

**LETTER**

## Mechanical vulnerability explains size-dependent mortality of reef corals

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**Abstract**

Understanding life history and demographic variation among species within communities is a central ecological goal. Mortality schedules are especially important in ecosystems where disturbance plays a major role in structuring communities, such as coral reefs. Here, we test whether a trait-based, mechanistic model of mechanical vulnerability in corals can explain mortality schedules. Specifically, we ask whether species that become increasingly vulnerable to hydrodynamic dislodgement as they grow have bathtub-shaped mortality curves, whereas species that remain mechanically stable have decreasing mortality rates with size, as predicted by classical life history theory for reef corals. We find that size-dependent mortality is highly consistent between species with the same growth form and that the shape of size-dependent mortality for each growth form can be explained by mechanical vulnerability. Our findings highlight the feasibility of predicting assemblage-scale mortality patterns on coral reefs with trait-based approaches.

**Keywords**

Biomechanics, colonial, demography, disturbance, life history, mortality, reef coral.

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**INTRODUCTION**

The demographic strategies of species that make up ecological communities have important ecological and evolutionary implications. Within-community variation in such traits, such as the age- or size-dependence of vital rates, influences community structure and dynamics (McGill *et al.* 2006; Litchman & Klausmeier 2008). However, separately estimating the demographic rates of each species in an assemblage is often logistically impossible, particularly when the assemblage is species-rich. Consequently, recent work in community ecology has focused intensively on the extent to which readily measurable species traits, such as adult body size and egg or seed size, can provide information about the likely demographic strategies employed by different species (Westoby & Wright 2006). This approach circumvents the need for logistically unfeasible species-by-species calibration of community-dynamics models. Such approaches have been used successfully, particularly in plant ecology, to capture fundamental life history and energetic trade-offs (Littler *et al.* 1983; Wright *et al.* 2004), coexistence mechanisms (Adler *et al.* 2013) and community assemblage patterns (Shipley 2010). Here, we test a trait-based approach to explaining interspecific variation in how mortality rates of reef corals vary with colony size; such differential susceptibility to mortality agents is integral to classical explanations for species coexistence on coral reefs and in other high-diversity systems (Connell 1978).

Mortality schedules are key components of life history and population ecology, and are also influenced directly by envi-

ronmental change (van Mantgem & Stephenson 2007). Mortality schedules determine longevity, and therefore influence the allocation of resources to growth, maintenance and reproduction that maximises lifetime reproductive output (Werner & Caswell 1977), as well as population structure (Werner & Gilliam 1984). At the species scale, mortality and fecundity schedules jointly determine the generation time of a species, and therefore influence the potential rate of evolution (Martin & Palumbi 1993). Therefore, understanding how mortality varies throughout an organism's life remains at the core of life history theory and population ecology. Age-dependent mortality curves are thought to have a limited number of possible shapes. Juvenile mortality rates often are higher than adult mortality rates, particularly for species with low levels of parental investment and numerous offspring and when recruitment is space-limited (Roughgarden *et al.* 1985). At the other end of the life cycle, mortality in unitary organisms consistently increases again at older ages for a variety of reasons, including the accumulation of deleterious mutations, biomechanical wearing, loss of physiological function and self-thinning of cohorts. When species exhibit both of these age-dependent responses, a 'U-shaped' or 'bathtub-shaped' mortality curve results. This form of mortality is well documented for many organisms (Paranjpe & Rajarshi 1986).

For colonial organisms such as reef corals and some plants, however, demographic rates such as growth, fecundity and mortality tend to depend more strongly on size (number of individual modules such as ramets or polyps) than age (Werner & Caswell 1977; Hughes & Connell 1987).

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Modularity allows organisms to escape allometric constraints that limit the size of individual modules (Jackson 1979), and consequently an organism's demographic contributions should be dependent on the number of modules (Hall & Hughes 1996). Modularity also introduces several life history possibilities not available to unitary organisms, such as the fission and fusion of colonies, which complicate demographic trajectories of colonies through time (Hughes & Connell 1987). In addition, mortality can occur at the level of the module, resulting in the partial mortality of colonies (Hughes & Connell 1987). Given that colonial organisms can exhibit both whole-colony and partial mortality, divergences from mortality models based on the biology of unitary organisms are to be expected.

