Skeletal damage in reef corals: relating resistance to colony morphology

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ABSTRACT: Corals vary in their ability to resist breakage from mechanical force. Biomechanical theory predicts that resistance to mechanical injury should be determined by the morphological properties of coral colonies. However, a general model to predict resistance of corals to mechanical impact from structural characteristics has been lacking. In order to determine whether resistance can be predicted from colony structure, I use a suite of 6 variables—skeletal density, branch thickness, branch spacing, branch length, colony height and colony (projected) area—to quantitatively describe the structure of colonies from 12 species of scleractinian coral. Experimental analysis of the resistance of colonies from each species, which range from massive and tabular growth forms to various branching models, showed that damage susceptibility varied widely. Resistance ranged from very high for species such as *Leptoria phrygia*, *Porites cylindrica* and *Porites* spp. in which there was no reduction in colony area as a result of mechanical stress, to low in species such as *Pocillopora damicornis*, *Seriatopora hystrix* and *Montipora* sp. which suffered over 60% damage. Regression tree analysis revealed a strong relationship between resistance and colony morphology, producing a model which accounted for 76% of the variation in resistance using only 4 of the structural variables: colony height, branch thickness, branch spacing and colony area. Skeletal density and branch length were relatively unimportant in determining susceptibility to breakage. The regression tree model showed potential for development as a predictive tool in reef management, as it was able to predict susceptibility to breakage of corals using 4 easily measured morphological variables with 57% reliability (estimated by cross-validation).

KEY WORDS: Coral · Skeletal density · Structure · Disturbance · Biomechanics · Morphology · Reef management

INTRODUCTION

Scleractinian corals, the dominant benthic organisms in most coral reefs, play key roles in habitat provision and reef construction (Grassle 1973, Endean 1976, Davies 1983). However, their rigid aragonitic skeleton is brittle and readily broken when exposed to mechanical forces associated with physical disturbances (Wainwright et al. 1976, Chamberlain 1978). A wide range of physical disturbances can cause structural damage to corals, including natural events such as

storms and cyclones (e.g. Woodley et al. 1981, Dollar & Tribble 1993), and human activities such as boat anchoring (e.g. Davis 1977, Palaganas 1991, Allen 1992), SCUBA diving and snorkelling (e.g. Hawkins & Roberts 1992, Chadwick-Furman 1997, Roupheal & Inglis 1998). Not all corals are affected equally by physical stress, and those with obviously different morphologies commonly differ in their response to mechanical force (Stoddart 1963, Woodley et al. 1981, Liddle & Kay 1987).

Variation in the response of corals to mechanical stress has significant ecological implications. In some situations, differential damage and mortality resulting from disturbance can be important in preventing a small subset of species from dominating a coral assemblage through competitive exclusion (Connell 1978),

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Improved understanding of the relationship between structural characteristics of corals and their susceptibility to damage may further clarify mechanisms by which physical disturbance affects the species diversity of coral assemblages.

The response of scleractinian corals to mechanical stress has important life-history implications. Structural damage results in a decrease in colony size and in the production of fragments (Highsmith 1982, Hughes & Connell 1987). The costs of damage to a coral include allocation of energy to repair injured tissue (Rinkevich & Loya 1989), increased risk of colonization by epilithic algae or bioeroders (Bak et al. 1977, Bak & Steward-Van Es 1980) and reduced reproductive output (Hall & Hughes 1996). A coral can also benefit from breakage if fragments that are produced are able to initiate new colonies. Indeed, for some species, fragmentation results in higher rates of recruitment success compared with sexually produced larvae (Highsmith 1982). The extent to which breakage is adaptive in the life history of corals is still debated (Hughes et al. 1992), but it is likely to vary between species and across habitats. In most situations the relative costs and benefits of breakage to a coral will depend on the extent of structural damage, which is determined by a coral's ability to withstand mechanical force.

The response of a coral to mechanical force is determined by 3 properties: resistance, resilience and stability (after Connell & Sousa 1983, Underwood 1989). Resilience and stability describe the processes of recovery, whilst resistance is the property which determines whether or not a coral will show any initial response to a particular disturbance. This fundamental property of organisms exposed to stress has also been called inertia or persistence, particularly in relation to population- or community-level response to disturbance (Underwood 1989). Basic principles of biomechanics suggest that resistance in rigid organisms such as scleractinian corals is determined by structural properties of the coral colony. Generally, these principles are borne out by observations of differential damage among corals exposed to physical disturbances of various types. Large storms (Woodley et al. 1981, Rogers 1993, Connell et al. 1997), boat anchoring (Davis 1977, Palaganas 1991), reef walking (Liddle & Kay 1987, Hawkins & Roberts 1993) and recreational diving (Hawkins & Roberts 1992, Reigl & Reigl 1996, Rouphael & Inglis 1998) have all been reported to damage corals with finer architecture, such as tabular or branching *Acropora*, more than corals with a solid architecture, such as *Porites* and faviids.

However, our ability to predict the resistance of a coral to mechanical forces remains poor, and depends upon arbitrary categories of colony morphology which have vague operational boundaries (i.e. arborescent,

digitate, tabular, massive, etc.). More analytical attempts at relating resistance to structural properties of corals have mostly focused on the effect of skeletal density on strength (Chamberlain 1978, Schuhmacher 1984). Other studies have examined the effects of the morphology of individual structural elements (i.e. branches) on susceptibility to breakage (Liddle & Kay 1987), or have compared the effects of skeletal density with morphology for a few closely related species (Schuhmacher & Plewka 1981b). However, none of these studies have sought general principles or models which explain resistance in terms of quantifiable structural characteristics of coral colonies.

The relationship between colony architecture and resistance also has implications for management of coral reefs. If colony structure is a reliable predictor of resistance to physical damage it may be possible to use information about the morphological composition of coral assemblages to predict the susceptibility of corals to breakage. In reef areas which are managed to protect against the impacts of human activities such as boat anchoring, reef walking and diving, an ability to predict the effects of anthropogenic physical disturbances can be critical to informed and effective management (Craik et al. 1990).

In this study, I investigate the biomechanical basis of resistance of corals to mechanical damage. I identify a suite of quantitative variables which describe morphological and material properties of corals such as branch morphology, branch arrangement and skeletal density. To test the resistance of corals I then measure structural damage in colonies exposed to experimental mechanical impact. I examine the relationship between resistance and colony structure, and develop a statistical model using non-linear classification techniques to predict damage susceptibility from simple morphological characteristics of coral colonies.

