CHAPTER 1: General introduction

Benthic and terrestrial habitats typically include sessile animal and/or plant assemblages (e.g., rocky reef kelp forests, tropical coral reefs and terrestrial plant communities). These organisms form the biological habitat structure among and within which associated organisms live and upon which many rely for both resources and protection. As a result, the abundance, distribution and diversity of these structural species are fundamental determinants of overall community structure (Dayton 1971; Menge 1976). Because space is generally a limiting resource in benthic and terrestrial habitats, stronger competitors may potentially exclude subordinates from establishing and/or maintaining suitable substrate for settlement and growth (Lang and Chornesky 1990). Given sufficient time without an external mortality agent to remove competitively dominant species, assemblages of structural species tend to approach low diversity equilibrium states (Connell 1979; Crow 1980 [terrestrial ecosystems]; Dayton 1971; Lang 1974; Connell 1978; Paine 1979; Paine and Levin 1981; Lang and Chornesky 1990 [marine ecosystems]). Subsequently, because of the dependence between structural species and their interstitial inhabitants, the diversity of the overall community declines (Menge 1976; Connell 1979; Bell and Galzin 1984; Stimson 1985; Sousa 2001).

Physical disturbance is a common, and often the overriding, mortality process that potentially inhibits competitive exclusion and its concomitant reduction in diversity (Sousa 1984). These disturbances are typically wind-driven phenomenon, such as elevated wave events in shallow marine systems (Denny and Wethey 2000) or windthrow in terrestrial systems, although they may also be caused by other sources (e.g., geothermal activity, Sousa 2001). For competitive inhibition to occur, the dominant competitors should be more susceptible to the disturbances than their subordinates; whether this is by sheer abundance or by increased biomechanical or physiological vulnerability (Sousa 1984). A widespread example of the trade-off between enhanced competitive ability and mechanical integrity occurs because of competition for light (where, as used in this thesis, mechanical integrity is an individuals ability to withstand mechanical force, and mechanical vulnerability, the reciprocal of mechanical integrity, is the inability of an individual to withstand mechanical force). Species that grow upwards, overtop and shade their neighbours tend to be competitively superior to other species in many systems (e.g., branching or foliaceous trees, kelp and corals; Wethey and Porter 1976; Grime 1977; Stimson 1985). These are precisely the attributes, however, that make such species particularly susceptible to mechanical breakage and mortality (e.g., Connell 1978; Chamberlain 1978; Wainwright et al. 1979; Woodley et al. 1981; Tunnicliffe 1981; Vogel 1996). The often diversity-promoting effects of recurrent physical disturbance are a central ecological idea (e.g., the intermediate-disturbance hypothesis; Connell 1978) and have been extensively documented and modelled (e.g., Levin and Paine 1974; Sousa 1979; Rogers 1993; Hubbell 1999; Molina and Sabatier 2001). However, our ability to quantitatively project the frequency and intensity of the conditions that cause mechanical destruction as well as understand the species- and size- selectivity of these events is limited (exceptions are limited primarily to temperate rocky shores; see Denny 1995).

Patterns of disturbance and recovery in ecological communities are essentially a function of two factors: return-time and magnitude (also referred to as frequency and intensity, respectively) (Sousa 1984; White and Pickett 1985). Long-term studies have identified that the structure of a community prior to hydrodynamic disturbance is in large part a function of the time since the last disturbance (Connell 1978; Paine and Levin 1981; Hughes 1989; Tanner et al. 1996; Connell et al. 1997; Hughes and Connell 1999). Typically, the longer the waiting time without extrinsic mechanical constraint (e.g., resulting from disturbance), the more mechanically vulnerable a community becomes to damage or destruction by physical disturbance, and thus to significant structural alteration (Hughes 1989; Whitman 1992; Connell et al. 1997). The second factor governing a community's response to physical disturbance is the magnitude of the disturbance. The magnitude of any disturbance imposes a mechanical threshold upon the community above which individuals will be damaged, displaced or killed. The effects of differential mortality of structural species have been well-documented following physical disturbance events (e.g., Crow 1980; Lugo et al. 1983; Reilly 1991 [terrestrial plant communities]; Dayton 1971; Levin and Paine 1974, 1975; Menge 1976; Sousa 1979; Denny 1995 [rocky shores]; Darwin 1842; Stoddart 1963, 1969; Shinn 1976; Highsmith et al. 1980; Knowlton et al. 1981; Woodley et al. 1981; Dollar 1982; Whitman 1992; Connell et al. 1997 [coral reefs]). Therefore, accurate projections of the return times and magnitudes of physical disturbances, as well as a firm understanding of the mechanical tolerances of the species comprising a structural assemblage, are essential to fully understanding the long-term dynamics of communities.

Using a tropical coral reef as a study system, this thesis aimed to quantify the mechanical vulnerability of corals, to predict the historical magnitudes and return times of previous physical (hydrodynamic) disturbances, and to estimate how the mortality imposed by these disturbances is likely to vary with species, colony size and location on the reef. Coral reefs provide the ideal system for a mechanistic investigation of the effects of disturbance on community dynamics for a number of reasons. First, coral reef communities are exposed to regular disturbances that significantly alter community structure (Whitman 1992; Tanner et al. 1994; Connell et al. 1997 and references therein). Moreover, a substantial amount of ecological research has utilized coral reefs as model systems, and this work has informed many of today's central ecological concepts (e.g., Levin and Paine 1974; Connell 1975, 1979). As a result, many of the interrelationships, patterns and processes governing the dynamics of these systems are well understood. Secondly, the vast majority of primary habitat structure of coral reefs is comprised of one group of animals (the scleractinian corals). Thus, the study of the biomechanical properties of the community requires knowledge of only one structural species assemblage. This eliminates the necessity to examine many different biomechanical forms, such as is necessary in biomechanical studies of terrestrial and temperate rocky shore systems (see Niklas and Spatz 2000; Denny 1995). Third, scleractinian reef corals are sessile, rigid and attached to the same carbonate substrate without complex or concealed rooting systems. Unlike flexible plants and animals, which are notoriously hard to biomechanically quantify (Koehl 1976; Carrington 1990; Johnston and Koehl 1994; Denny 1995; Gaylord and Denny 1997a, b), the biomechanical properties of rigid organisms are characterised relatively easily. Fourth, scleractinian reef corals typically form sub-tidal platforms that span a narrow depth range (0-5m below the lowest astronomical tide; Veron 1993). This narrow range eliminates the confounding effects of light on morphology (and, consequently, indirectly altering mechanical integrity; Oliver et al. 1983). Fifth, shallow reef platforms provide a continuum of hydrodynamic regimes from the highly exposed reef front (crest) to the relatively sheltered and hydrodynamically benign reef back (Done 1983; Hardy and Young 1996). These platforms therefore exhibit strong spatial differences in disturbance magnitude, thus creating a natural hydrodynamic gradient over which mechanical vulnerability is likely to vary. Finally, the broadcast dispersal strategy of these corals allows for recruiting larvae from a single species to potentially settle anywhere along the continuum of hydrodynamic habitats, thus ensuring that community members are from a heterogeneous mixture of genotypes (Babcock et al. 1986; Baird and Hughes 1997).

To achieve my aims, the first half of this thesis identifies the biomechanical limitations of coral colonies and develops a novel approach for comparing intra- and inter-specific differences between colony vulnerability (Chapters 2 and 3). The second half of the thesis focuses on the prediction of colony dislodgement on the reef, a component that required a comprehensive spatial and temporal multi-scale oceanographic approach to predict the magnitude and return time of water motion over the reef (Chapters 4 and 5). Taken together, these components constitute a framework for predicting the effects of hydrodynamic disturbance in sessile space-limiting systems.

Chapter 2 begins by describing the development of a geometric model which utilizes classical engineering theory to identify the principle factors that define the mechanical strength of individual colonies under the influence of water motion. The factors identified as part of this model are: 1) the tensile strength of the colony/substrate interface, 2) the projected shape of the colony perpendicular to water motion and 3) the maximum water velocity produced by passing waves. Chapter 2 then focuses on the first of these factors by undertaking a comprehensive examination of the material strengths of corals skeleton and the reef substrate over a spatial hydrodynamic gradient at Lizard Island, the Great Barrier Reef (GBR), Australia.

Chapter 3 describes the development of a theoretical technique to objectively quantify the mechanical vulnerability of coral colonies based on their projected shape (the second of the mechanical factors identified in Chapter 2). The resulting measure, the maximum predicted stress (MPS), is the amount of tensile stress at the coral/substrate interface of a colony for a given water velocity. Empirical measurements of MPS were taken for three morphologically disparate species at the Lizard Island study site to determine how mechanical vulnerability differs between and within species as a function of their size. Additionally, I examine the potential causes and implications of the upper bound of the MPS of colonies over a distinct hydrodynamic gradient which identifies the existence of a mechanical threshold constraining mechanical diversity.

Chapter 4 focuses on spatial and temporal quantification of water motion on a typical coral reef. The objective of this chapter is to investigate the third factor that determines the mechanical integrity of coral colonies (identified in Chapter 2), the maximum water velocity. Using a 37-year historic record of wind speed and direction of the study site area, I undertook an extensive field and modelling exercise to quantify the temporal and spatial variability of water motion at scales ranging from seconds to centuries and from metres to an entire reef. Because the study reef at Lizard Island is typical of many reefs in the GBR Lagoon, the results are suggested to be broadly applicable to other reefs throughout the GBR and potentially worldwide.

In Chapter 5, the results of the previous three chapters are drawn together in the development of a novel method of estimating rates of colony mortality on coral reefs. This method calculates the expected mortality rate due to colony dislodgement from the reef substrate based on the colony’s projected shape and size, the strength of the substrate to which it is attached and the return time of the maximum survivable water velocities at its position on the reef.

CHAPTER 2: The mechanical integrity of coral colonies

2.1 Introduction

Severe wave exposure is the most widespread and destructive form of ecological disturbance that influences coral reef communities (Woodley et al. 1981; Done 1983; Rogers 1993). Cyclonic winds produce large wave climates that subject the primary biological habitat structure, scleractinian corals, to elevated levels of hydrodynamic force which potentially prunes branches or other projections from colonies or dislodges entire colonies from the substrate altogether (Woodley et al. 1981). While colonies may recover from branch removal (partial mortality; Tunnicliffe 1981; Hall and Hughes 1996; Hall 2001), whole-colony dislodgement usually results in mortality. Colony fragments may reattach to the substrate and grow (asexual recruitment; Smith and Hughes 1999), but the colony no longer exists in its original form. Depending on the magnitude of the hydrodynamic disturbance, these mortality events may significantly alter coral assemblage structure and thereby the entire reef community (e.g., Porter et al. 1981; Woodley et al. 1981; Hughes 1984; Dollar and Tribble 1993).