Scleractinian corals are the principal framework builders on coral reefs, and provide much of the habitat structure on which coral reef organisms depend. With few exceptions, they are colonial, with individual modules (polyps) propagating both asexually (colony growth), and founding new colonies by sexual reproduction and fragmentation. Previous studies have found that whole-colony mortality rates of reef corals decline monotonically with size (Fig. 1, solid line; Connell 1973; Hughes & Connell 1987). Such a pattern was predicted to be a consequence of a module mortality rate that is independent of colony size, such that larger colonies are likely to experience mortality of some, but not all of their modules (i.e. partial colony mortality), whereas small colonies are more likely to die completely, or to escape injury entirely (Fig. 1; Jackson 1979; Hughes & Jackson 1985). For instance, Hughes & Jackson (1980) found that colonies suffering partial mortality during a year disproportionately belonged to larger size classes.

Reef-building corals are exposed to a variety of mortality agents, including damage and dislodgement by tropical storms (Porter *et al.* 1981), scouring and burial by sand and rubble (Lenihan *et al.* 2011), predation (Rotjan & Lewis 2008), tissue death by disease (Garret & Ducklow 1975) and starvation due to the breakdown of symbiosis with zooxanthellae at elevated

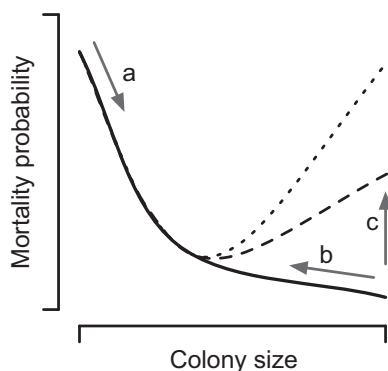
water temperatures, a phenomenon known as bleaching (Glynn 1993). Some of these mortality agents have been substantially exacerbated by climate change and other anthropogenic effects on reefs (Hughes *et al.* 2003). For example, warmer surface waters increase the prevalence of coral bleaching and disease (Hoegh-Guldberg *et al.* 2007). However, other types of disturbance have occurred routinely for millennia on reefs. For instance, wave forces generated by winds, particularly by tropical storms and cyclones, are often the dominant process acting to limit coral colony size (Done 1983) and strongly influence coral cover change (De'ath *et al.* 2012). Colony dislodgment by routine storms typically results in mortality, although unattached colonies may live for days or weeks (Knowlton *et al.* 1981), and can even reattach and reoccupy a smaller size class although the probability of reattachment is generally low (Smith & Hughes 1999). Furthermore, the biomechanical vulnerability of corals to storms differs among species and individuals as a function of colony shape, with susceptible species typically becoming increasingly vulnerable to dislodgment as they grow (Massel & Done 1993; Madin & Connolly 2006). In contrast, other mortality agents, such as thermal bleaching and crown-of-thorns starfish predation, are not size-selective (Moran 1986; Baird & Marshall 2002). Therefore, if hydrodynamic dislodgment is a major cause of routine whole-colony mortality, then the differential susceptibility of large colonies of different growth forms could substantially alter mortality schedules. Specifically, species that become more mechanically vulnerable with size should exhibit bathtub-shaped mortality patterns (Fig. 1c), whereas more robust species should exhibit the monotonically decreasing mortality rates observed in previous work.

Here, we test whether the mortality schedules of coral species depend on how their vulnerability to mechanical disturbance changes as they grow. We use a broad range of colony sizes for 11 Indo-Pacific coral species, including multiple representatives of each of five colony growth forms, to determine whether and how colony shape influences mortality. Our results reveal that variation in mortality rate among coral species is strongly and predictably dependent upon the key trait of colony morphology, in a manner consistent with the predictions of theory that predicts vulnerability to dislodgment from biomechanical first principles (Madin & Connolly 2006).