METHODS

Twelve species of scleractinian corals were selected for use in the study. The 12 species represent a range of morphologies and families that are common on the Great Barrier Reef (GBR) (Veron 1986) (Fig. 1). Six colonies of each species were selected at sheltered sites around One Tree Island (23° 30' S, 152° 03' E), a small offshore cay with well-developed reef in the southern GBR. Six structural characteristics—skeletal density and 5 morphological variables—were measured for each colony. The 5 morphometric variables were simple to measure in the field and represented characteristics of both branch morphology and branch arrangement (colony architecture): branch length, branch thickness, branch spacing, colony height and

Fig. 1. Representative colonies from each of the 12 species of Scleractinia used in the study. Growth form (in brackets) after Veron (1986): (a) *Acropora formosa* (branching); (b) *Acropora humilis* (branching); (c) *Acropora hyacinthus* (plate); (d) *Acropora palifera* (branching); (e) *Leptoria phrygia* (massive); (f) *Montipora* sp. (plate); (g) *Porites cylindrica* (branching); (h) *Porites annae* (massive); (i) *Pocillopora damicornis* (branching); (j) *Porites* spp. (massive); (k) *Seriatopora hystrix* (branching); (l) *Stylophora pistillata* (branching). (Photographs a, b, f, g, i, j, k & l courtesy of J.E.N. Veron. Photographs c, d & e courtesy of D. Wachenfeld)

colony (planar) area. The colonies that were selected were of average size for each species in this location (determined from pilot surveys), and were located in water <10 m deep.

Measurement of structural characteristics. The skeletal density of each colony was calculated from 3 replicate sub-samples per colony. Several of the branching species were known to exhibit gradients in skeletal density within the corallum (Oliver 1984, Hughes 1987). Samples of the skeleton taken from these species included sections of varying density across the expected range within the colony. For example, in the branching species with axial gradients in

skeletal density, the samples were branch sections extending from the base to the tip of the branch. Thus, the density measure for each sample is integrative, providing an average skeletal density for the colony.

Samples were cleaned of tissue by immersion in a chlorine bleach bath, air dried for 5 to 7 d, and weighed to the nearest gram. The volume of each sample was determined by volumetric displacement in fresh water. Samples were coated in paraffin wax prior to measurement to prevent water infiltration of skeletal pores, an important influence on gross skeletal density and strength (Wainwright et al. 1976). The measured volumes were adjusted for the contribution of paraffin wax used to coat each sample, which was calculated from the mass of wax adhering to the sample and the known density of paraffin wax. Skeletal density (kg m^{-3}) was then calculated for each sample, representing the ratio of aragonitic matrix to pore space in the skeleton sample.

The large range of structure and form which is typical of most coral assemblages poses particular problems when comparing the morphology of different colonies. In particular, it has proven difficult to develop generalised morphometric models which permit quantitative comparisons between colonies with vastly different architectural models or growth forms (such as tabulate, arborescent and massive). As a result, previous studies have either confined their comparisons to species that are similar in growth form (e.g. Chamberlain & Graus 1975, Schuhmacher & Plewka 1981a), or have resorted to qualitative categories of general growth form (e.g. Kay & Liddle 1989). Based on work by Graus et al. (1977), I have attempted to overcome this limitation by modeling all colony forms as geometric variants of a basic branching plan. Using this approach, colonies with either massive growth form (e.g. *Porites* sp., *Leptoria phrygia*) or tabular growth form (e.g. *Montipora* sp., *Acropora hyacinthus*) are considered equivalent to a single, vertically growing branch, and are described as non-branching. Most other growth forms are considered to have multiple branches, and are described as branching species. Encrusting corals were not represented in this study.

The morphological variables were measured *in situ*, or calculated directly from *in situ* measurements. In each colony 5 branches were selected haphazardly to measure branch thickness, branch length and branch spacing. Although there can be substantial intra-co-

lony variation in these variables, I was primarily interested in whole-colony response to mechanical stress, and an average value for each variable was derived for each colony. Branch thickness was estimated by calculating the cross-sectional area, assuming an ellipsoid cross-section and using the major and minor branch diameters. Branch diameters were measured at the base of the selected branches, just above the first major bifurcation above the colony base. Branch length was a direct linear measurement from the branch base (as defined above) to the branch tip. Branch spacing was the distance between the tip of the selected branch and that of the nearest neighbouring branch. Colony height was a single measurement for each colony, and was measured as the maximum vertical extension of skeletal elements (not total height above substratum).

Planar area was measured from video images taken vertically above each colony before and after disturbance. Video stills were captured using an external Snappy (Play Incorporated) video capture device, and processed in a photograph editing package to delineate colony perimeter. Total planar area was then calculated using Image Tool, a public domain image analysis software package developed by the University of Texas Health Science Centre at San Antonio (UTH-SCSA 1998).

Experimental disturbance. To test the resistance of each colony to physical disturbance, a standardised force was applied to each coral colony using a specially developed test apparatus similar to that used to simulate the effects of trampling on terrestrial flora (Wagar 1967, Keilomaki 1973). The impact apparatus consisted of a 12.5 kg metal disk with basal area of 180 cm², which slid down a guide pole 1.2 m long. The base of the vertical guide pole was placed on top of the subject colony and the disk was released, falling along the pole to apply a single, instantaneous vertical force to the coral. The mass, size and application of the weight simulated a moderate-sized boat anchor falling onto a coral.

The response of each coral colony to the test disturbance was measured by the relative change in planar (projected) area of the colony. Planar area was measured prior to disturbance, and then immediately after the test disturbance. Post-disturbance measurements were based on the planar area of the original coral skeleton that remained intact and attached (i.e. fragments were removed). Planar area estimates the area of benthic space controlled either directly or indirectly by a sessile organism (pre-emptive space), and is therefore an important indicator of the relative fitness of a coral colony in a reef assemblage (Jackson 1979). Additionally, changes in planar area can be used to measure damage across a range of growth forms. Relative damage was defined as the absolute change in

planar area divided by the initial planar area of the colony.