Because of logistical difficulties in recording colony dislodgement during hydrodynamic disturbances, and the fact that such disturbances are both rare and variable in magnitude, quantifying the differential effects of hydrodynamic force as a function of biomechanical properties of colonies during elevated hydrodynamic events is problematic (Done 1983; Denny and Wethey 2001). An alternative approach to understanding these purely physical events, and subsequently inferring ecological change, is through the application of physical principles to the available data on coral biomechanics and disturbance regimes (Denny 1988). Using such principles opens the possibility of predicting the ecological change that will result from hydrodynamic disturbance. This capability may provide an important tool for forecasting the effects of the increase in the intensity of cyclones in coming decades (Walsh et al. 2001) which is hypothesised to be associated with ongoing climate change (Mitchell et al. 1990, Houghton et al. 1996; Nott and Haine 2001). Therefore, with the aid of classical engineering theory, this chapter attempts to approach the first component of this method by comprehensively examining the mechanical integrity of scleractinian corals on coral reefs.

The mechanical integrity of a colony is expected to depend on five primary factors: colony size, morphology, material strength, gravity and hydrodynamic habitat (Wainwright et al. 1982; Denny 1988; Vogel 1996). To introduce and assess the importance of each of these factors, a simple geometric model was conceived that approximates a coral colony by a rigid cylinder attached to the substrate at one end. A cylindrical model was favoured because coral colonies and colony branches can be most closely modelled by radially growing elements where diameter varies as a function off height above the substrate to which the colony is attached (Denny 1988; Kaandorp 1999).

In ecological terms, larger colonial organisms are more generally successful than smaller colonial organisms (Jackson 1979). An example of one of the mechanisms driving this phenomenon is the causal relationship between increased colony size and increased surface area, regardless of morphology, which increases potential resource transfer at this interface (e.g., nutrients, gases and wastes; Jackson 1979; Vogel 1996). Moreover, the competitive ability and reproductive output of corals generally increase with colony size (e.g., Stimson 1985; Lang and Chornesky 1990; Hall and Hughes 1996). In the context of mechanical integrity, however, size establishes the degree to which a colony interacts with the water column, and thus hydrodynamic force (Denny 1988). For the model cylinder of height h and diameter d, the size of a whole-colony or the branch of a colony is defined by

$$A = hd \tag{2.1}$$

where A is the projected area of the colony perpendicular to horizontal water flow.

Colony morphology determines how skeletal mass is spatially distributed in three dimensions and, therefore, also determines the amount of the area upon which hydrodynamic force acts. For example, Graus et al. (1977) found that colonies of *Acropora palmata* in a highly exposed habitat oriented their branches in a way that reduced the hydrodynamic force, whereas colonies in more sheltered habitats did not. Morphology is also responsible for the manifestation of mechanical stress within different regions of a colony (Wainwright et al. 1982). Maintaining a small basal attachment relative to overall colony size, for example, will result in a greater concentration of stress in the colony's base. A colony's morphology is defined by a shape-index, S, where

$$S = \frac{h}{d} \tag{2.2}$$

Consequently, a structure that is taller than it is wide (high h, low d) will have a shape-index of greater than one, whilst a short, stubby structure will have a shape-index of less than one.

The magnitude and frequency of hydrodynamic disturbance to which a colony is exposed depends in large part upon its habitat (i.e., spatial position) on the reef (e.g., Connell et al. 1997). Within these different habitats, the periodic nature of waves subjects the inhabitants of a coral reef to continual changes in water velocity and acceleration (Denny 1988). Such motion induces three types of hydrodynamic force. The first two of these are lift, which acts perpendicular to flow and tends to lift the colony off the substrate, and drag, which acts parallel to flow and tends to push the colony laterally over the substrate. These forces are the result of the viscosity of seawater and are directly related to the size and shape of the colony and the squared flow velocity (Vogel 1996). The magnitude of lift is characteristically small relative to that of drag for coral colonies (Vosburgh 1982; unpublished flume tank data). Lift may become more important for colonies with low shape indices or table-like morphologies, especially if colonies are not strictly aligned with flow or if flow is not strictly parallel with the substrate (Vosburgh 1982; Denny 1999). However, even in lift-promoting scenarios for colonies, this force will never be comparable to drag and the small gain in resolution of force estimation is considered trivial compared to the problems dealing calculating lift for highly variable morphologies (see Wainwright et al. 1979). The third type of hydrodynamic force is a consequence of the inertial properties of water and is a function of colony volume and the acceleration of water past the colony (Vogel 1994). This force will only become significant relative to drag when colonies are large (i.e., greater than 2m diameter) and water acceleration is large relative to velocity (i.e., for Reynolds Numbers between 10^3 and 10^5; Denny 1999). For oceanic and locally generated wind waves with wave periods greater than three seconds, acceleration is substantially smaller than velocity per wave cycle and the inertia force can thus also be ignored (Komar 1997; cf. Massel and Done 1993). In other words, drag force can be expected to dislodge a colony well before lift or inertial forces would. Therefore, the maximum hydrodynamic force to which a coral will be subjected on a reef can be approximated solely by the equation for drag, given by

$$F_h = \frac{1}{2}\rho_w h d u^2 C_d \qquad (2.3)$$

where ρ_w is the density of seawater, u is the flow velocity and C_d is the drag coefficient, which is approximately equal to one for a cylinder at Reynolds numbers between 10^3 and 10^5 (Gerhart et al. 1992; Vogel 1996).

Because the density of coral skeleton is relatively homogeneous throughout a given colony, as a colony gets larger, gravitational force increases proportionally to volume. Gravitational force can have both positive and negative effects on colony integrity. For heavy colonies with low shape-indices, gravitational force counteracts hydrodynamic forces that tend to topple a colony by pulling the colony towards the substrate. However, for heavy colonies with high shape-indices, gravitational force can compound the action of hydrodynamic force, particularly when colonies are not strictly vertical. Gravitational force is given by the equation

$$F_g = \frac{\rho_a g \pi h d^2}{4} \qquad (2.4)$$

where ρ_a is the density of the coral's skeleton, $\pi h d^2/4$ is the colony's volume and g is the universal gravitational constant (~9.81ms^{-2}).

The application of force to a colony is resisted by a colony's internal mechanical stress (Wainwright et al. 1982). A colony, or part of a colony, will fail (i.e., break, for brittle materials) if the level of stress within its structure becomes greater than the strength of the material of which it is composed (Wainwright et al. 1982). There are three primary types of mechanical stress: shear, compression and tension (Gere and Timoshenko 1994). Shear stress is produced in a colony (or colony branch) as it resists force tending to push consecutive cross-sectional layers laterally over one another (Fig. 2.1a,b). Because significant boundary layers do not have space or time to form significantly (relative to colony size) in wave-swept habitats (Vogel 1996), and thus hydrodynamic force can be assumed to act uniformly on the projected area of colonies and branches, the resultant shear stress τ is greatest at the centre of the basal attachment area (Fig. 2.1a,b). For the model cylinder, maximum shear stress is given by

$$\tau_{\max} = \frac{8\rho_w u^2 S}{3\pi} \tag{2.5}$$

(see Appendix 2.1).

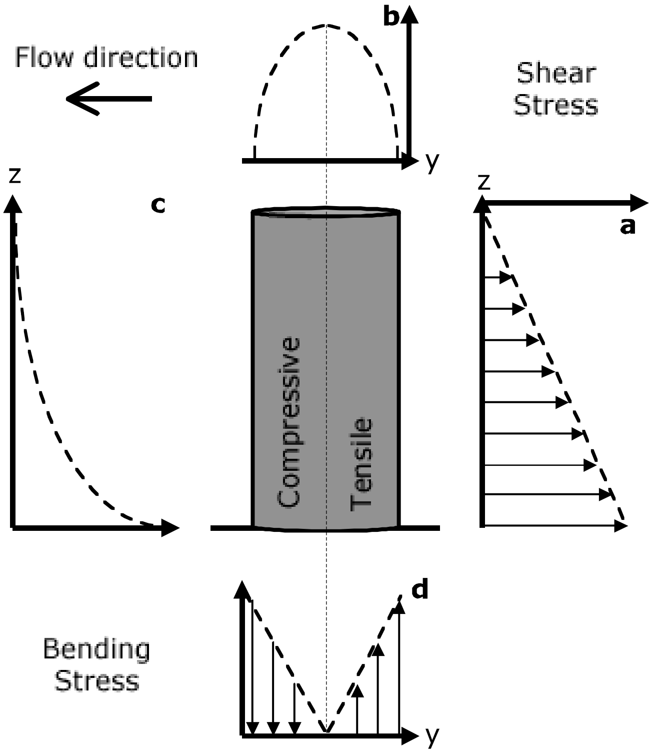

Fig. 2.1: A graphical model of shear and bending stresses within a coral colony (shaded cylinder) given an evenly distributed horizontal hydrodynamic force. a) Shear stress resists lateral sliding of consecutive horizontal layers where stress decreases linearly from a maximum stress at the colony base to zero at the top of the colony. b) At a given distance from the colony base, shear stress is maximal at the colony's neutral plane (dotted line). Compressive and tensile stresses (the "bending stress") develop within a colony equally on opposite sides of the neutral plane. c) Bending stresses decrease quadratically with distance from the base and d) are maximum at the periphery of the base and minimum at the neutral plane.

Compressive and tensile stresses are produced as a colony or branch resists hydrodynamic forces that bend them about their attachment regions, and are also maximal at the base (Fig. 2.1c,d). For a structure with a symmetrical cross-section, such as the typical circle- or oval-shape found at the base of a colony or branch (Veron 1993), the material at the side upon which hydrodynamic force is applied will be in tension and the opposite side will be *equally* under compression (Fig. 2.1d). The maxima of these two stresses occur at the periphery of the cross-section and a plane running down the axis of the structure exists where there is no bending stress (the neutral plane) (Fig. 2.1d). The maximum compressive and tensile stress σ_{max} (i.e., the bending stresses, which are equal but opposite in direction) at the base and periphery of the model cylinder are given by

$$\sigma_{\max} = \frac{8\rho_w u^2 S^2}{\pi} \tag{2.6}$$

(see Appendix 2.1). Gravitational force produces compressive stress that is maximal at the base of the cylinder and is given by

$$\sigma_{\max,g} = h\rho_a g \tag{2.7}$$

Total compressive and tensile stress is the sum of hydrodynamic stress and gravitational stress. That is, gravity adds to maximum compressive stress and subtracts of maximum tensile stress.

Coral colonies are composed of aragonite and the substrate to which they are attached is composed predominantly of magnesium calcite (Barnes 1970, Macintyre and Marshall 1988). Both of these materials belong to the group of brittle crystalline carbonates (similar to limestone and concrete) that are superior in strength when subjected to compressive and shearing loads, but renowned for their inadequacy under tension (Wainwright et al. 1982; Franklin and Dusseault 1989). The compressive strength of crystalline carbonate material is typically an order of magnitude greater than its tensile strength (Callister 1994; Franklin and Dusseault 1989). Moreover, tensile strength becomes progressively weaker as force is applied over a greater cross-sectional area due to a greater likelihood of mechanically significant material flaws (Wainwright et al. 1982). Therefore, because tensile and compressive strength increase equally with distance from a colony's neutral plane, it is expected that the tensile strength of the weaker material at the colony/substrate interface will limit the colony's overall strength.