## MATERIAL AND METHODS

### Field data

Thirty colonies of each of 11 scleractinian coral species were first tagged at Lizard Island, Australia, on the reef crest between South and Palfrey Islands (14.699839 °S, 145.448674 °E) in November 2009. The study site is obliquely exposed to the south easterly trade winds and oceanic storms that generate routine large swells at Lizard Island. Based on a recent description of the coral assemblage structure at this site (Dornelas & Connolly 2008), species were selected to include multiple representatives of five different growth forms: tabular (*Acropora cytherea* and *A. hyacinthus*), arborescent (*A. intermedia* and *A. robusta*), corymbose (*A. spathulata*, *A. millepora*,



**Figure 1** Alternative models of coral mortality. Past studies have shown that whole-colony mortality rates tend to decrease monotonically with size [indicated by the arrow at (a)]. Monotonic decrease is hypothesised to occur because mortality agents act independently at the module (polyp) scale and therefore have a greater chance of killing smaller colonies and reducing the size of larger colonies [illustrated by the leftward arrow at (b)]. Storm wave mortality processes also cause whole-colony dislodgement and death, which can lead to higher mortality rates in large colonies for some species [upward arrow at (c)], potentially generating bathtub relationships of mortality rate with size.

and *A. nasuta*), digitate (*A. cf. digitifera* [‘fat dig’ morph: Wolstenholme *et al.* (2003)] and *A. humilis*) and massive (*Goniastrea pectinata* and *G. retiformis*). The *Acropora* species were identified according to Wallace (1999) and the *Goniastrea* species according to Veron (2000). Colonies were photographed from above with a scale plate for estimation of planar area. Colonies were revisited for three subsequent years and rephotographed (2010–2012). There were no tropical cyclones, mass bleaching events, crown-of-thorns starfish or disease outbreaks during the study period. Thus, our study documents ‘background’ mortality, which typically accounts for the majority of mortality events in reef coral assemblages (Hughes & Connell 1999). Dead or missing colonies were replaced with new, tagged colonies in order to maintain approximately 30 colonies per species every year. Colonies were considered dead when the skeleton of the tagged colony was found. Following an exhaustive search for tagged colonies using photographs from prior years, missing colonies were categorised as ‘gone,’ if the exact position formerly occupied by the colony could be ascertained (implying that the colony was dislodged). The exact position of a total of 14 colonies were not identified over the course of the study, due mainly to substantial community change in the colony’s vicinity that made its original position difficult to triangulate unambiguously. For the results presented here, those 14 colonies were excluded; however, repeating our analyses considering those colonies as ‘gone’ had no effect on our conclusions: model selection identified the same best-fitting models, and all relationships identified as statistically meaningful in the analyses below remained so. Photographs were corrected for barrel distortion, colonies were outlined, and the scale used to calculate planar area. Area estimates were (natural) log-transformed for analyses. Mortality data were pooled across the 3 years for analysis, resulting in 73 to 110 observations of annual survival or mortality for each species (see Appendix S1).

### Model selection

A generalised linear model (GLM) with a binomial response variable (mortality) and logit link function was used to determine which of the proposed models best predicted mortality as a function of colony size (planar area). We compared models with three alternative forms of size-dependent mortality: where the mortality response was a quadratic function of colony size (allowing for bathtub-shaped or hump-shaped relationships), where it was a linear function of colony size (allowing only monotonically decreasing or increasing relationships), and where mortality was independent of colony size. For each of these three forms of size dependence, we fitted a model where each species had its own size-dependent response to mortality, and a model where species with the same growth form had the same size-dependent mortality relationships. This yielded six alternative models: two groupings (species separate or species pooled), each with three forms of size-dependence (quadratic, linear and size-independent). For each growth form, we selected the best-fitting model using second order AIC (AICc), which corrects for small sample sizes. Analyses were conducted using the ‘glm’

function in the statistical programming language R (R Core Team 2013).

In a separate set of analyses, we fitted generalised additive models (GAMs) with a cubic regression spline smoother and a binomial error distribution separately for each species as a further check on whether the best GLM model adequately captured the underlying shape of the mortality-size relationship. For instance, an asymmetric bathtub shape (with mortality rate decreasing more slowly or quickly at small versus large sizes) might not be detected by the GLM analysis, as the quadratic mortality model enforces a symmetric mortality curve. GAMs were run using the ‘gam’ function from the ‘mgcv’ package for R (Wood 2011).