Analyses. The relationship between resistance and structural characteristics of colonies was tested using regression techniques. Colonies were not grouped by species for these analyses, since I sought a model which would predict resistance from quantifiable morphological variables independent of qualitative categories. Simple linear regressions were used to relate damage caused by the impact treatment to each of the structure variables in turn. The degree of linear association between structural variables was quantified using the Pearson correlation coefficient. Strong correlation between predictor variables rendered multiple linear regression inappropriate for examining the relationship between raw structural characteristics and resistance. Instead, principal component analysis (PCA) was used to reduce the 6 structural characteristics to a smaller number of uncorrelated components. These components were then used in multiple linear regression analysis to test for a relationship between damage and the combined structural characteristics.

Biomechanical theory suggests that the interactions between morphological characteristics are important in determining structural properties of an organism. Residual plots indicated that the relationships between variables was complex, suggesting that a non-linear technique that was insensitive to heteroscedasticity might better represent the structure-resistance relationship. Regression tree analysis explains variation of a single response variable in terms of multiple explanatory variables, without being limited to linear relationships and without strict requirements of homoscedasticity (De'ath & Fabricius 2000). Regression trees were thus used to explore non-linear relationships between the structure variables and damage.

The regression tree is constructed by repeated binary splitting of the data. At each split the model tests all predictor variables to determine the variable and its value which maximises the sums of squared differences between the 2 resulting sets of response values. In this way the model determines a non-linear sequence of binary splits which explains the maximum amount of variation in the response variable. The optimal size of the regression tree model is estimated by plotting the predicted residual sums of squares for the model against tree size and identifying the minima. The power of the model as a predictive tool is tested in an internal cross-validation procedure. In this procedure, the tree is generated from a randomly selected subset (90%) of the data, and its predictive ability is tested on the 10% of the data which were excluded from model generation. An estimate of the mean and standard error for cross-validated model error was derived by bootstrapping ($n = 50$).

PCA was used to explore the correlation among structural characteristics of coral colonies, and to examine the taxonomic consistency in colony structure. An ordination plot of component scores for each colony was produced using the first 2 components from a PCA of the 6 structural variables. Confidence ellipses (90%) were then plotted for species groups and the relationships between species groupings were examined. The degree of reliability with which colonies of the same species are grouped in the PCA provides an indication of the validity of using the chosen suite of variables to describe the structure of colonies differing widely in growth form.

RESULTS

Structural characteristics of corals

Skeletal density

Skeletal density ranged from a mean of 1226 kg m⁻³ for *Porites annae* to 2201 kg m⁻³ for *Seriatopora hystrix* (Table 1). The 3 species of Pocilloporidae had the highest skeletal densities, followed by the plate-forming species, *Acropora hyacinthus* and *Montipora tuberculosa*. The other species were of intermediate skeletal densities (1387 to 1610 kg m⁻³).

Colony area

Planar colony area ranged from a mean of 210 cm² for *Porites* spp. to 1085 cm² for *Acropora hyacinthus* (Table 1). The plate-forming species *A. hyacinthus* and *Montipora tuberculosa* were, on average, the 2 largest species, with an average colony area >900 cm². Mean colony area exceeded 500 cm² for *Leptoria phrygia*, *Porites cylindrica* and *Acropora formosa*. The pocilloporid species *Stylophora pistillata*, *Pocillopora damicornis* and *Seriatopora hystrix* were among the smallest species in the study, with a mean colony area <400 cm².

Colony height

Colony height ranged from a mean of 0.5 cm for *Montipora* sp. to 29 cm for *Leptoria phrygia* (Table 1). The plate-forming species *Montipora* sp. and *Acropora hyacinthus* were the 2 shortest species, followed by *Acropora humilis*, *Pocillopora damicornis* and *Seriatopora hystrix*. The tallest species were *L. phrygia*, *Acropora formosa* and *Porites cylindrica*, all with a mean colony height >26 cm.

Table 1. Response to mechanical stress (% decrease in planar area) and structural characteristics of colonies from 12 coral species. Values are mean ($\pm$ SE) for 6 colonies of each species

Taxon	Colony area (% decrease)	Skeletal density (kg m ⁻³)	Initial colony size (cm ²)	Colony height (cm)	Branch length (cm)	Branch thickness (cm ²)	Branch spacing (cm)
<i>Acropora formosa</i>	29.00 (9.4)	1598.6 (96.4)	580.4 (129.4)	26.3 (2.3)	18.0 (1.8)	2.0 (0.3)	3.7 (0.6)
<i>Acropora humilis</i>	9.48 (4.5)	1458.4 (39.4)	344.8 (78.6)	5.8 (0.4)	5.8 (0.4)	2.1 (0.2)	1.1 (0.1)
<i>Acropora hyacinthus</i>	55.46 (12.0)	1284.5 (34.5)	1084.8 (166.7)	1.0 (0.1)	2.5 (0.2)	1114.5 (170.3)	0.0 (0.0)
<i>Acropora palifera</i>	15.19 (5.1)	1525.7 (88.7)	477.6 (41.9)	22.3 (1.1)	8.4 (0.9)	10.1 (1.2)	2.5 (0.2)
<i>Leptoria phrygia</i>	-0.86 (3.0)	1610.1 (36.5)	715.3 (143.1)	29.1 (2.0)	29.1 (2.0)	850.1 (159.3)	0.0 (0.0)
<i>Montipora</i> sp.	67.85 (13.2)	1337.1 (51.6)	928.3 (198.3)	0.5 (0.1)	0.5 (0.0)	948.1 (215.1)	0.0 (0.0)
<i>Pocillopora damicornis</i>	63.08 (6.6)	1716.7 (53.7)	324.6 (29.5)	7.5 (0.3)	7.5 (0.3)	1.5 (0.2)	0.8 (0.1)
<i>Porites annae</i>	2.74 (1.8)	1226.4 (87.9)	346.9 (51.4)	22.0 (1.1)	22.0 (1.1)	496.9 (87.1)	0.0 (0.0)
<i>Porites cylindrica</i>	-0.06 (0.8)	1387.1 (51.5)	621.5 (55.6)	28.5 (1.1)	9.9 (0.5)	4.8 (0.4)	1.3 (0.2)
<i>Porites</i> spp.	0.77 (1.9)	1486.5 (57.9)	209.8 (38.5)	13.9 (0.8)	13.9 (0.8)	225.4 (43.6)	0.0 (0.0)
<i>Seriatopora hystrix</i>	63.88 (8.0)	2200.6 (186.1)	336.7 (53.6)	8.1 (0.9)	8.1 (0.9)	0.2 (0.0)	0.3 (0.0)
<i>Stylophora pistillata</i>	27.35 (6.3)	1705.3 (79.5)	384.9 (35.1)	17.5 (0.8)	6.5 (0.3)	1.8 (0.1)	1.1 (0.0)