The model developed above illustrates several key biomechanical features that will be examined further in this chapter for reef corals. First, shear and bending stresses induced by hydrodynamic force are a function of the shape of the colony and are independent of colony size (Eq. 2.6). Moreover, because bending stress is proportional to the square of the shape index, this stress becomes increasingly significant in taller and narrower colonies and branches, whereas shear stress only becomes a critical factor in colonies which are substantially shorter than they are wide (Eq. 2.5). All hydrodynamically-induced stresses increase quadratically with flow velocity (Eq. 2.6). On the other hand, gravitational compressive stress is a function of colony height and is independent of colony shape (Eq. 2.7). This relationship exists because the increase in gravitational force resulting from increase in mass (i.e., due to increase in width) is counteracted by its proportional increase in basal area over which the gravitational force acts. In general, as a given shape gets larger, gravitational stress will augment hydrodynamic compressive stress and diminish tensile stress at the colony base. Finally, because compressive and tensile stresses run parallel to the axis of the colony or colony branch, the material immediately at the other side of the basal attachment interface (the substrate) is subjected to the same level of stress. Therefore, the strength of a structure in bending will be limited by the weaker of these two materials.

Using this model, the aim of this study was to theoretically and empirically explore how the mechanical properties of coral skeleton and the reef substrate limit colony integrity on coral reefs. These aims were achieved by 1) determining which mechanical stress-types limit colony strength, 2) comparing the skeletal strengths of morphological disparate reef corals to the substrate strength, 3) examining spatial variation in coral and substrate strength on a reef and 4) theoretically assessing the likelihood of branch "pruning" or whole-colony dislodgement during hydrodynamic disturbance.

2.2 Methods

2.2.1 Relative importance of stress-types

The relative contributions of shear, compressive and tensile stresses as a function of colony shape and size where estimated using the above model. Levels of these three stress-types were explored for a range of colony sizes (10^{-5} - $10^{1}m^{2}$ projected area, representing coral spat to the largest known *Porites* colony; see Veron 1993) and colony shapes (10:1 – 1:10 height to width ratios, representing a range from thick branching through to semi-encrusting colonies) at a number of different flow velocities (1, 2 and $10ms^{-1}$). The gravitational component of compressive and tensile stresses was calculated using a range of skeletal densities from published studies (see Hughes 1987 for synthesis).

2.2.2 Mechanical testing of coral skeleton and reef substrate

The fieldwork for this study was conducted on the exposed southeast reef at Lizard Island, in the Great Barrier Reef (GBR) lagoon, Australia (14°40' S, 145°28' E). Skeletal material was collected from replicate colonies (n = 10-20) of seven morphologically disparate species of reef coral (*Acropora intermedia* [branching]; *Acropora hyacinthus* [tabular]; *Acropora gemmifera* [corymbose]; *Acropora palifera* [subgenus *Isopora*, convoluted hemispherical]; *Favia favus* [hemispherical]; and *Porites sp*. and *Goniastrea favulus* [encrusting/hemispherical]; Veron 1993). Samples were taken from the periphery and base of colonies, where whole-colony mechanical stress is the greatest (Fig. 2.1d). Additionally, pavement substrate material was chiselled from a number of haphazardly selected areas at the reef crest. Samples were soaked in a mild bleach solution to kill any tissue and epiphytic organisms and then were water blasted to remove dead tissue and dried. The density of samples was measured using Archimedes Principle by measuring the weight first in air and then suspended in distilled water (density equals dry weight divided by dry minus wet weight; Hughes 1987). A number of cores were taken from the skeletal and substrate samples using a 12.5mm diameter diamond-tipped coring piece mounted in a standard drill press, and those with any sign of bioerosion or boring were discarded. The ends of cores were cut at perpendicular angles with a diamond rock-saw and ground with 400μm corundum grit to ensure that force was applied evenly to the cores. Cores for testing under tension were prepared by attaching a plate with hook to the end of each core using epoxy and cutting a 1mm rounded groove (to minimise stress concentrations) around centre of each core to reduce cross-sectional area. Cores broke at the groove rather than at the skeleton/epoxy interface. Compression and tension tests were run using a standard INSTRON testing unit. A spherical seat was used for compression tests to correct for any inaccuracy associated the potential of having slightly non-perpendicular core ends. Purely tensile stress was ensured by using steel wire loops that fit into the steel hooks attached to either end of cores. Tests were run until brittle failure, at which point skeletal strength was calculated by dividing the force of fracture by cross-sectional area.

2.2.3 Spatial gradients in strength of coral skeleton and reef substrate

Typical of many reefs within the GBR lagoon, the profile of the southeast reef at Lizard Island emerges steeply from approximately 20m of water to a distinct reef crest and an extensive reef flat. To determine intra-specific variation in skeletal strength over this profile, sampling was undertaken on the three most abundant of the seven study species (*Acropora palifera* [subgenus *Isopora*], *Acropora gemmifera* and *Acropora* *hyacinthus*; Fig. 2.2) horizontally from the reef crest (0m) to 120m shoreward across the flat. Because an very strong relationship between skeletal density and skeletal strength was found (see below), skeletal strength was estimated using the measurements of density of small samples taken from the colony base, thereby reducing unnecessary damage to living colonies. Skeletal samples were collected from ten randomly chosen colonies at four positions over the reef 40m apart (reef crest, mid, flat, back; see bottom of Fig. 2.5 for details) along two haphazardly positioned reef profiles (transects). Density was calculated and subsequently converted to estimates of compressive and tensile strength using equations derived from the laboratory testing (Eqs. 2.11 and 2.12 below).

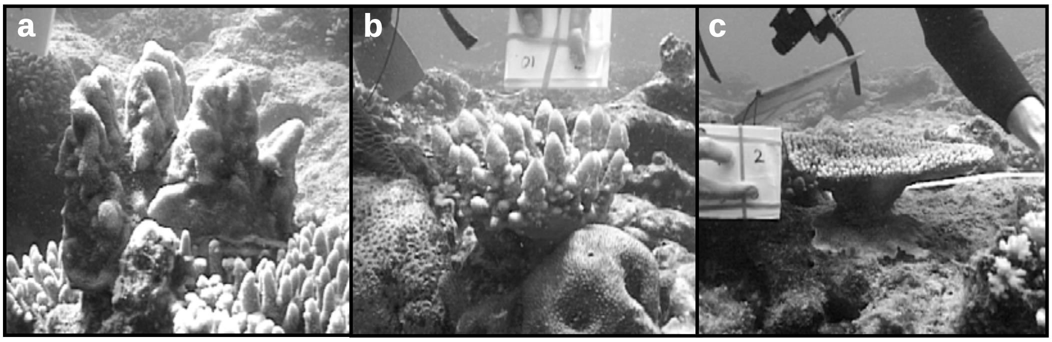

Fig. 2.2: The study species: a) *Acropora palifera* (subgenus *Isopora*), b) *Acropora gemmifera* and c) *Acropora hyacinthus*.

To assess the strength of the substrate over the reef profile, a geomechanical technique, known as dynamic probing, was utilized (Peck et al. 1974; Polous and Davies 1980; Bock 1984; Foruria 1984). This technique involved dropping a known mass a known distance onto a rod (with a known diameter) which was thereby forced into the substrate. The tip of the rod was cone-shaped and hence the standard apparatus is commonly referred to as a dynamic cone penetrometer (DCP). Penetration resistance is the number of blows (drops of the mass) per penetration interval and can be correlated to many material properties, including density and compressive strength (Peck et al. 1974). Because this study was concerned only with the mechanically relevant portion of substrate for corals (the upper 0-20cm), and to enable mobility and replication of tests on the reef, a scaled-down version of the widely used DCP unit was built. To use published DCP correlations for density and strength of carbonate materials, the data (blows per unit distance, or the “N-value”) were converted using a specific energy equivalence ratio (Poulos and Davies 1980; Appendix 2.2).

Substrate tests using the modified DCP unit were undertaken at the same two sites and four positions where skeletal samples were collected. Ten points at each position were haphazardly chosen less than a metre apart in areas that were primarily composed of hard, non-living substrate. At each point, the probing unit was operated for up to 100 blows and the penetration distance into the substrate was measured at ten blow intervals via calibration markings that were etched into the side of the rod. The area that the probe sampled was less than 1cm^2. Measurements were converted to DCP “N-values” and density and compressive strength were estimated at 5mm depth intervals for each replicate at each position at the two sites (Appendix 2.2). These estimates were calibrated with the laboratory core results discussed above, and the best estimate of tensile strength was calculated using the ratio of compressive and tensile strength found for the laboratory cores.

The relative differences between coral skeletal and reef substrate tensile strengths were presented as a ratio (ψ) where a value of less than one indicates stronger substrate and a value of greater than one indicates stronger coral skeleton. Coral and substrate were approximately lognormally distributed (see Results). Therefore, for each combination of species and reef position, median and 95% confidence ranges were calculated using a Monte Carlo simulation of 10^6 independent combinations of coral and substrate strength drawn randomly from their respective empirical lognormal distributions.

2.2.4 Limiting strength of coral colonies: dislodgement versus pruning

A colony or colony branch will fail when the bending stress becomes greater than the strength of the material of which it is composed. Assuming gravitational stress is negligible relative to hydrodynamic stress, the ratio of internal stress to material strength for a colony is

$$\varphi_c = \frac{\sigma_{\max,c}}{\sigma_{[c,s]}} \tag{2.8}$$

where $\sigma_{max,c}$ is the maximum bending stress in the colony and $\sigma_{[c,s]}$ is the smaller of the two values of coral skeleton or reef substrate strength. When φ_c is greater than one, the colony will fail. For a branch on the colony

$$\varphi_b = \frac{\sigma_{\max,b}}{\sigma_{[c]}} \tag{2.9}$$

where $\sigma_{max,b}$ is the maximum bending stress in a branch and $\sigma_{[c]}$ is the strength of coral skeleton. Dividing φ_c by φ_b and substituting Equation 6 gives

$$\varphi = \psi\left(\frac{S_c}{S_b}\right)^2 \tag{2.10}$$

where ψ is the ratio of the limiting strength of the colony $\sigma_{[c,s]}$ and the branch $\sigma_{[c]}$ and S_c and S_b are the shape indices of the colony and colony branch, respectively. If φ is greater than one the colony fails first, if it is less than one, branches fail first, and for unity, dislodging and pruning occur simultaneously.