### Association between mortality models and colony mechanical vulnerability

To evaluate the extent to which differences in shape of the size-dependent mortality relationship were explained by vulnerability to dislodgment, we quantified the mechanical dislodgement vulnerability (colony shape factor, *CSF*) of coral colonies based on their planar area and growth form using equations parameterised for other colonies at the same study location. *CSF* is a dimensionless variable that captures the projected area of a colony subjected to hydrodynamic drag, the cantilever bending moment at the colony base (i.e. the second moment of the projected area) and the dimensions of the basal attachment (Madin & Connolly 2006). *CSF* is a key predictor of mechanical vulnerability, because dislodgement can be mechanistically predicted based on maximum water velocity generated by waves and the strength of the reef substrate to which colonies attached, both of which are assumed to be similar on average for all colonies at the study site. Specifically:

$$CSF = \frac{16}{d_{\parallel}^2 d_{\perp} \pi} \int_{y=0}^h y w(y) dy$$

$d_{\parallel}$  and  $d_{\perp}$  are the two basal attached diameters measured from the horizontally aligned photographs, and the integral term is the second moment of area of the colony outline perpendicular to wave action [ $w(y)$  is the projected width,  $y$  is distance above the substrate and  $h$  is the height of the colony].

In 2010, 395 colonies representing the five growth forms (arborescent, tabular, corymbose, digitate and massive) were photographed along the three perpendicular axes required to calculate *CSF*: two horizontal photographs, one each parallel and perpendicular to prevailing wave action, and one vertically to capture planar area. Photographs were corrected for barrel distortion, colonies were outlined, and the scale plate used to estimate colony planar area and the variables required to estimate *CSF* (see Appendix S2). Multiple regression was used to capture expected colony *CSF* as a function of growth form (categorical) and colony size (planar area), and allowed for interactions between the two predictor variables because growth form was expected to influence both the intercept and slope of model relationships. The regression analysis was conducted using the ‘lm’ function in the statistical programming language R (R Core Team 2013).

The resulting regression model was used to estimate *CSF* for colonies of the 11 focal species based on their size and growth form. We then looked at the relationship between colony mortality rate and *CSF* for the largest 10, 20, 30, 40 and 50% of colonies of a species. Spearman correlations were used to determine if species with larger, mechanically vulnerable colonies tended to exhibit bathtub mortality curves. To verify that any differences in mortality rate for larger colonies reflected increasing mortality with size, consistent with the mechanical vulnerability hypothesis, and were not artefacts of coincidentally higher baseline mortality in growth forms with high *CSF*, we also examined relationships between colony mortality rate and *CSF* for the smallest 10, 20, 30, 40 and 50% of colonies of a species. To be consistent with our hypothesis, the predicted positive relationship between *CSF* and mortality rate should hold for larger colonies, but not smaller colonies.