Branch length

Branch length and colony height are closely related (Pearson correlation = 0.744, $p = 0.000$), particularly for colonies with growth forms that were geometrically characterised as single, non-dividing, vertically growing branches. Therefore branch length showed a similar range to colony height, varying from a mean of 0.5 cm (*Montipora* sp.) to over 29 cm (*Leptoria phrygia*) (Table 1). Branch length in colonies with branching growth form ranged from 5.8 cm (*Acropora humilis*) to 18 cm (*Acropora formosa*). *Acropora palifera* colonies used in this study were distinctly ramose (i.e. secondary branching was common), with an average branch length of 8.4 cm.

Branch thickness

Branch cross-sectional area was the most variable of the morphological characteristics measured, with average branch cross-section ranging from 0.2 cm² in *Seriatopora hystrix* to 1115 cm² in *Acropora hyacinthus*. This large range is due in part to the geometric definition of colonies in which massive and tabular growth forms were classified as single, vertically growing branches (see 'Methods'). In these corals, the cross-sectional area of the colony is identical to the branch cross-sectional area. Species formed 2 distinct groups based on branch thickness. The 7 species with a branching architecture had an average cross-sectional area close to or less than 10 cm². The remaining 5 species, comprising massive and tabular species, had branches >200 cm² in cross section (Table 1).

Fig. 2. Mean ($\pm$ SE) reduction in planar area of 12 species of scleractinia caused by the same mechanical force ($n = 6$ colonies per species). Symbols show families: (●) Acroporidae; (○) Pocilloporidae; (■) Poritidae; (□) Favidae

Branch spacing

The distance between adjacent branches is an important variable for distinguishing among ramose species. Mean branch spacing varied from 0.3 cm (*Seriatopora hystrix*) to 3.7 cm (*Acropora formosa*) in the 7 species with a branching growth form (Table 1, Fig. 1). *Acropora palifera* was the next most openly branched species after *A. formosa*. The most compact of the branching species after *S. hystrix* was *Pocillopora damicornis*, with a mean branch spacing of 0.8 cm. *Porites cylindrica*, *Stylophora pistillata* and *Acropora humilis* were intermediate, ranging from 1.1 to 1.3 cm. The 5 species with massive or tabular growth form were characterised geometrically as single branches, and were given a zero value for branch spacing.

Colony damage—resistance to mechanical force

There was large variation in resistance to mechanical stress among the corals tested, with colonies suffering reductions in planar area (damage) of between 0 and 100%. Six species contained undamaged colonies: *Leptoria phrygia*, *Porites annae*, *Porites* sp., *Porites cylindrica*, *Acropora formosa* and *Acropora humilis*. Colonies which were totally damaged (i.e. colony area reduced by 100%) during the mechanical impact tests were from 3 species: *Acropora hyacinthus*, *Montipora tuberculosa* and *Seriatopora hystrix*.

The average reduction in planar area differed significantly between species (ANOVA: $df = 11$, $F = 14.8$, $p = 0.000$), ranging from 0 to 68% (Table 1, Fig. 2). The species with the highest resistance (<5% damage) to mechanical stress were *Leptoria phrygia* and the 3 species of *Porites*: *P. cylindrica*, *Porites* sp., *P. annae*. All were characterised by a massive (solid) architecture, except *P. cylindrica*, which was branched. The species least resistant to physical impact (>50% damage) were *Acropora hyacinthus*, *Pocillopora damicornis*, *Seriatopora hystrix* and *Montipora tuberculosa*. Colonies of *A. hyacinthus* and *M. tuberculosa* had a tabulate or plating architecture, while the 2 Pocilloporid species were branched. Species of intermediate resistance (mean damage range: 9 to 29%) all had architectural models characterised by branching: *Acropora formosa*, *Stylophora pistillata*, *Acropora palifera* and *Acropora humilis*.

Relating colony structure and resistance

Resistance to mechanical damage in corals was not reliably predicted by any morphological variable alone. The maximum amount of variation in damage

explained by linear relationship with a single morphological variable was 35% (colony height). Branch length was less useful again for predicting resistance, with $r^2 = 0.25$. The remaining 4 variables (skeletal density, colony size, branch thickness and branch spacing) each explained less than 5% of the observed variation in response to experimental mechanical stress (Fig. 3).

Residual plots indicated complex relationships between the structure variables, suggesting that multiple linear regression against the raw predictor variables was inappropriate. PCA reduced these 6 related variables to 3 independent components with eigenvalues >1 that together explained 77% of the variation (Table 2). The first component, which explained 31% of the variation in the data, correlated strongly with branch cross-sectional area, branch spacing, colony size and skeletal density. Component 2 explained an additional 29% of the variation, and separated the data on the basis of colony height and branch length.

Fig. 3. Damage against each morphological variable, showing coefficient of variation (r^2) from univariate linear regressions. Note $\log_{10}$ scale for branch thickness.

Component 3 explained a further 17% of variation in the data, and was additionally correlated with branch spacing, colony size and branch length.

Although the first 3 principal components together explained 77% of the variation in the predictor variables, they were not effective at representing variation in resistance. The multiple linear regression of resistance against the 3 principal components was highly significant ($p = 0.000$), but the regression explained only 34% of the variation in resistance ($\alpha = 0.278$, $\beta_1 = -0.066$, $\beta_2 = -0.168$, $\beta_3 = 0.023$, $r^2 = 0.343$). The predictive value of the morphological variables, either alone or in linear combination, was therefore relatively low.

Regression trees were much more effective at representing the relationship between colony structure and resistance (Fig. 4). Regression tree analysis yielded a model which represented 76% of the variation in the data using only 4 morphological variables. The regression tree model reliably predicted resistance from colony structure, with cross-validated reliability averaging 57% ($\pm 0.7\%$).

