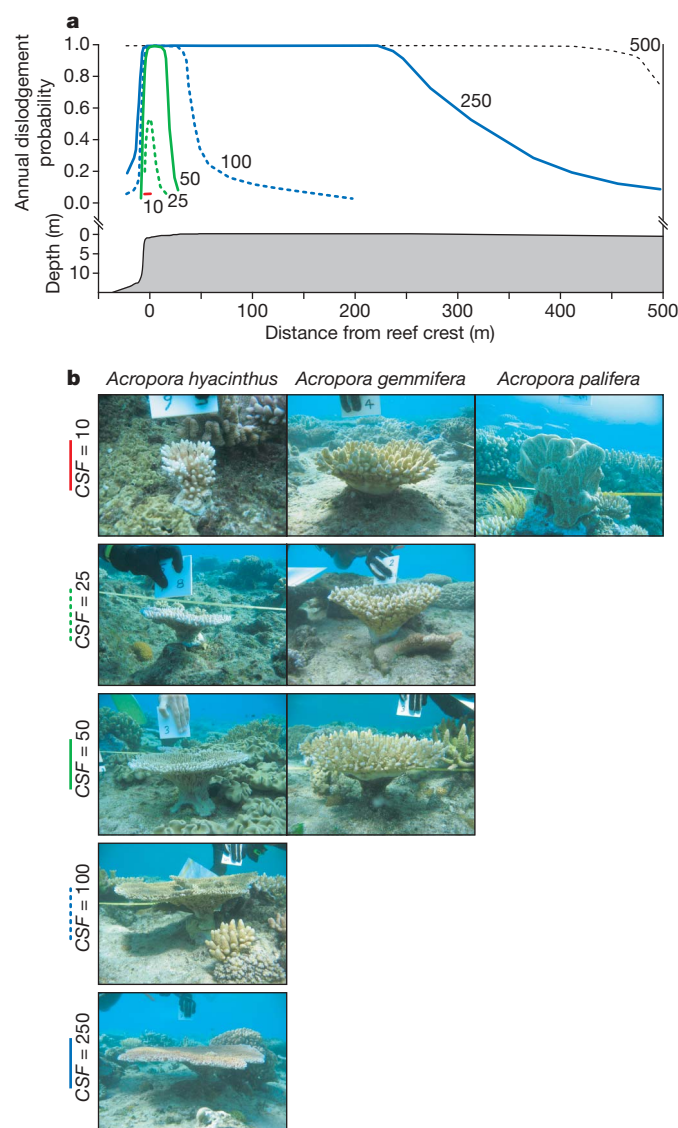


Figure 3 | Annual probabilities of colony dislodgement predicted from the 37-yr history of water velocity on the study reef. a, Yearly dislodgement estimates as a function of distance from the reef crest for six *CSF* values (10, 25, 50, 100, 250 and 500) that span the realistic range of values for a wave-exposed reef platform **b**, Images of colonies of the three species with *CSF* values approximately equal to five of those represented in the upper panel (no colonies at the study site were near *CSF* = 500).

coral were selected at these sites on the basis of two criteria: (1) individuals were abundant from the reef crest to 80 m across the flat towards the back of the reef, and (2) the species each had characteristic morphologies which were likely to exhibit different changes in *CSF* with increasing size (Fig. 3b). The first species, *Acropora hyacinthus*, is fast-growing and forms horizontal tables up to several square metres in size, and is typically attached to the substrate by a short central stalk. The second species, *Acropora gemmifera*, forms digitate colonies with a geometrically variable substrate attachment. The final species, *Acropora palifera* (subgenus *Isopora*), forms sturdy submassive mounds with the largest attachment area relative to colony size.

Eight belt transects (each 80 m long and 2 m wide) were laid perpendicular to the crest and parallel to the prevailing wave motion. The transects extended across the reef flat from the crest towards the reef back and all colonies of the three study species within the 160-m² transect areas were digitally photographed and their distance from the reef crest was recorded. For each colony, photographs were taken from above, as well as parallel and perpendicular to the reef crest (and thus the direction of prevailing wave climates⁹) to obtain the digital information required to calculate *CSFs*. For each photograph, the colony's outline, its basal points (where the outline of the colony coincided with the substrate) and the length of a 10 cm scale-plate were digitised and recorded as xy-coordinates. A computer program (available from the authors) measured the area encompassed by the colony outline, the width of the colony and the dimensions of the base from the digital images, then calculated the bending moment (per water velocity squared) numerically by calculating the product of each pixel within the colony outline and the height of that pixel from the colony base, and then summing this quantity over all pixels in the colony outline (equation (4)). Using these quantities, along with the basal width parallel to flow, $d_{||}$ (calculated by the same program), the *CSF* for each colony was calculated according to expression (1). Planar area, which gives an indication of the two-dimensional space occupied by a colony, was estimated from the colony photograph from above.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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