## RESULTS

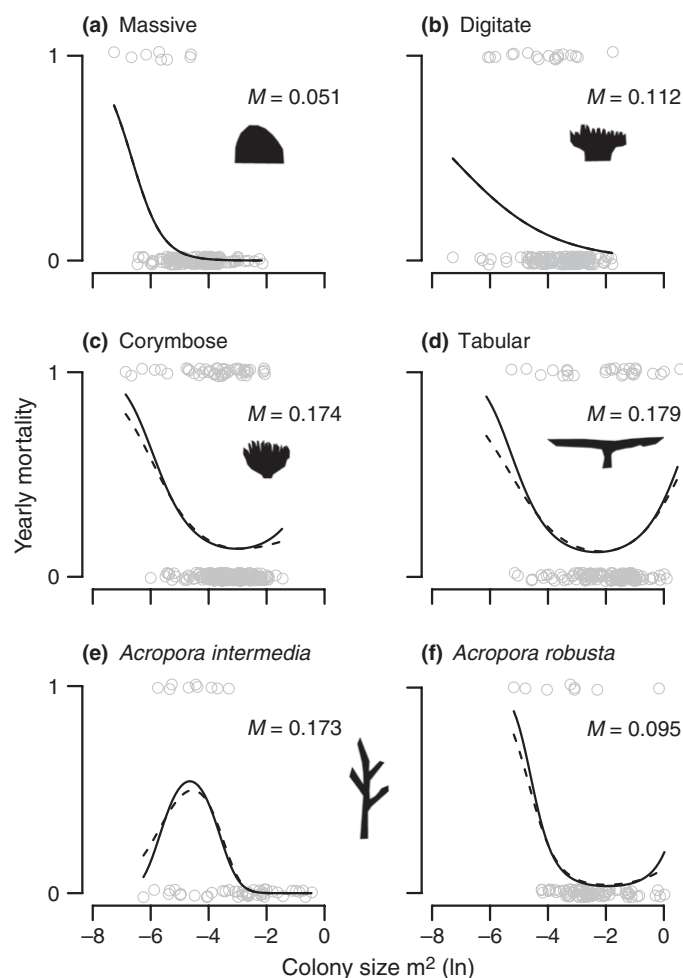
### Model selection

In all cases except for the arborescent colonies, growth form was a better predictor of yearly mortality than species (Table 1, Fig. 2), with the quadratic model best describing tabular and corymbose colonies, and the monotonic model best describing digitate and massive colonies. Consistent with our expectation, the monotonic models implied decreasing (rather than increasing) mortality rates with size (Fig. 2a, b), and the quadratic models implied bathtub-shaped (rather than hump-shaped) mortality schedules, with a clear minimum at

**Table 1** GLM results for (the logistic transform of) yearly mortality probability as a function of the natural logarithm of colony size

	Estimate	SE	z-value	Pr(>  z )
<b>Arborescent (n = 141)</b>				
( <i>Acropora intermedia</i> )	-22.070	10.149	-2.175	0.030*
( <i>Acropora robusta</i> )	20.638	10.227	2.018	0.044*
Area: <i>Acropora intermedia</i>	-9.565	4.727	-2.024	0.043*
Area: <i>Acropora robusta</i>	1.988	1.071	1.857	0.063
Area <sup>2</sup> : <i>Acropora intermedia</i>	-1.029	0.536	-1.918	0.055
Area <sup>2</sup> : <i>Acropora robusta</i>	0.513	0.215	2.387	0.017*
<b>Tabular (n = 156)</b>				
(Intercept)	-0.586	0.562	-1.044	0.296
Area	1.215	0.536	2.268	0.023*
Area <sup>2</sup>	0.266	0.106	2.513	0.012*
<b>Corymbose (n = 271)</b>				
(Intercept)	0.618	1.900	0.325	0.745
Area	1.624	1.002	1.620	0.105
Area <sup>2</sup>	0.268	0.127	2.106	0.035*
<b>Digitate (n = 163)</b>				
(Intercept)	-4.328	0.976	-4.435	0.000***
Area	-0.593	0.234	-2.536	0.011*
<b>Massive (n = 162)</b>				
(Intercept)	-12.458	2.981	-4.179	0.000***
Area	-1.872	0.533	-3.509	0.000***

The species-level model best-fit the arborescent species; whereas the growth-form-level model best-fit all other species. \*\*\*:  $P < 0.001$ , \*:  $P < 0.05$ .

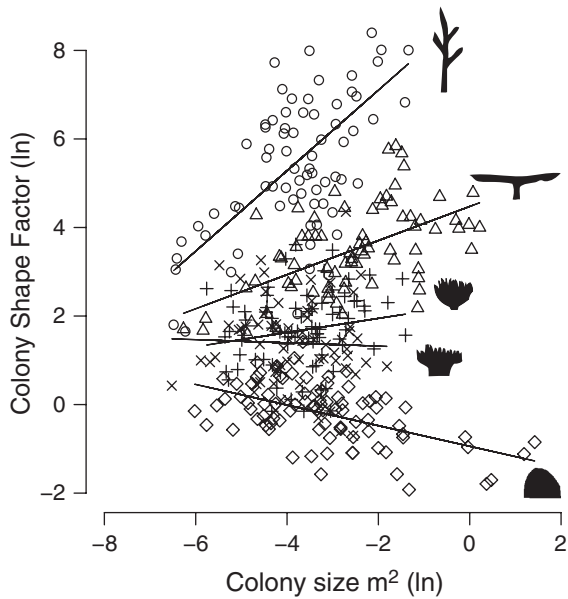


**Figure 2** Mortality rate as a function of colony size. Panels show the best-fit GLM for mortality (solid lines), along with the observations (grey points: 1 indicates mortality, 0 indicates survival; points have been randomly offset from 1 and 0 to help visualise densities with size). Where the growth form model was the best-fitting model, the data have been pooled across species (a–d). Arborescent species are plotted separately (with the same silhouette) as model selection favoured different mortality parameters (e, f). Dashed lines (sometimes concealed by the GLM fit) show best-fit GAMs for each species or growth form respectively. Yearly mortality rates ( $M$ ) are given for each panel.

intermediate colony sizes (Fig. 2c, d). Among the arborescent corals, *Acropora robusta* and *A. intermedia* had significant and marginally non-significant quadratic terms respectively. However, these quadratic effects were in opposite directions (Fig. 2e, f); consequently, growth form was a poor predictor of mortality for these species. GAMs supported the robustness of the qualitative patterns identified by the model selection (Fig. 1, dashed lines).