2.3 Results

2.3.1 The relative importance of stress-type

Levels of shear stress were several orders of magnitude lower than compressive and tensile stresses in scenarios where the mechanical failure of a colony via bending was likely to occur (Fig. 2.3). The only combination of parameters in which shear stress became similar in magnitude to compressive and tensile stress was the scenario in which the colony shape index was so small that bending was almost non-existent (e.g., 1:100; encrusting form) and when the colony was exposed to unrealistic flow velocities (e.g., greater than $30ms^{-1}$). Because brittle crystalline materials are much stronger in shear than in tension, shear stress is never likely to limit the integrity of a colony or its branches on a coral reef.

As water velocity increases, the compressive and tensile stresses increase equally on each side of the model colony. Eventually a colony size is reached where gravitational compressive stress began to significantly augment compressive stress and diminish hydrodynamic tensile stress, and divergence of the two stress-types occurs (Fig. 2.3). As mentioned above, the maximum tensile strength of a brittle crystalline material is generally an order of magnitude smaller than its compressive strength. If this general rule marks the upper bound for tensile strength in coral skeleton (demonstrated empirically below), then tensile strength will limit the integrity of coral colonies until the point at which the divergence of the two stress-types, tensile and compressive, reaches an order of magnitude (Fig. 2.3). However, as flow velocity increases, the divergence between compression and tension diminishes. Therefore, colonies that mechanically fail due to hydrodynamic force are limited by the tensile strength of their skeleton or that of the substrate to which they are attached.

Compressive strength will only be limiting due to gravity in a scenario where both colony size is very large (e.g., greater than $2m^2$) and the limiting material is considerably weaker than that which is characteristic of crystalline carbonates (e.g., due to a high proportion of bioerosion and/or boring per unit volume).

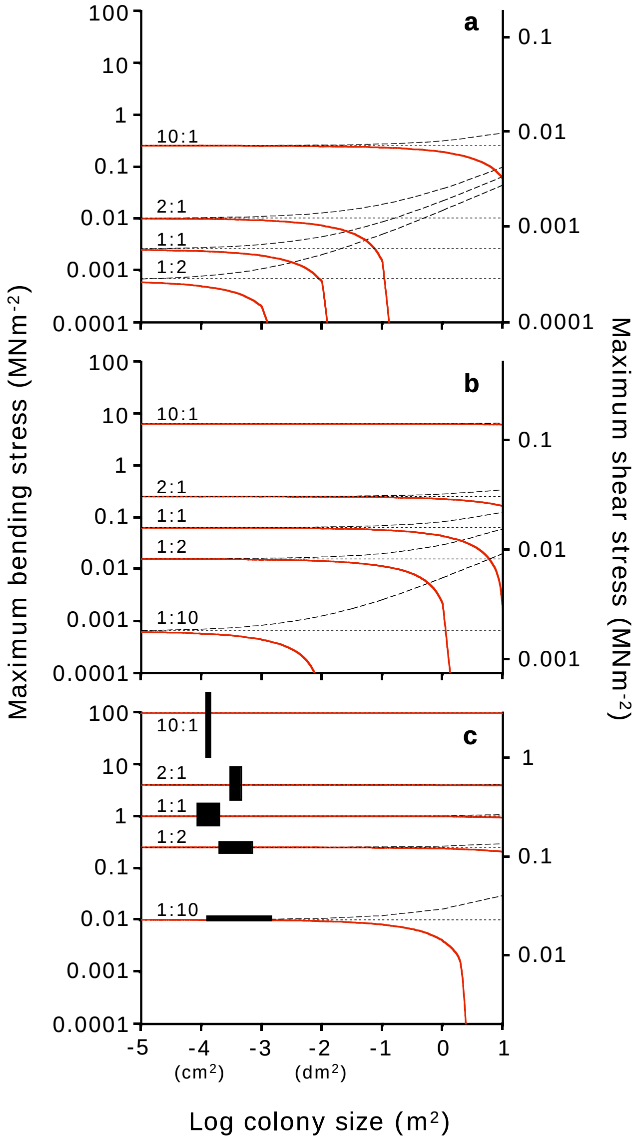

Fig. 2.3: The maximum quantities of the three stress types (tensile [solid line], compressive [dashed line] and shear [dotted line]) as a function of log colony size (x-axis) for five shape indices ranging from encrusting (1:10) through isometric (1:1) to branching (10:1). Relative differences in stress-types are illustrated at three flow speeds: a) $1ms^{-1}$, b) $2ms^{-1}$ and c) $10ms^{-1}$. The projected shape of model cylinders of the various shape indices is given as a visual guide in c).

2.3.2 Mechanical testing of coral skeleton and reef substrate

Coral skeleton and reef substrate were on average 11.5-times stronger under compression than they were under tension, and this disparity increased for species' with stronger skeleton (Fig. 2.4). The ratio of compressive to tensile strength was on average 5-fold for hemispherical and semi-encrusting *Favia favus* and *Goniastrea favulus*, whereas the greatest average difference (17-fold) was for the staghorn *Acropora intermedia*. The reef substrate was on average 10.1-times stronger in compression than in tension, closely approximating theoretical estimates for crystalline carbonate materials (i.e., to within an order of magnitude). By taking the average ratio of compressive to tensile strength (11.5), rough estimates of tensile strength for species from other studies, which in all cases only measured compressive strength, were calculated (Fig. 2.4).

There was a marked relationship between skeletal strength and species' morphology for both the above three species and for species from the literature (Fig. 2.4). Skeleton from structurally delicate growth forms, such as branching and tabular morphologies, sustains significantly greater mechanical loads than does skeleton from more robust species. The skeleton of the staghorn *Acropora intermedia*, for example, was on average 10-times stronger in tension than skeleton from hemispherical/semi-encrusting *Porites sp.* The strength of the substrate was in general very low compared to that of coral skeleton for laboratory core measurements. The only species whose skeletal material exhibited a lower tensile than that of substrate was the hemispherical/encrusting *Porites sp.*

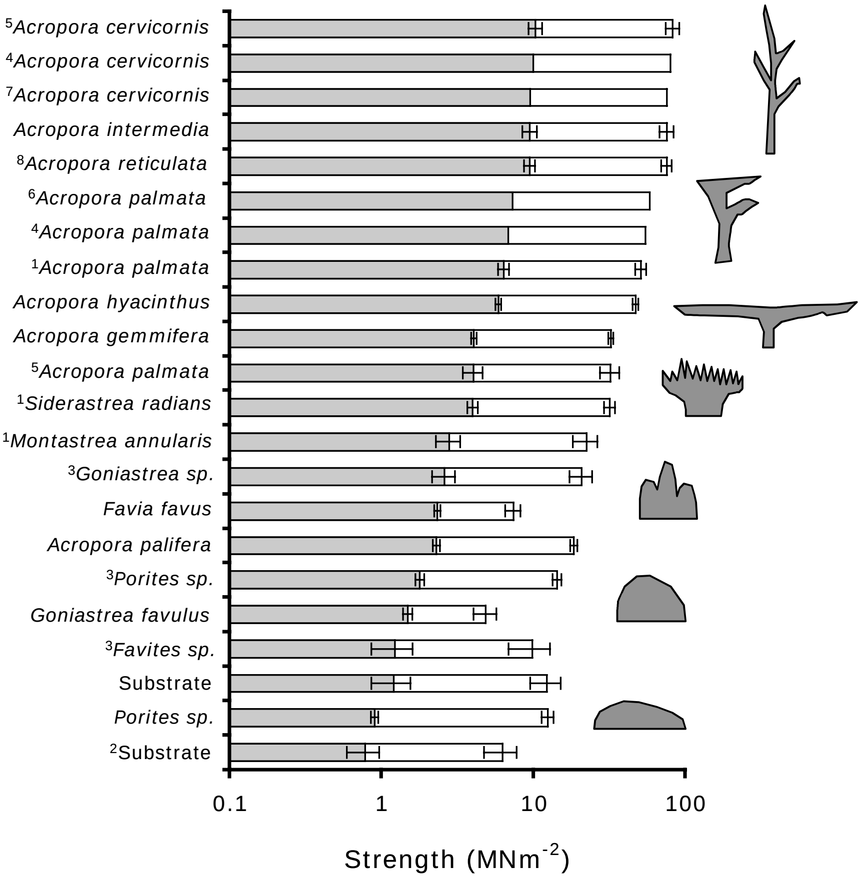

Fig. 2.4: Compressive (open bars) and tensile (shaded bars) strengths of skeleton for a range of morphologically disparate coral species from this study and the literature (log10 scale). [1]Chamberlain (1978), [2]Foruria (1984), [3]Foster (1974), [4]Schuhmacher (1984), [5]Schuhmacher and Plewka (1981), [6]Shapiro (1980), [7]Tunnicliffe (1978), [8]Vosburgh (1982) (skeletal and substrate materials from this study have no index). Note that compressive and tensile stresses are vectorially opposed and have both been plotted along the positive x-axis only for the purpose of comparison.

A clear exponential relationship ($r^2 = 0.85$ for compression 0.87 for tension) was found between the strength of coral skeleton and its density (Fig. 2.5). In compression, the relationship was

$$\sigma = 0.12e^{2.7\rho_a}, \qquad (2.11)$$

indicating that for the maximum density of aragonite (2.94cm^{-3}; Hughes 1987), the predicted maximum compressive strength would be approximately 315.9MNm^{-2}, which is similar to projections made for this value by Chamberlain (1978). In tension, the relationship was

$$\sigma = 0.08e^{1.8\rho_a}, \tag{2.12}$$

indicating a predicted maximum possible strength of aragonite in tension of 16.8MNm^{-2}. The regression models (Fig. 2.5) indicate that as skeletal density increases, the compressive strength of coral skeleton increases at a greater rate than for tensile strength. Compressive strength is an order of magnitude greater than tensile strength at densities greater than approximately 2gcm^{-3}. Below this point, the disparity is smaller. The strength of the surface reef substrate was substantially lower for both stress types of a given density when compared to coral skeleton (Fig. 2.5). The disparity between substrate and skeleton strength will be addressed in detail below.

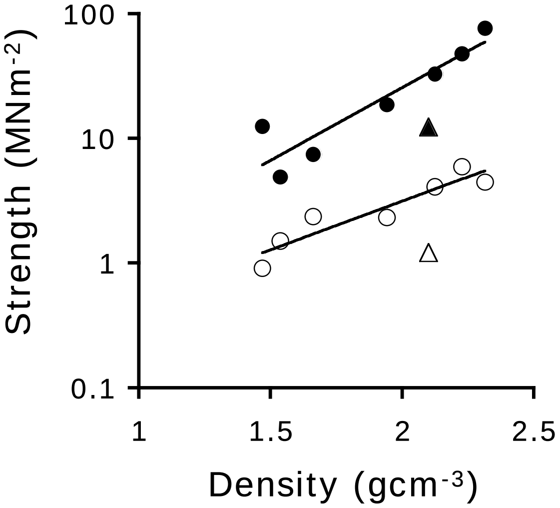

Fig. 2.5: Compressive (solid) and tensile (open) strength of coral skeleton (circles) and reef substrate (triangles) as a function of density. Each circle represents the average strength and density of the seven coral species measured in this study (in order from left to right along the x-axis: *Porites sp., Goniastrea favulus, Favia favus, Acropora palifera, Acropora gemmifera, Acropora hyacinthus* and *Acropora intermedia*). The regression model lines were calculated for coral skeleton (solid lines, see text for details).