The optimal regression tree divided the 72 colonies into 5 groups on the basis of colony height, branch thickness, branch spacing and colony area (Fig. 4). The first division of the tree separated colonies >11.6 cm in height. Tall colonies (>11.6 cm) were subsequently divided on the basis of branch cross-sectional area, producing leaves (terminal ends of regression tree stems) with very different values of the response variable, damage. Thus, colonies that were >11.6 cm in height and which had a mean branch thickness >3.9 cm formed a terminal group that was most resistant to physical impact (mean damage = $3.6 \pm 0.8\%$ SE; $n = 29$). Colonies of the same height, but which had thinner branches (<3.9 mm), formed a group of intermediate resistance ($26.1 \pm 3.4\%$ SE; $n = 13$). The regression model split colonies <11.6 cm in height into

Table 2. Results from principal component analysis of 6 structure variables: colony size, colony height, branch spacing, branch length, branch thickness and skeletal density. Only components with eigenvalue >1 are shown. Variable loadings with absolute values ≥ 0.4 are shown in bold

Explanatory variable	Component		
	1	2	3
Colony size	0.59	-0.18	-0.46
Colony height	-0.14	-0.94	-0.09
Branch spacing	-0.67	-0.23	-0.61
Branch length	-0.23	-0.77	0.53
Branch thickness	0.84	-0.18	0.17
Skeletal density	-0.52	0.40	0.34
Eigenvalue	1.86	1.75	1.02
% of variance	31.02	29.19	16.92

Fig. 4. Regression tree model of the relationship between damage and structural characteristics of corals (error = 0.24). The model predicts damage with 57% reliability (cross-validation error = 0.43 ± 0.01) using 4 morphological variables: colony height, branch thickness, branch spacing and colony area

2 groups based on branch spacing. Short colonies (<11.6 cm) with branch spacing >0.81 cm were subdivided into a terminal group with intermediate resistance ($22.4 \pm 4.7\%$ SE; $n = 8$). Short colonies with branch spacing <0.81 cm were further split on the basis of colony size into the final 2 leaves. Colonies <1126.5 cm² in area formed a terminal group with intermediate damage ($21.0 \pm 2.2\%$; $n = 4$) while colonies >1126.5 cm² were those with the highest level of damage ($72 \pm 2.6\%$; $n = 18$). In other words, corals with least resistance to physical impact (those which exhibited the greatest damage) were colonies that were <11.6 cm in height with narrowly spaced branches (<0.81 branch spacing) and >1126.5 cm² in planar area (Fig. 4).

Taxonomic consistency of colony structure and resistance

The PCA scores plot shows that the first 2 principal components are effective at explaining most (60%) of the variation in structural characteristics among the coral colonies, and that much of the structure in the data relates to species groupings of colonies (Fig. 5). Component 1, strongly correlated with branch thickness, colony area, branch spacing and skeletal density, separates low plate-forming colonies of *Montipora* sp. and *Acropora hyacinthus* from the small branching colonies of *Acropora humilis*, *Seriatopora hystrix* and

Pocillopora damicornis. Component 2 also separates the tall solid colonies of *Leptoria phrygia* and *Porites annae* from tall branching colonies of *Porites cylindrica* and *Acropora formosa*. Component 2, correlating with colony height and branch length, as well as skeletal density, reveals differences in structure between branching colonies of *A. formosa*, *Acropora palifera* and *Stylophora pistillata*. It also separates colonies of *Porites* spp. from other colonies with a massive growth form. Confidence ellipses (90%) further illustrate the effectiveness of the 2 components in representing similarities between colonies of the same species. These results indicate that there is strong taxonomic consistency in the grouping of coral colonies on the basis of structural characteristics and validate the use of a simplified geometric branching model to represent the range of growth forms.

The taxonomic consistency of corals grouped by structural similarities suggested that the predictions of the regression

tree model could be usefully interpreted in relation to coral taxa comprising each group (Table 3). Group 1 (mean damage = 3.6%) predicted by the regression tree model comprised the 3 species with massive growth form (*Porites* sp., *Leptoria phrygia* and *Porites annae*) plus colonies from the thick-branched species *Acropora palifera* and *Porites cylindrica*. Group 2 (mean damage = 26.1%) contained the branching species *Acropora formosa* and *Stylophora pistillata*. Group 3 (mean damage = 22.4%) was characterised by 2 different branching species: *Acropora humilis* and 2 colonies of *Pocillopora damicornis*. Group 4 (mean damage = 21.0%) contained only 4 colonies from the 2 plate-forming species *Acropora hyacinthus* and *Montipora* sp. Group 5 contained the colonies with lowest resistance to damage (mean damage = 71.9%), and included colonies of *A. hyacinthus* and *Montipora* sp. as well as the small branching species *P. damicornis* and *Seriatopora hystrix*.

DISCUSSION

Although scleractinian corals feature a wide range of growth strategies and colony shapes, the results of this study demonstrate that the structural characteristics of colonies from a range of species can be effectively represented by 6 quantifiable variables. These variables (colony area, colony height, branch length, branch thickness, branch spacing, skeletal density)

Fig. 5. Principal component biplot illustrating the relationships between coral colonies based on the 6 structural characteristics. Confidence ellipses (90%) are plotted for each species. (▲) *Acropora formosa*; (■) *Acropora humilis*; (▲) *Acropora hacinthus*; (▲) *Acropora palifera*; (■) *Leptoria phrygia*; (■) *Montipora* sp.; (●) *Pocillopora damicornis*; (●) *Porites annae*; (●) *Porites cylindrica*; (●) *Porites* spp.; (◆) *Seriatopora hystrix*; (◆) *Stylophora pistillata*

describe colony structure without recourse to qualitative categories such as growth form. By representing all colonies, regardless of overall form or shape, as geometric variants of a basic branching plan, colony structure can be compared between and within species with vastly different growth strategies. This scheme may not be appropriate for all corals, and would be difficult to apply to most encrusting species. However, within its limitations it provides a standardised framework for morphometric description that may, if applied in future studies, facilitate comparisons of

structural characteristics of corals between different studies and sites.

Commensurate with the range of structural characteristics represented among colonies in this study was large variation in resistance to mechanical force. Colonies of some species, such as *Montipora tuberculosa*, *Seriatopora hystrix* and *Pocillopora damicornis*, were highly susceptible to breakage, while others, such as *Leptoria phrygia*, *Porites cylindrica*, *Porites* sp. and *Porites annae*, were very resistant. The results of the only other published study from the GBR that explicitly

tests resistance of whole colonies to mechanical stress (Liddle & Kay 1987) are consistent with those reported here. In their study of the effects of trampling on 4 species of corals, Liddle & Kay (1987) found that *P. damicornis* was the most susceptible of 4 species exposed to experimental trampling, with *Acropora palifera* relatively resistant to damage and *Porites* sp. suffering no structural damage.