### Association between mortality models and large colony mechanical vulnerability

Mechanical vulnerability (*CSF*) of coral colonies was strongly dependent on colony size and growth form as well as interactions between these variables (Fig. 3; see Table S1). We found a strong positive relationship between mechanical vulnerabil-

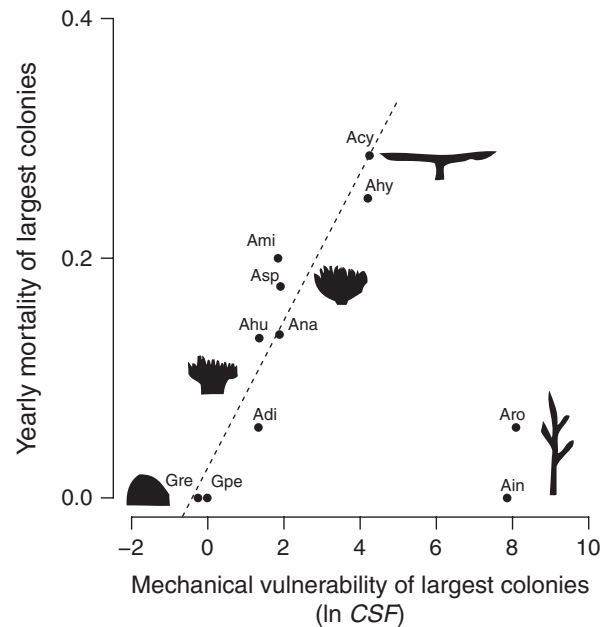


**Figure 3** Relationships between colony shape factor (*CSF*) and colony size for the five study growth forms: arborescent (circles;  $n = 73$ ), tabular (triangles;  $n = 76$ ), corymbose (pluses;  $n = 78$ ), digitate (crosses;  $n = 68$ ) and massive (diamonds;  $n = 86$ ). Lines show the best-fit multiple regression model, which was subsequently used to estimate *CSF* for the tagged colonies.

ity and yearly mortality for 9 of the 11 species – the two arborescent species were clear outliers (Fig. 4; Table 2a, b). Tabular and corymbose species had high whole-colony mortality and mechanical vulnerability (high *CSF*) at large colony sizes, consistent with their bathtub-shaped mortality schedules. Massive and digitate species had low mortality and low mechanical vulnerability (low *CSF*) at large sizes, consistent with their monotonically decreasing mortality schedules. The outliers, the arborescent species, are mechanically vulnerable, but had low rates of whole-colony mortality for larger colonies. No significant relationships were found between biomechanics and mortality for the subsets of smaller colonies of each species (Table 2c, d).

## DISCUSSION

Our findings show that reef coral species have either monotonically decreasing or bathtub-shaped mortality relationships with colony size. With the exception of arborescent corals, the size-dependence of whole-colony mortality was closely linked to the species trait of colony shape, as predicted by mechanical vulnerability theory (Madin & Connolly 2006). Past studies of coral mortality have only documented monotonically declining relationships (Connell 1973; Jackson 1979). However, by focusing predominantly on massive and foliaceous species, these studies have likely captured only part of the wider spectrum of mortality patterns of corals. Here, we broadened the scope of previous work by considering mortality-size relationships for a wider range of coral species and growth forms, from slow growing, mechanically robust, massive species through to fast growing, delicate, branching species. Massive species showed the monotonic relationships



**Figure 4** Mean annual mortality of the largest 20% of colonies for each species plotted against their mean estimated mechanical vulnerability (*CSF*). Abbreviations represent the first letter of the genus name and first two letters of the species name (see Methods for full species names). The dashed line shows the relationship between the variables when the two arborescent species (bottom right) are removed (Table 2b).

observed in prior work. However, species with mechanically vulnerable larger individuals (e.g. species with tabular and corymbose growth forms) conformed better to the bathtub mortality-size relationship that is common in unitary organisms as a function of age.