2.3.3 Spatial gradients in strength of coral skeleton and reef substrate

Significant declines were found in skeletal and substrate density and strength from the crest shorewards towards the back of the reef (Fig. 2.6a,b). For the three study species, skeletal density and strength differed significantly between species (F = 6.8, df = 2, P < 0.000) and among the four stations (F = 14.2, df = 3, P < 0.001). Tukey's posthoc analysis grouped *Acropora hyacinthus* and *Acropora gemmifera* into the same homogeneous subset, with significantly denser and stronger skeleton than *Acropora palifera*. Additionally, the crest and mid-transect positions grouped into a homogeneous subset and the reef flat and back grouped into another.

The density and strength of coral skeleton from these three species were substantially greater than those of the reef substrate. The density and compressive strength of reef substrate differed significantly among locations on the reef and vertically with depth into the substrate (F = 12.9, df = 3, P = 0.030). Posthoc analysis separated the crest with significantly denser and stronger substrate from the mid and flat positions that, in turn, were significantly greater than the reef back. In comparison to coral skeletal strength, the estimates of substrate tensile strength (determined using the empirical ratio of compressive to tensile strength) showed over an order of magnitude more variation. Furthermore, the reef substrate was significantly denser and stronger within the first few centimetres of crust than deeper layers, and became increasingly weak with depth (F = 16.4, df = 5, P = 0.023, Fig. 2.7a,b). Between 150 and 180mm into the substrate, the average strength was approximately six times lower than the 30mm surface layer.

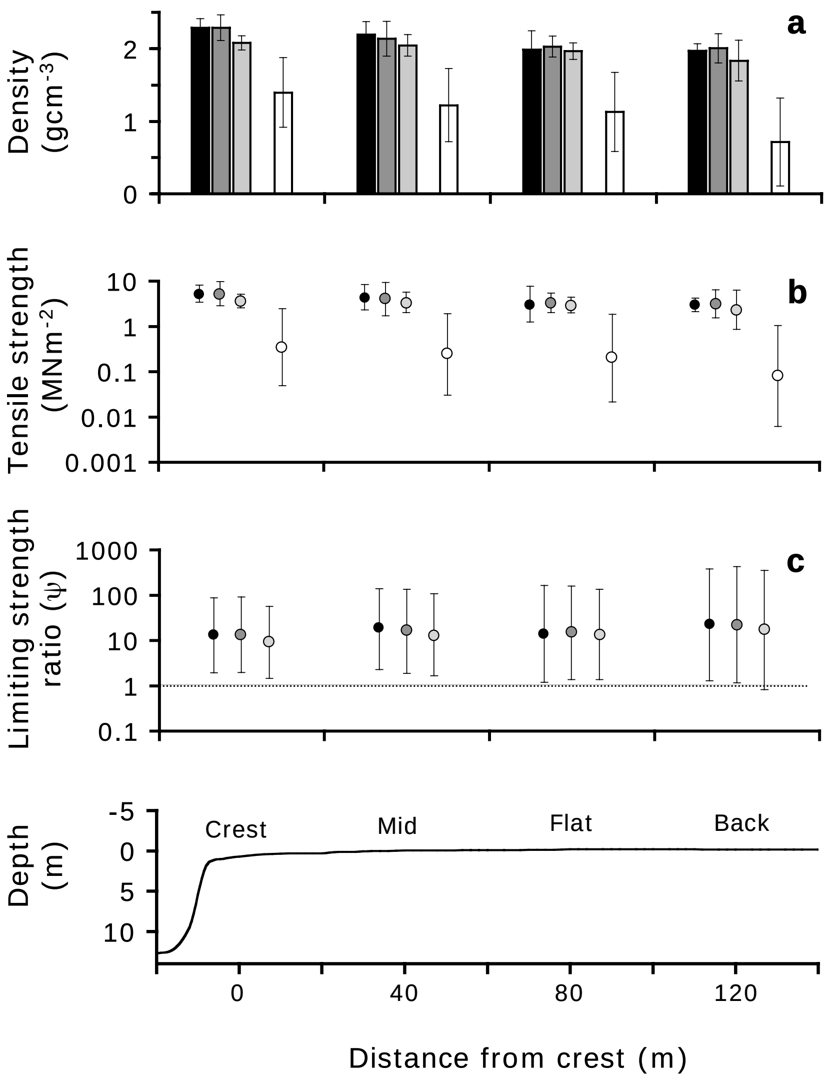

Fig. 2.6: a) Mean material density of *Acropora hyacinthus* (black), *Acropora gemmifera* (dark), *Acropora palifera* (grey) and the substrate (white) at four position across the reef profile (±95% confidence intervals). b) Mean tensile strength for the same coral species and substrate over the reef profile (±95% confidence intervals). c) Median limiting strength ratios for the three coral species relative to reef substrate (±95% confidence ranges, see text for details).

Using strength estimates from the upper 6cm of reef substrate, the limiting strength ratio *ψ* (the ratio of skeleton to substrate strength) became progressively larger toward the reef back where coral skeleton was approximately 5-10 times stronger than the substrate (Fig. 2.6c). Moreover, the 95% ranges of the limiting strength ratios for each species at each position over the reef showed variation of approximately two orders of magnitude. At the reef back, where variation was the greatest, 95% of Monte Carlo simulations ranged between one (substrate and skeletal strength equal) and over 400 (skeleton 400-times stronger than substrate). Illustrated by a dotted line in Fig. 2.6c, almost every colony was limited by the tensile strength of the substrate.

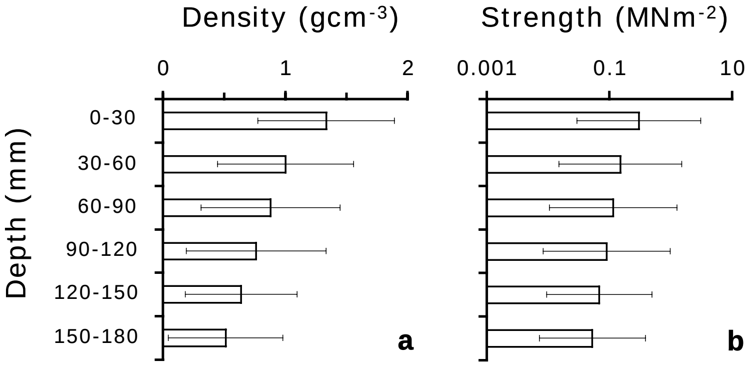

Fig. 2.7: Mean substrate density (a) and tensile strength (b) as a function of substrate depth (±95% confidence intervals).

2.3.4 Limiting strength of coral colonies: dislodgement versus pruning

Whether a whole-colony or its branches are likely to fail first as hydrodynamic force increases (i.e. as a result of increased flow velocity) depends on the relative shape of these structures and the limiting strength ratio (ψ) of skeletal and substrate materials (Fig. 2.8). An approximately isometrically shaped colony (i.e., a shape-index of one), for example, with branches that have a shape-index of two (i.e., height is twice width) is likely to be initially pruned given that its skeleton and the substrate are similar in strength ($\psi = 1$). However, if the substrate is an order of magnitude weaker in tension than the colony's skeleton (dashed line, Fig. 2.8), then it is unlikely that this colony will ever lose branches before the whole-colony is physically dislodged. The limiting strength ratios found in this study (>10, Fig. 2.6c) illustrated, in general, that branch removal is highly unlikely to occur before whole-colony dislodgement (Fig. 2.8). However, pruning may potentially occur on colonies with low whole-colony shape indices and high branch shape indices or in scenarios where skeletal strength has been significantly weakened (e.g., as a result of bioerosion).

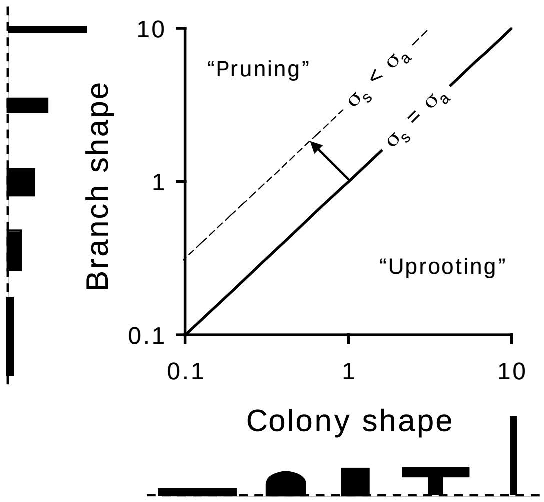

Fig. 2.8: Plot of a model colony's overall shape against its average branch shape. The solid line represents the theoretical threshold between whole-colony dislodgement and branch removal given that skeletal and substrate strengths are equal. The dashed line indicates the displacement of the threshold if coral skeleton is an order of magnitude stronger than the substrate. For colonies attached to a substrate weaker than the strength of its skeleton, pruning is unlikely to occur unless the shape index of branches is significantly higher than that of the whole colony.

2.4 Discussion

This study has demonstrated that the mechanical limitations of coral colonies during hydrodynamic disturbance are primarily dependent on three of the expected five factors outlined in the Introduction: 1) the colony shape, which determines the extent that a colony interacts with water flow, 2) the maximum horizontal water velocity, which determines the amount of hydrodynamic drag force exerted on the colony, and 3) the limiting tensile strength of the carbonate materials at the colony/substrate interface. Results strongly suggest that substrate strength limits the integrity of coral colonies during hydrodynamic disturbance for the majority of species and growth form that are vulnerable to mechanical dislodgment on the reef. Furthermore, branch pruning, which subsequently reduces the force acting on a colony, is likely to be a rare phenomenon except in cases where branch shape-indices are substantially greater than whole-colony shape-indices or where skeletal strength has been significantly weakened by agents such as bioerosion.

2.4.1 Limits to colony size

An unexpected result of this study was the insignificant contribution of gravitational stress to hydrodynamic mechanical stress for all but the very largest colonies on coral reefs (i.e., > 1m^2 projected area; Fig. 2.3). This contribution further decreased as hydrodynamic forces reached levels where colonies were at risk of mechanical failure. Although gravitational force will not significantly alter the outcome of destruction during hydrodynamic disturbance because the vast majority of colony sizes are typically less than 1m^2 projected area (Done 1982; Veron 1993), gravity clearly presents two size-related phenomena: 1) "size refuges" for low shape-index colonies and 2) the absence of large high shape-index colonies on coral reefs. Gravitational force counteracts hydrodynamic bending by holding low shape-index (i.e., short and wide) colonies on the reef. As these encrusting/hemispherical colony shapes increase in size, colony mass potentially becomes great enough to counter maximal hydrodynamic forces (illustrated by rapid divergence of tensile stress in Fig. 2.2). Moreover, a size can be attained where a colony may no longer needs to be attached to the substrate for a given hydrodynamic regime (Fig. 2.8; see Appendix 2.1 for derivation). This figure demonstrates the velocity thresholds above which unattached model colonies, for a range of sizes and shapes, will be toppled. Except for the most benign flow habitats, size refuges only operate for larger colonies with lower shape indices. Large hemispherical colonies (e.g., *Porites spp.* and *Diploastrea heliopora*) may reach these refuges given sufficient time between hydrodynamic disturbances in their habitats (Massel and Done 1993). However, colonies of the size where gravitational force is predicted to overwhelm hydrodynamic force are typically rare on coral reefs (Done 1983) and, contrary to theoretical expectation, are usually found in hydrodynamically sheltered back-reef habitats (Veron 1993).