The resistance of corals to mechanical damage can be related to quantifiable structural characteristics using non-linear modeling techniques. Four morphometric variables—colony height, branch thickness, branch spacing and colony size—were able to predict the susceptibility of corals

Table 3. Distribution of species among groups predicted by regression tree analysis (see Fig. 4) (n = 6 colonies per species)

	Group 1	Group 2	Group 3	Group 4	Group 5
<i>Acropora formosa</i>	0	6	0	0	0
<i>Acropora humilis</i>	0	0	6	0	0
<i>Acropora hacinthus</i>	0	0	0	3	3
<i>Acropora palifera</i>	6	0	0	0	0
<i>Leptoria phrygia</i>	6	0	0	0	0
<i>Montipora</i> sp.	0	0	0	1	5
<i>Pocillopora damicornis</i>	0	0	2	0	4
<i>Porites annae</i>	6	0	0	0	0
<i>Porites cylindrica</i>	5	1	0	0	0
<i>Porites</i> spp.	6	0	0	0	0
<i>Seriatopora hystrix</i>	0	0	0	0	6
<i>Stylophora pistillata</i>	0	6	0	0	0

to breakage with 56% reliability. Interestingly, other structural characteristics such as skeletal density and branch length, which have been used elsewhere to indicate resistance to breakage in corals, were relatively unimportant in determining resistance in this study. The 4 predictor variables can all be easily measured in the field without destructive sampling.

The model resulting from regression tree analysis of these variables is based on colony architecture, yet there was high taxonomic consistency within groups predicted by the model. This suggests that resistance can be predicted for coral species, at least where there is not large intraspecific variation in structural properties. Where there is large morphological variation among conspecific colonies, it may be more meaningful to allocate colonies to morphological types (based on preliminary analysis) rather than to taxonomic groups. Although it includes a more numerous and diverse suite of species than has hitherto been attempted in any single study, this model has been developed on a relatively small sub-sample of possible coral forms. Therefore, despite the relatively strong predictive ability of the model, caution is necessary in attempting to extrapolate to corals with structural models outside the range of those tested here. Further testing of the model on other species of corals from different areas would further validate (or invalidate) its general applicability.

The importance of morphological characteristics over skeletal density in corals is particularly interesting, considering the emphasis on density in many studies seeking to explain variation in resistance among corals (e.g. Chamberlain 1978, Schuhmacher 1984, Hughes 1987). This emphasis on skeletal density is probably due to theoretical predictions and laboratory tests which have shown that porosity has a large effect on the strength of rigid, ceramic-like materials such as coral skeleton (Wainwright et al. 1976, Chamberlain 1978). Maximum skeletal density in corals is constrained by an upper limit of 2940 kg m⁻³, which is the density of solid aragonitic CaCO₃ (Graus et al. 1977). Pores within the coral skeleton mean that actual densities (excluding reports based on extremely porous branch tips) commonly range from <1000 kg m⁻³ to around 2500 kg m⁻³ (Hughes 1987). My measurements of the skeletal density of 12 species of corals encompass a similarly large range, from 1226 to 2201 kg m⁻³. Yet, I found no correlation between skeletal density and susceptibility of whole colonies to damage from mechanical stress.

The relationship between porosity and strength for ceramic material is described empirically by the function: $\sigma = \sigma_0 e^{-nV}$, where σ is the actual strength of the material, σ_0 is the strength of the same material with no porosity, V is the porosity (the fraction of the total

bulk occupied by void), and n is a constant between 4 and 7 (Ryskewitch, in Wainwright et al. 1976). The exponential relationship between strength and porosity means that small changes in porosity can have a large effect on strength. However the most dense coral skeleton reported to date is 2800 kg m⁻³ (Gladfelter 1982, Hughes 1987) and even this skeleton is 18 to 30% weaker than solid, void-free aragonite. The skeleton from the species with highest mean density in this study (*Seriatopora hystrix* = 2201 kg m⁻³) had a porosity of 25%, which is 63 to 83% weaker than a solid equivalent. Because the relationship between porosity and strength is exponential, the greatest reduction in strength will occur initially, as porosity increases from zero. At intermediate values of porosity, further increases will have significantly less effect on strength. For example, doubling porosity from 10 to 20% causes a much greater reduction in strength than doubling porosity from 40 to 80%. Among the coral species used in this study, the difference in strength between the skeleton of species with the highest (*S. hystrix*) and lowest mean densities (*Porites annae* = 1226 kg m⁻³) is only 15 to 27%. In most situations, therefore, reductions in strength due to skeletal densities are not likely to be as important as the effects of variation in other structural characteristics. In most instances, greater changes in strength appear to be associated with variations in morphological variables such as colony height and size, branch thickness and branch spacing. This conclusion is supported by a comparison of the relative importance of skeletal density and morphological characteristics for *Acropora palmata* and *Acropora cervicornis* by Schuhmacher & Plewka (1981a). They showed that resistance to the mechanical forces of waves is accomplished by adaptations in growth form rather than adaptations in skeletal density, and they concluded that 'skeletal strength does not appear to be of major adaptive value in the two *Acropora* species' (Schuhmacher & Plewka 1981a).

A strong relationship between morphological characteristics and resistance to mechanical damage has also been noted for plants. In particular, the relative sensitivity of perennial plants to trampling appears to be strongly associated with plant morphology (Bates 1935, Kuss 1986, Sun & Liddle 1993). Morphological features such as leaf size, plant height, internode length and shoot density can all be important in determining resistance to trampling among plants (Sun & Liddle 1993). Experimental analyses by Liddle & Kay (1987) on the effects of trampling on reef-flat corals found similar patterns: morphological features of colonies (such as branch thickness and branch length) are major determinants of the ability of sessile organisms to resist structural damage.