We hypothesised that the continuum between the linear and bathtub models would be controlled by the disproportionate vulnerability of large colonies to processes that cause whole-colony mortality. Specifically, we predicted mechanical vulnerability to dislodgement to be a source of differences in mortality schedules among species. Hydrodynamic forces generated by large wave events have very different effects on coral colonies based on their size and growth form (Madin & Connolly 2006). Top heavy, tabular and branching species tend to be disproportionately dislodged when they grow large compared to bottom-heavy, massive species that tend to resist dislodgement and are therefore more likely to suffer partial mortality by scouring or impact injuries rather than be dislodged (Hughes & Jackson 1985; Madin & Connolly 2006). The strongest monotonic pattern was displayed by massive and digitate growth forms, for which large colonies are resistant to being overturned by storm waves; whereas the strongest bathtub pattern was displayed by the tabular and corymbose species, for which large colonies are susceptible to being overturned by storms resulting in colony death (Madin & Connolly 2006). The strong, positive relationship between species' predicted probability of large-colony dislodgement, and their tendency to exhibit bathtub mortality patterns, indicates that interspecific differences in mechanical vulnerability have strong effects on the demography and life history of corals. Mechanical vulnerability, in turn, is strongly dependent on colony shape.

**Table 2** Statistical significance and strength of relationships between mechanical vulnerability and mortality rate of the largest and smallest 50, 40, 30, 20 and 10% of colonies for each species

Largest								
	(a) All species				(b) Arborescent species removed			
	<i>t</i> -value	<i>df</i>	<i>Pr</i> (>   <i>t</i>  )	<i>cor</i>	<i>t</i> -value	<i>df</i>	<i>Pr</i> (>   <i>t</i>  )	<i>cor</i>
50%	0.012	9	0.990	0.004	2.859	7	0.024*	0.734
40%	0.196	9	0.849	0.065	3.998	7	0.005**	0.834
30%	0.195	9	0.849	0.065	4.202	7	0.004**	0.846
20%	0.205	9	0.842	0.068	5.729	7	0.001**	0.908
10%	0.341	9	0.741	0.113	3.825	7	0.007**	0.822
Smallest								
	(c) All species				(d) Arborescent species removed			
	<i>t</i> -value	<i>df</i>	<i>Pr</i> (>   <i>t</i>  )	<i>cor</i>	<i>t</i> -value	<i>df</i>	<i>Pr</i> (>   <i>t</i>  )	<i>cor</i>
50%	1.856	9	0.096	0.526	2.084	7	0.076	0.619
40%	1.814	9	0.103	0.517	1.529	7	0.170	0.500
30%	1.912	9	0.088	0.537	0.738	7	0.485	0.269
20%	0.344	9	0.739	0.114	1.165	7	0.282	0.403
10%	-0.244	9	0.813	-0.081	-0.129	7	0.901	-0.049

Analyses were run for (a, c) all 11 study species and (b, d) following the removal of the two arborescent species. \*\*:  $P < 0.01$ , \*:  $P < 0.05$ .

The morphologies of corymbose, arborescent and tabular species facilitate fast growth (Hughes & Connell 1987). Such species have earlier reproduction than slower-growing species such as massive corals (Babcock 1991; Baria *et al.* 2012). Moreover, by allowing colonies to form canopies above the substrate, tabular, corymbose and arborescent growth forms provide a competitive advantage in access to light and the dissolved nutrients and particulates supplied by water flow (Jackson 1979; Stimson 1985). Such canopy-forming morphologies have long been known to be vulnerable to dislodgment during cyclones, and indeed this has been viewed as a key mechanism of diversity maintenance on coral reefs (Connell 1978). Our study quantifies this differential vulnerability to dislodgment, and shows that strong differences in size-dependent mortality between these growth forms can be driven even by the hydrodynamic events that occur in 'normal' years, where major cyclones do not occur.