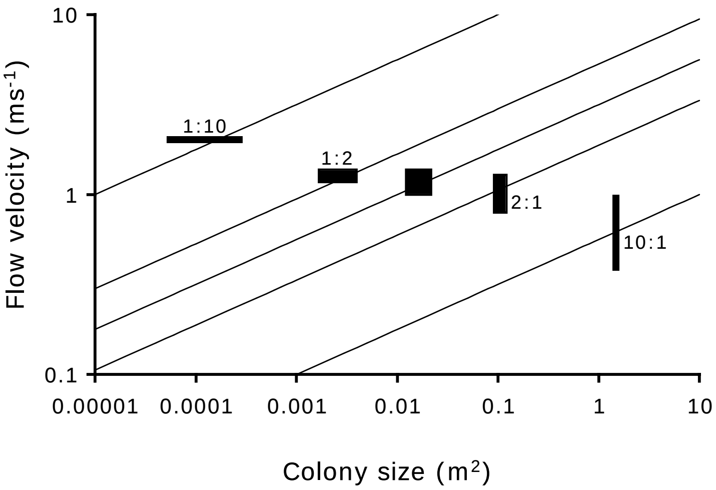

Fig. 2.9: The theoretical dislodgement thresholds (solid lines) for unattached colonies as a function of colony size, flow velocity and colony shape index (illustrated by black projected shapes). Unattached colonies that assume a position above the threshold will be predicted to topple over.

In contrast to low shape-index colonies, gravity augments bending moments for high shape index colonies (e.g., thick branching and tabular). For example, as a branch deviates from vertical, the bending stresses at its base become progressively greater. Therefore, large colonies with high shape indices are unlikely to exist on shallow reefs without some form of support to alleviate severe bending stresses (e.g., hay-stacking of staghorn and elkhorn colonies, Tunnicliffe 1979, Chamberlain 1978, and peripheral fusion of neighbouring tabular colonies, T. P. Hughes pers. comm.).

2.4.2 The limiting strength of coral colonies

Quantification of substrate strength on the reef at Lizard Island and comparison with the skeletal strengths of a range of coral species suggested that, for the majority of reef corals, the substrate would limit a colony's mechanical integrity (Fig. 2.4). Moreover, the highly variable and independent nature of substrate strength at small spatial scales (<1cm) demonstrated that at larger spatial scales (e.g., the scale of colony attachment area) strength would approach the reef local mean (Fig. 2.6). That is, as a colony grows its basal area spreads increasingly over the substrate. Initially, when the base has a small diameter, little substrate is occupied and, by chance, the strength of this substrate, and consequently the colony, will be more unpredictable. However, as the colony spreads further, the probability that both strong and weak substrate is intercepted increases and the overall substrate strength will approach the local average.

The differences in the magnitude and variability of substrate and skeletal strength are likely to result from the different processes by which they are created. Coral reef substrate is formed by diagenetic cementation of coral rubble and other reef materials following adequate primary stabilisation (Rasser and Riegl 2002). The resulting internal structure varies with respect to the type of rubble framework, the degree of bioerosion and the amount of filling of both borings and cavities by lithified internal sediment, and the degree of submarine cementation (Macintyre and Marshall 1988). Magnesium calcite is the predominant compound found in submarine cements, although this is often infused with aragonite (Macintyre and Marshall 1988). The reef substrate is therefore a heterogeneous conglomerate containing a mix of partially eroded rubble, a range of crystalline materials, variable sized voids, material interfaces, micro-flaws and living organisms. Given this characteristically variable nature, a high level of mechanical variation in the substrate material was not unexpected. The greater substrate strength at the crest versus the flat is probably attributable to greater cementation and therefore binding strength of materials at the crest, where wave action is stronger. This phenomenon has been noted in past studies and syntheses (e.g., Macintyre 1985; Buddemeier and Oberdorfer 1986; Macintyre and Marshall 1988; Rasser and Riegl 2002), but its nature on the reef in space and time, and particularly how this may influence colony survival during hydrodynamic disturbances, has not been conclusively investigated.

Reduction in the density of reef substrate and coral skeleton at the scale of the colony via bioerosion reduces these materials' strengths (Wainwright et al. 1982; Tunnicliffe 1981). By selecting test cores devoid of bioerosion for laboratory testing, the resulting strengths are likely to accurately represent the upper range of possible material strengths on the reef. This accuracy was necessary in the present study to construct a reliable relationship between skeletal density and strength. The collection of coral skeletal and the geomechanical probing of substrate over reef transects, however, measured the strength of haphazardly selected materials that were likely to contain bioerosion. Therefore, these results likely provided accurate estimates of material strength on the reef, inclusive of bioerosion.

The "One Hoss Shay" principle (Denny 1988) suggests that to minimise material requirements (i.e., to increase metabolic savings), every point within a load-bearing structure should be only exactly as strong as is mechanically necessary. Therefore, when pushed to the point of failure, every point will theoretically break simultaneously. Why, then, do corals build skeletons much greater in strength than the substrate to which they are attached? Initially, it was expected that increased skeletal strength would reduce the chance of hydrodynamic branch pruning. However, for the average deficiencies in substrate strength found in this study (ψ = 10-20), the attachment areas of branching morphologies are likely to fail well before their branches fail (Fig. 2.8). Five other possible explanations exist for the unexpectedly high skeletal strengths found. First, high strength may be maintained in the unlikely event that a coral will intercept equally strong substrate. Second, the reef substrate at Lizard Island may be mechanically inferior to that of other reefs. Third, a significant proportion of scleractinian evolutionary history may have occurred on stronger substrates such as granite or volcanic materials. Four, high strength may reduce predation of coral tissues. Finally, corals may have little control over the density of skeletal formation, which may be related to ambient levels of dissolved calcium carbonate in the water column.

2.4.3 Spatial gradients of substrate and skeletal strength over the reef

The strength of reef substrate significantly increased towards the reef crest, coinciding with increasing hydrodynamic exposure. Additionally, the substrate strength was substantially greater at the surface than deeper, where bending stress of a coral colony is greatest. Although both of these gradients in reef lithification are well known to reef geologists (see Macintyre and Marshall 1988 for review), their levels on the reef may have significant ecological consequences by contributing to the determination the range of colony shapes that can persist spatially over on a reef. Reef lithification is a near-surface phenomenon that tends to be correlated with water motion (Macintyre and Marshall 1988). Therefore, the vertical (depth) and horizontal (across reef) gradients in substrate strength found in this study are likely to be a common occurrence on seaward or windward profiles of many coral reefs, both of which are areas that are prone to hydrodynamic disturbance.

The existence of two conflicting physical gradients (hydrodynamic and substrate strength) generates a scenario in which stronger substrate coincides with the areas of greater hydrodynamic action on a reef profile (Chapter 4 and this chapter, respectively). In the absence of a substrate or colony strength gradient, a hydrodynamic gradient might limit the various shapes on colonies nearer to the crest through increased rates of colony removal. Conversely, in the absence of a hydrodynamic gradient (flow velocity constant over the reef), colonies further from the crest where the substrate becomes (on average) weaker might be dislodged (on average) more readily. The summation of these two thresholds creates a theoretical continuum where colonies at the crest are removed due to severe hydrodynamic force and colonies furthest from the crest are removed because the substrate is too weak to contend with hydrodynamic forces. These scenarios open the possibility that a mechanical refuge exists in the middle of this gradient. Testing this idea requires devising techniques for quantifying colony morphology from a mechanical perspective and is the objective of the next chapter. An objective quantification of colony mechanical vulnerability will allow for investigation of inter- and intra-specific differences in colony mechanical vulnerability and how these differences potentially constrain species growth over the hydrodynamic gradient through differential rates of colony dislodgement.

CHAPTER 3: Measuring and comparing biomechanical variation in reef corals

3.1 Introduction

Hydrodynamic disturbance is a ubiquitous source of mortality in coral reef communities (Connell 1978; Rogers 1993; Hughes and Connell 1999). Strong winds that produce larger than normal wave climates can pummel shallow reef platforms and dislodge the sessile reef corals that reside there (Woodley et al. 1981; Dollar and Tribble 1993). Because corals form the primary habitat structure on reefs, a large number of associated organisms that live among and within them are also adversely affected if corals are dislodged (e.g., Woodley et al. 1981; Porter et al. 1981; Lewis 1998). For these reasons, the fundamental role of disturbance as a process structuring reef communities has received much attention (Darwin 1842; Stoddart 1963, 1969; Shinn 1976; Highsmith 1980; Knowlton et al. 1981; Woodley et al. 1981; Dollar 1982; Dollar and Tribble 1993; Connell et al. 1997). In particular, much past research has focused on how coral reef communities recover following disturbance events. This research has subsequently elucidated some of the mechanisms by which such destructive events can promote the maintenance of community diversity over time (Connell 1978; Pearson 1981; Colgan 1987; Tanner et al. 1994).

Despite the demonstrated importance of hydrodynamic disturbance in driving the dynamics of coral reef communities, no framework currently exists for quantitatively linking a colony's morphological characteristics to its susceptibility to hydrodynamic disturbance. It is often assumed that, given the same external physical conditions, a delicate branching colony will mechanically fail (e.g., be dislodged) before a robust hemispherical colony. However, formalising these differences in physical terms would allow quantification of species- and size-specific differences in vulnerability to physical disturbance. Such a predictive, mechanistic understanding of the effects of disturbance on a community is essential if we are to accurately model coral reef community dynamics over time.

Results presented in Chapter 2 established that the potential dislodgement of a colony by water motion is a function of three factors: 1) the maximum horizontal water velocity, 2) the tensile strength of the substrate to which the colony is attached and 3) the colony’s projected shape perpendicular to water flow. The first two of these factors characterised properties of a colony’s external environment. The third factor, however, the projected shape of a colony, represents an intrinsic property of the colony and determines the degree to which hydrodynamic force is translated as mechanical stress at the colony/substrate interface. Only upon this variable does the animal exert any degree of ecological and evolutionary control (Graus et al. 1977; Jackson 1979; Chappell 1980; Veron 1993; Kaandorp 1999), and thus it is this factor which is the focus of this chapter.