Ecological implications of tolerance

The large variability in resistance among the species tested here suggests that the adaptive value of breakage will likewise vary considerably between species. Some corals such as *Leptoria phrygia*, *Porites cylindrica* and *Porites* spp. are very unlikely to suffer structural damage, and therefore will rarely produce fragments and need to repair skeletal injuries. However, fragmentation and the need to repair structural damage is likely to be a common occurrence for other species such as *Montipora* sp., *Seriatopora hystrix*, *Pocillopora damicornis* and *Acropora hyacinthus*. Previous research has shown that the regenerative ability of corals can be ranked according to morphological attributes. Corals with more solid morphologies (*Porites mayeri*, *Porites lichen* and *Goniastrea retiformis*) are slower to regenerate injury than corals with branching or tabular morphologies (*Acropora robusta*, *P. damicornis* and *A. hyacinthus*) (Hall 1997). Similarly, survival rates of fragments vary among species (Highsmith 1982, Smith & Hughes 1999), and the ability of a species to establish daughter colonies from broken fragments can be important in determining the net adaptive value (or cost) to a coral of skeletal damage. However, stochastic events such as disease outbreaks and storm-generated waves exert strong influence on regeneration and fragment survival (Bak & Crieis 1981, Woodley et al. 1981, Bak et al. 1982), and the benefits of a strategy which favours recovery or fragmentation are likely to be variable and uncertain. Further understanding of the relative benefits of different damage response strategies will require a detailed comparison of the resistance, injury regeneration capacity and fragment survivorship of a range of coral species that span a variety of growth forms.

The biomechanical relationship between colony structure and resistance to damage suggests that the structural characteristics of corals will be important in determining the energy regime which a coral can inhabit. Charles Darwin, in his formative journeys on the 'Beagle', contrasted the 'great rounded masses' of *Porites* corals and the 'exceedingly strong honey-combed masses' formed by *Millepora* colonies which dominated the exposed outer margin of Cocos-Keeling Atoll with the 'generally brittle and thinly branched' species inhabiting the lagoon. By virtue of their structure, '*Porites* and *Millepora* alone seem able to resist the fury of the breakers' (Darwin 1897). Differences among species in their resistance to structural damage have also been suggested as an explanation for differences in community structure between sheltered and exposed reef sites by recent workers (e.g. Chamberlain & Graus 1975, Graus et al. 1977, Schuhmacher & Plewka 1981a, Done 1982), and many species show polymorphism in

relation to wave exposure (e.g. Geister 1975, Graus et al. 1977, Schuhmacher & Plewka 1981a, Veron 1986).

Perhaps the most important role of the structure-resistance relationship, however, is in determining how a coral assemblage responds to physical disturbances. Differential mortality of corals has been reported following many disturbance events which cause mechanical stress, including both natural and anthropogenic disturbances (e.g. Davis 1977, Woodley et al. 1981, Liddle & Kay 1987, Connell et al. 1997, Roupheal & Inglis 1998). Many theoretical models which describe mechanisms for maintenance of biological diversity are built on observations that species vary in their tolerance of disturbance events (e.g. Connell 1978). Variability in the resistance of corals to structural damage results in patchiness in the effects of a physical disturbance. In some cases disturbances can be critical to prevent a small subset of species from monopolising resources (e.g. Connell 1978, Hughes & Connell 1999). The results of the present study elucidate a mechanism which can explain the differential effects of physical disturbances. There is a strong relationship between the architectural properties of coral colonies and their resistance to breakage, suggesting that the changes to community composition which result from physical disturbance will depend in part on the morphological characteristics of the coral species which comprise an assemblage.

Resistance and reef management

The model described in this study has potential application in assessing the risk of damage to different community types from human activities. In many managed reef areas, such as the Great Barrier Reef Marine Park, the dual goals of preservation and multiple use are approached through the use of zoning plans (Kelleher 1986). In zoning plans which aim to protect reef sites from physical damage caused by human activities, information about the susceptibility to damage of species comprising the coral assemblage is critical. The strong relationship between colony structure and resistance in corals demonstrated in this study suggests that a framework for predicting the susceptibility to damage of reef sites is practicable. With information on species composition and the structural characteristics of key species, the aggregate of the resistance of the key species can be used to rank reef sites by relative susceptibility to damage. Species can be weighted differently according to their abundance, or by some assessment of ecological or aesthetic value (Done 1995). Finally, information about exposure (i.e. type and frequency of activities; proportion of colonies subjected to mechanical stress) can be combined with

predictions of susceptibility to estimate the overall risk of damage to the coral assemblage at a particular site. Knowledge of recovery processes, including injury regeneration and fragment survival, would further aid evaluation of the risk of lasting damage to a reef assemblage.