In contrast to species with other growth forms, the arborescent species had high-predicted mechanical vulnerability to disturbance, but very low whole-colony mortality rates, contrary to our hypothesis (Fig. 2e, f). We attribute this result to two characteristics of arborescent species that cause them to depart in important ways from the assumptions implicit in the mechanical vulnerability model. Specifically, the theory assumes that dislodgment occurs via the mechanical failure of the reef substrate at the point of colony attachment (Madin & Connolly 2006), because the substrate is typically weaker than coral skeleton (Madin 2005). However, arborescent staghorn species such as *A. intermedia* are known to form 'thickets' with multiple attachment points as they grow, fragment readily, and have relatively high rates of fragment reattachment and survival, relative to other growth forms (Tunncliffe 1981; Smith & Hughes 1999). There is often dead skeleton near the points of attachment of such colonies to the substrate, due to

cultivation of filamentous algae by damselfishes (e.g., *Stegastes nigricans*). Thus the anomalous mortality-size patterns seen in arborescent species may be due to fragmentation caused by breakage of bio-eroded, dead skeleton, rather than mechanical failure of the reef substrate at a single point of colony attachment.

Our study suggests that coral species fall into one of three mortality groups: those with bathtub-shaped patterns, those whose whole-colony mortality rate decreases with colony size, and a third group (which includes at least some arborescent species), whose colony growth dynamics cause them to violate the assumptions of the mechanical dislodgment theory that we have tested here. The group to which a species belongs can be explained based on growth form, which influences colony susceptibility to hydrodynamic dislodgement. The mechanistic link between the size-dependent mortality pattern and colony shape suggests that our findings can be extended to other common growth forms not considered here (e.g. columnar, foliaceous, encrusting, etc.), whose growth forms imply particular patterns of change in mechanical vulnerability with colony size (Madin & Connolly 2006). Our findings are relevant for other reef habitats, because hydrodynamic flow will eventually limit the size to which mechanically vulnerable species can grow. However, in sheltered habitats, bathtub-shaped mortality schedules will be less apparent, due to the greater chance of colonies dying for other reasons, before becoming large enough to be mechanically dislodged by the weaker hydrodynamic forces prevailing there.

Differences in mortality schedules are important for understanding population resilience to acute disturbances and chronic environmental change, as well as potential rates of evolutionary adaptation. For instance, the potential for corals to adapt to global warming has been questioned in part on the grounds that generation times of corals are on the order

of decades (Hoegh-Guldberg *et al.* 2007). However, species whose growth forms confer strongly bathtub-shaped mortality schedules will have generation times substantially shorter than this. For example, integrating the tabular mortality curve (Fig. 2d) with the growth curve for this growth form from Madin *et al.* (2012: Fig. 4a) gives an estimated average life-span of 3–4 years, two- to three-fold less than other estimates (e.g., Carpenter *et al.* 2008). Such species, which are often the most vulnerable to temperature stress, may therefore benefit from faster adaptation rates than previously supposed (Baird *et al.* 2009; Pandolfi *et al.* 2011). Because the species that conformed to the bathtub mortality model also tend to be the fast growing *Acropora* species, they also have greater capacity for population recovery. Conversely, when they are dislodged, they are more likely to be broken up into rubble, and transported off the reef, in contrast to more mechanically robust forms (Hughes 1999). Thus, while they will likely contribute disproportionately to reef primary production and horizontal reef progradation, they are also likely to make disproportionately small contributions to vertical reef growth. In other words, mortality schedules have implications, not only for demographic and life history strategies, but also for ecosystem functioning.

There have been growing calls for ecology to become more predictive, particularly in light of the need to anticipate the consequences of anthropogenic environmental change (Pereira *et al.* 2011). McGill *et al.* (2006) suggested that predictability might be enhanced by focusing on traits as explanatory variables for species differences, rather than calibrating species differences individually. Our results show that, in reef corals, morphology is an excellent predictor of mortality, capturing most of the variation among species in our study. Moreover, the effect of growth form on mortality rate can be explained by how their mechanical vulnerabilities change with colony size (Madin & Connolly 2006), suggesting that mechanistic links between species traits and demographic rates can help form a foundation for anticipating the long-term, assemblage-level consequences of environmental change in systems whose diversity is too great for species-by-species approaches to be feasible.

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#### STATEMENT OF AUTHORSHIP

JM performed the analyses and wrote the first draft of the manuscript. All authors collected the data and contributed to manuscript revisions.

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