The primary objective of this study was to apply the biomechanical theory developed in Chapter 2 to develop a technique to quantitatively predict the maximum stress that a colony transmits to the reef substrate under a given water velocity. This objective was achieved through the development of a measure, the maximum predicted stress (MPS), which defines the amount of stress that a colony experiences at its base for a given level of water velocity. If the water velocity is such that the basal stress created within the colony is equal to or greater than the strength of the substrate, breakage at the colony/substrate interface will occur. The second objective of the study was to use the MPS to compare the mechanical vulnerability of individuals from populations of three morphologically disparate species to quantify differences in mechanical integrity. The third objective of this chapter was to characterise the relationship between MPS and colony size to determine how mechanical vulnerability changes as a result of colony growth. The fourth and final objective of this study was to ascertain whether the patterns of MPS found within colonies of the study populations varied from the reef crest to the reef back in a manner consistent with predictions based on the associated gradient in hydrodynamic exposure.

3.2 Methods

3.2.1 Calculating the maximum predicted stress

For the purpose of the present study, four simplifying assumptions were made to reduce the number of model parameters. Due to the highly variable nature of coral colony growth and distribution on a reef, the first assumption was that there was no appreciable sheltering effect by neighboring colonies. The second assumption was that pressure drag is the primary process transmitting force to coral colonies, and therefore that forces associated with lift and water acceleration are secondary and negligible (see Chapter 2 and Denny [1999] for justification). Pressure drag, F_{drag}, is produced by loss of fluid momentum due to viscosity and is generally expressed in the form (Vogel 1996)

$$F_{drag} = \frac{1}{2}\rho_w C_d U^2 A_{proj} \tag{3.1}$$

where ρ_w is the density of water, C_d is the drag coefficient (a measure of the extent to which water interacts with shape), U is the water velocity and A_{proj} is the projected area of the colony perpendicular to flow. The second assumption was that the drag coefficient of a coral colony is approximately equal to one. For corals, the only study that has examined drag coefficients for corals found that drag coefficients ranged between 0.82 and 1.02 for a tabular species, *Anacropora reticulata* (Vosburgh 1982). Other experiments on a variety of biological shapes show that drag coefficients typically range between 0.5 and 1.5 (Vogel 1996; Gaylord et al. 1994; unpublished data). Because colonies are generally circular in horizontal cross section, coral colonies are geometrically similar to rigid cylinders with variable diameters. For the range of Reynolds numbers corresponding to a colony in its hydrodynamic habitat (approximately 10^3 - 10^5), a cylinder will have a constant drag coefficient of one (see Gerhart et al. 1992). The third assumption was that no appreciable vertical velocity-gradient in water flow exists from the substrate to the top of the coral colonies. This assumption is made because the periodic water motion caused by waves prevents the development of any substantial boundary relative to the height of even a small coral colony (Vogel 1996), and in shallow marine habitats the water motion generated by waves varies insignificantly as a function of height above the substrate (see Chapter 4 for further justification). With these assumptions in mind, the force acting on a colony (for a given water velocity squared) is directly proportional to the colony's projected area:

$$\frac{F_{drag}}{U^2} = \frac{\rho_w}{2} A_{proj} \tag{3.2}$$

The application of force to a structure attached to a solid substrate, such as a coral colony, produces three types of internal stress: compressive, tensile and shear (Wainwright et al. 1979; Chapter 2). Coral colonies are limited by the maximum tensile stress at the periphery of the base of the colony (Chapter 2). Tensile and compressive stresses are produced as a colony resists bending about the substrate to which it is attached, and does so equally on either side of the neutral axis (Fig. 3.1a). Finding the stress produced by a force that bends a colony requires the calculation of theoretical moments of area about the substrate (Fig. 3.1). The magnitudes of these moments are equal to the product of the hydrodynamic force weighted by the perpendicular distance to each axis from the point upon which it acts. A given force will produce a greater bending moment when applied to the top of a colony than when applied at the bottom of a colony (i.e., the colony acts as a lever). As the force is directly proportional to projected area (for a given flow velocity squared) and the force acts equally over the projected area (Eq. 3.2), the bending moment (per water velocity squared) is the double integral of the force applied to each point on the colony, weighted by that point's distance from the base:

$$\frac{M}{U^2} = \frac{\rho_w}{2} \iint_A f(x,y)g(y)dA, \tag{3.3}$$

where *f(x,y)* is a function describing the outline of the colony in the (x,y) plane perpendicular to flow, and *g(y)* is a linear weighting function simply equal to *y*.

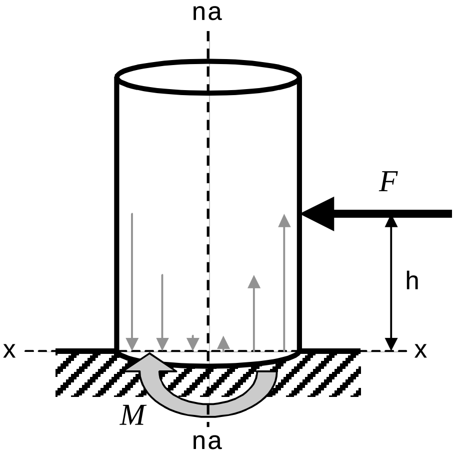

Fig. 3.1: The magnitude of the bending moment (*M*) about the substrate and subsequent compressive and tensile stresses (grey downward and upward arrows respectively) are a function of the force (*F*) and the height at which the force acts above the substrate (*h*). Compressive and tensile stress is zero at the neutral axis (na) and maximum at the periphery.

By approximating the basal cross-sectional area of a colony as an oval, the maximum predicted stress (MPS) produced at the periphery in the base of a coral colony (for a given water velocity squared) is given by:

$$\sigma_{mps} = \frac{16\rho_w M}{\pi(d_{para}^2 d_{perp})} \tag{3.4}$$

(see Appendix 3.1 for derivation). d_{para} is the width of the base (i.e. diameter) of the colony parallel to water flow and d_{perp} is the width perpendicular to water flow. Because this is actually a measure of stress (units: Nm^{-2}) per flow velocity squared (units: m^{2}s^{-2}), the units for MPS are Ns^{2}m^{-4}. The higher the MPS, the greater the maximum stress produced at the colony/substrate interface for a given water velocity and the more mechanically vulnerable the colony is. If velocity increases to the point where the MPS is equal to or greater than the limiting strength of the colony, breakage will theoretically occur at the base. Thus, hydrodynamic events potentially impose an upper limit to MPS, with those colonies exceeding these limits being dislodged from the substrate under excessive hydrodynamic force.

3.2.2 Data collection

The study was conducted at two sites at Lizard Island in the northern GBR lagoon, Australia. The study sites, South Island and Bird Islet, were typical of exposed reefs in this region in that they are composed of steep reef slopes, shallow exposed crests and extensive reef flats. Three species of scleractinian reef coral were selected at these sites based on two criteria: 1) that individuals were abundant from the reef crest to 80 metres across the flat towards the back of the reef, and 2) that the species each had characteristic growth forms which were likely to exhibit different levels of maximum predicted stress (MPS). The first species, *Acropora palifera* (subgenus *Isopora*), forms sturdy sub-massive mounds with the largest attachment area relative to colony size (Fig. 2.2a). The second species, *Acropora gemmifera*, forms corymbose (bushy) colonies with a geometrically variable substrate attachment (Fig. 2.2b). The final 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 (Fig 2.2c).

To take the required photographs to calculate MPS, four belt transects (each 80m long and 2m wide) were laid at each site 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 $160m^2$-transect areas were digitally photographed and their position along the hydrodynamic gradient (distance from the reef crest) was recorded. For each colony, two photographs were taken on the horizontal plane, as well as parallel and perpendicular to the reef crest, to obtain the information required to calculate MPS.

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 10cm scale-plate were digitised and recorded as xy-coordinates. A computer program (available from the author) measured the area encompassed by the colony outline, the width of the colony at the base and the bending moment according to Eq. 3.3. The latter was solved numerically because the two-dimensional colony outlines could not feasibly be described as continuous parametric functions. Using the basal width d_{perp}, the projected area A_{proj}, the bending moment M_{bend} (extracted from the colony photograph taken perpendicular to the crest) and the basal width d_{para} (from the parallel photograph), the MPS for each colony was calculated according to Eq. 3.4.

3.2.3 Data analysis

Because the range of MPS values was distributed lognormally, the magnitude of differences in MPS between species and between sites was visualised by calculating means and standard errors on log-transformed data. A two-way ANOVA was used to determine whether any differences were statistically significant. Agreement with the assumptions of ANOVA was assessed through inspection of normal qq plots of standardised residuals and plots of standardised residuals against predicted values.

The horizontal projected area of a colony perpendicular to the prevailing wave motion, A_{proj}, was used as a proxy for colony size. The use of this proxy was justified by the fact that for the study's purposes, the horizontal projected area represents the primary surface area upon which force is acting, thus differences in three-dimensional size between colonies should not have contributed to differences in force-induced stress between colonies. For each species, the relationship between colony size and MPS was explored using regression analysis. Both variables were log-transformed and data clouds exhibited increasing variance with increasing colony size. Therefore, a regression model was formulated in which standard deviation was a linear function of colony size (see Appendix 3.2 for derivation). This model was fit to data by numerical maximum likelihood methods (using the function “optim” in the software program R). Because assumptions of standard linear regression were violated (i.e., variance is not independent of colony size), nonparametric correlation was used to estimate the association between colony size and MPS.

Regression analysis was also used to quantify the general relationship between the log-transformed MPS levels of colonies and their distance from the reef crest. Unevenness of variances over the reef again required the use of a regression model with standard deviation as a linear function of distance from the crest. Levels of MPS in colonies of *Acropora hyacinthus* were not normally distributed for various intervals over the reef. However, variation in MPS values was well-characterised by a truncated normal distribution (i.e., an upper limit to MPS), with the point of truncation increasing linearly with increasing distance from the crest. An appropriate regression model was developed to incorporate this error distribution (see Appendix 3.2).

3.3 Results

3.3.1 Study species and sites

The three focal species exhibited marked differences in maximum predicted stress (MPS) (Fig. 3.2; F = 85.6, df = 2, P = 0.012). Differences between the two study sites were marginally non-significant (F = 8.1, df = 1, P = 0.072). There was no species by site interaction, indicating that inter-specific differences were consistent across sites (F = 1.5, df = 2, P = 0.225). *Acropora hyacinthus* colonies displayed the greatest MPS levels with an average of 9.1kNs^{2}m^{-4}, indicating that this species experiences approximately twice the stress at its basal attachment for a given water velocity than does *Acropora gemmifera*, which averaged 4.6kNs^{2}m^{-4}. Therefore, it would take approximately half of the water velocity to dislodge an average colony of *Acropora hyacinthus* that it would to dislodge an average colony of *Acropora gemmifera*. The most mechanically robust species was *Acropora palifera,* whose sampled population average an MPS of only 1.5kNs^{2}m^{-4}. Lower mean values of MPS were found at South Island, although these values were not statistically different from those found at Bird Islet. Consequently, data from the two sites were pooled to improve the power of the subsequent regression analyses.