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LITERATURE CITED

- Allen WH (1992) Increased dangers to Caribbean marine ecosystems. *BioScience* 42:330–335
- Bak RPM, Crieis SR (1981) Survival after fragmentation of colonies of *Madracis mirabilis*, *Acropora palmata* and *A. cervicornis* (Scleractinia) and the subsequent impact of a coral disease. *Proc 4th Int Coral Reef Symp* 2:221–227
- Bak RPM, Steward-Van Es Y (1980) Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites*, *P. purpurea* and *Porites asteroides*. *Bull Mar Sci* 30: 883–887
- Bak RPM, Brouns J, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. *Proc 3rd Int Coral Reef Symp* 1:143–148
- Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: influence of time, location of interaction and epifauna. *Mar Biol* 69:215–222
- Bates GH (1935) The vegetation of wayside and hedgerow. *J Ecol* 23:470–487
- Chadwick-Furman NE (1997) Effects of SCUBA diving on coral reef invertebrates in the US Virgin Islands: implications for the management of diving tourism. *Proc 6th Int Coelenterate Biol Conf* 1:91–100
- Chamberlain JA Jr (1978) Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* 4:419–435
- Chamberlain JA, Graus RR (1975) Water flow and hydromechanical adaptations of branched reef corals. *Bull Mar Sci* 25:112–125
- Connell J (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:769–772
- Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. *Am Nat* 121:789–824
- Connell JH, Hughes TP, Wallace CC (1997) A 30 year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Craig WR, Kenchington R, Kelleher G (1990) Coral-reef management. In: Dubinsky Z (ed) *Ecosystems of the world, coral reefs*. Elsevier Science Publishers, New York, p 453–467
- Darwin C (1897) *The structure and distribution of coral reefs*. D Appleton and company, New York
- Davies P (1983) Reef growth. In: Barnes D (ed) *Perspectives on coral reefs*. Brian Clouston Publisher, Manuka, p 69–106
- Davis GE (1977) Anchor damage to a coral reef on the coast of Florida. *Biol Conserv* 11:29–34
- De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for the analysis of complex ecological data. *Ecology* (in press)
- Dollar S, Tribble G (1993) Recurrent storm disturbance and recovery: a long-term study of coral communities in Hawaii. *Coral Reefs* 12:223–233
- Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95–107
- Done TJ (1995) Ecological criteria for evaluating coral reefs and their implications for managers and researchers. *Coral Reefs* 14:183–192
- Endean R (1976) Destruction and recovery of coral reef communities. In: Jones OA, Endean R (eds) *Biology and geology of coral reefs*. Academic Press, New York, p 215–254
- Geister J (1975) The influence of wave exposure on the ecological zonation of Caribbean coral reefs. *Proc 3rd Int Coral Reef Symp* 1:24–29
- Gladfelter E (1962) Skeletal development in *Acropora cervicornis*. III. Patterns of calcium carbonate excretion in the axial corallite. *Coral Reefs* 1:45–51
- Grassle JF (1973) Variety in coral reef communities. In: Jones OA, Endean R (eds) *Biology and geology of coral reefs*. Academic Press, New York, p 247–270
- Graus RR, Chamberlain JA Jr, Boker AM (1977) Structural modification in corals in relation to waves and currents. In: Frost S, Weiss MP, Saunders JB (eds) *Reefs and related carbonates—ecology and sedimentology*. The American Association of Petroleum Geologists, Tulsa, OK, p 135–153
- Hall VR (1997) Interspecific differences in the regeneration of artificial injuries on scleractinian corals. *J Exp Mar Biol Ecol* 212:9–23
- Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* 77:950–963
- Hawkins J, Roberts CM (1992) Effects of recreational SCUBA diving on fore-reef slope communities of coral reefs. *Biol Conserv* 62:171–178
- Hawkins JP, Roberts CM (1993) Effects of recreational SCUBA diving on coral reefs: trampling on reef-flat communities. *J Appl Ecol* 30:25–30
- Highsmith RC (1982) Reproduction by fragmentation in corals. *Mar Ecol Prog Ser* 7:207–226
- Hughes TP (1987) Skeletal density and growth form of corals. *Mar Ecol Prog Ser* 35:259–266
- Hughes TP, Connell JH (1987) Population dynamics based on size or age: a reef-coral analysis. *Am Nat* 129:818–829
- Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: a long-term perspective. *Limnol Oceanogr* 44: 932–940
- Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. *TREE* 7:292–295
- Jackson JBC (1979) Morphological strategies of sessile animals. In: Larwood G, Rosen BR (eds) *Biology and systematics of colonial organisms*. Academic Press, London, p 499–555
- Kay AM, Liddle MJ (1989) Impact of human trampling in different zones of a coral reef flat. *Environ Manag* 13:509–520
- Kelleher G (1986) Managing the Great Barrier Reef. *Oceanus* 29:13–19
- Keilomaki S (1973) Tallaamisen vaikutus mutik-katypin kuusi-kon pintakasvillistukseen. Summary: ground cover response to trampling in a spruce stand of *Myrtillus* type. *Silva Fenn* 7:96–113
- Kuss FR (1986) A review of major factors influencing plant responses to recreation impacts. *Environ Manag* 10:637–650
- Liddle MJ, Kay AM (1987) Resistance, survival and recovery

- of trampled corals on the Great Barrier Reef. *Biol Conserv* 42:1–18
- Oliver JK (1984) Intra-colony variation in the growth of *Acropora formosa*: extension rates and skeletal structures of white (zooxanthellae-free) and brown tipped branches. *Coral Reefs* 3:139–147
- Palaganas VP (1991) Anchor damage on the coral reef of Sombrero Island, Batangas, Philippines. *Proc 7th Int Symp Coastal Ocean Manag* 1:1–14
- Reigl B, Reigl A (1996) Studies on coral community structure and damage as a basis for zoning marine reserves. *Biol Conserv* 77:269–277
- Rinkevich B, Loya Y (1989) Reproduction in regenerating colonies of the coral *Stylophora pistillata*. In: Spanier E, Steinberger Y, Luris M (eds) *Environmental quality and ecosystem stability*. ISEEQS Publishers, Jerusalem, p 257–265
- Rogers CS (1993) Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12:127–137
- Rouphael AB, Inglis GJ (1998) Impacts of recreational SCUBA diving at sites with different reef topographies. *Biol Conserv* 82: 329–336
- Schuhmacher H (1984) Reef-building properties of *Tubastrea micranthus* (Scleractinia, Dendrophyllidae), a coral without zooxanthellae. *Mar Ecol Prog Ser* 20:393–399
- Schuhmacher H, Plewka M (1981a) The adaptive significance of mechanical properties versus morphological adjustments in skeletons of *Acropora palmata* and *Acropora cervicornis* (Cnidaria, Scleractinia). *Proc 4th Int Coral Reef Symp* 2:121–128
- Schuhmacher H, Plewka M (1981b) Mechanical resistance of reefbuilders through time. *Oecologia* 49:279–282
- Smith L, Hughes T (1999) An experimental assessment of survival, re-attachment and fecundity of coral fragments. *J Exp Mar Biol Ecol* 235:147–164
- Stoddart D (1963) Effects of Hurricane Hattie on the British Honduras reefs and cays. *Atoll Res Bull* 95:1–142
- Sun D, Liddle MJ (1993) Plant morphological characteristics and resistance to simulated trampling. *Environ Manag* 17: 511–521
- Underwood AJ (1989) The analysis of stress in natural populations. *Biol J Linn Soc* 37:51–78
- UTHSCSA (1998) ImageTool. 1.28. University of Texas Health Science Centre at San Antonio (accessed: 5/3/1999); available at <http://ddsdx.uthscsa.edu/dig/itdesc.html>
- Veron J (1986) *Corals of Australia and the Indo-Pacific*. Angus and Robertson, North Ryde
- Wagar JA (1967) Simulated trampling as a technique in recreation research. XIV IUFRO Congress Munchen Section 26:239–245
- Wainwright SA, Biggs WD, Currey JD, Gosline JM (1976) *Mechanical design in organisms*. Edward Arnold (Publishers) Limited, London
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton NC, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe WJ, Wahle CM, Wulff JL, Curtis SG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749–755

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