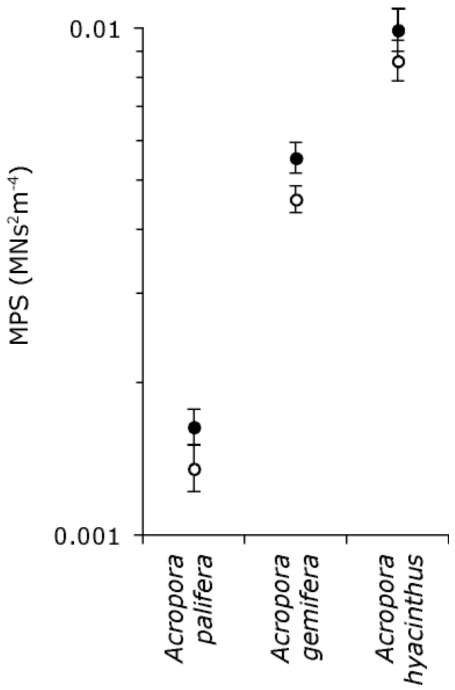

Fig. 3.2: Average and standard errors of log-transformed MPS levels in colonies of the three study species at the two study sites, South Island (open circles) and Bird Islet (solid circles).

3.3.2 Maximum predicted stress and colony size

Clear differences existed between the three study species with respect to changes in MPS levels attributable to colony size (Fig. 3.3). For small colonies where projected shapes were similar, stress did not differ substantially between species. For instance, a colony with a projected area of 0.001m^2 had an MPS of approximately 0.001MNs^{2}m^{-4} for all species. As colonies got larger, however, MPS diverged among species (Fig. 3.3). Stress in colonies of *Acropora palifera* displayed no significant association between colony size and MPS (Spearman’s r = -0.214, p = 0.005). Levels of MPS in this species trended downward for larger colonies, indicating that they become more mechanically robust with size. In contrast, *Acropora gemmifera* showed a significant association between MPS and colony size (Spearman’s r = 0.479, p < 0.001) with slope of 0.5 on a log-log scale, indicating a square-root relationship. 95% prediction intervals (approximately 2 standard deviations to either side of the mean) were calculated to indicate the bounds within which approximately 95% of observations should fall. These prediction intervals show that variability in MPS increases with size in this species, thus indicating the potential for different morphologies to either alleviate or exacerbate susceptibility to stress at larger sizes depending on their growth strategy.

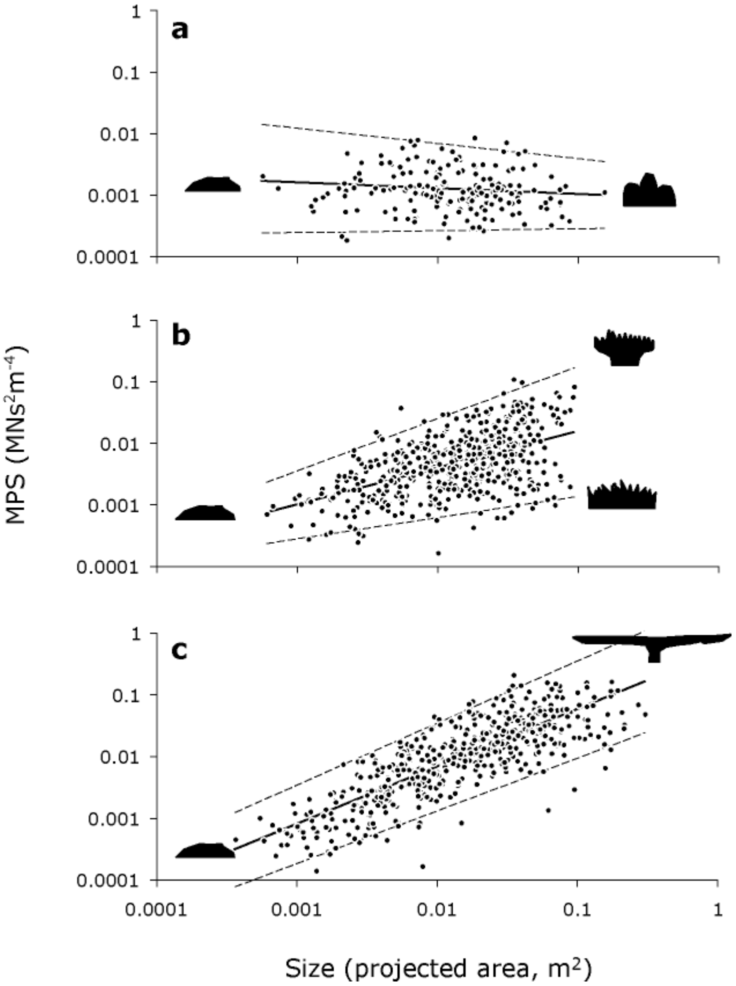

Fig. 3.3: Relationship between MPS and colony size (both variables log-transformed) for individual colonies of the three study species: a) *Acropora palifera*, b) *Acropora gemmifera* and c) *Acropora hyacinthus*. Solid lines show best-fit linear regressions of log(MPS) on log(colony size), with standard deviation modeled as a linear function of colony size (see Appendix 3.2). Dashed lines are 95% prediction intervals, i.e., intervals between which 95% of observations are expected to fall. Silhouettes of colony projections illustrate characteristic changes in shape during growth.

The strongest association between MPS and size was found for *Acropora hyacinthus,* in which colony stress increases steeply with increase in colony size (Spearman's r = 0.823, $p < 0.001$). A slope of 0.9 on a log-log scale indicated that susceptibility to bending stress in this species increases approximately linearly with colony size (measured as the projected area of the colony). For this species, the largest colonies on average retained levels of stress over 100-times greater than the smallest colonies. This large disparity indicated that for a constant substrate strength, a small colony of *Acropora hyacinthus* can withstand 100-times the water velocity of the largest colonies sampled from the population at Lizard Island.

3.3.3 Maximum predicted stress over a hydrodynamic exposure gradient

Although average MPS remained relatively constant over the reef for the three study species, variation in MPS tended to increase (Fig. 3.4). This trend was least clear for the submassive species *Acropora palifera* for which MPS levels in colonies appeared to be independent of distance over the reef (Fig. 3.4a). On the other hand, there was an obvious increase in variation of MPS levels for the corymbose *Acropora gemmifera* colonies with increasing distance from the reef crest (Fig. 3.4b). The lower 95% prediction interval was set by small colonies, which had low levels of MPS and were distributed broadly over the reef. However, the upper 95% prediction interval increased by an order of magnitude between the crest and reef back, indicating the presence of increasingly vulnerable colonies with distance from the crest.

In contrast to both *Acropora palifera* and *Acropora gemmifera*, the population of tabular *Acropora hyacinthus* colonies showed evidence of mechanical truncation: colonies that would have been expected to exist at the high end of the MPS distribution appeared to have been removed from the population closer to the reef crest (Fig. 3.4c).

Moreover, the truncation became progressively less pronounced with increasing distance from the reef crest, suggesting the imposition of a mechanical threshold to MPS sometime in the recent past. The estimated point of truncation is illustrated as a dotted line in Fig. 3.4c, along with dashed lines indicating the 95% prediction intervals for a non-truncated distribution with the same mean and variance. Variation in MPS levels was especially large for *A. hyacinthus*, spanning two orders of magnitude at the crest and nearly three orders of magnitude at the reef back.

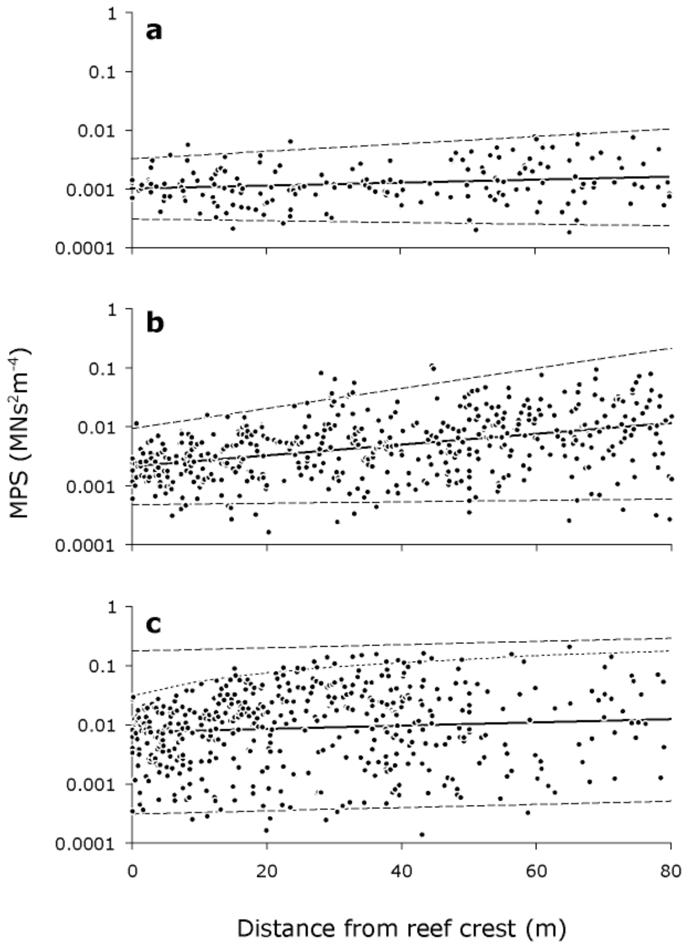

Fig. 3.4: Relationship between log-transformed MPS levels and distance (up to 80m) from the hydrodynamically exposed reef crest for individual colonies of the three study species: a) *Acropora palifera*, b) *Acropora gemmifera* and c) *Acropora hyacinthus*. Solid lines show best-fit linear regressions of log(MPS) on distance over reef, with standard deviation modelled as a linear function of distance (see Appendix 3.2). Dashed lines are 95% prediction intervals. For *Acropora hyacinthus*, regression line and 95% prediction intervals were estimated for a non-truncated population where the point of truncation varied linear with distance over the reef (Appendix 3.2). The estimated point of truncation is indicated with a dotted line.

3.4 Discussion

Using a simple photographic procedure and engineering theory, this study produced a technique to objectively quantify the intrinsic mechanical differences between coral species, colony sizes, and locations on a coral reef. The distinct mechanical differences found to exist between species illustrated a hierarchy of mechanical integrity and, therefore, of survival probability during a hydrodynamic disturbance. Moreover, variation of MPS within species illustrated that large colonies are not necessarily more vulnerable to hydrodynamic force (as suggested by geometric modelling in Chapter 2), although if colony shape changes as a colony grows, size becomes an indirect determinant of mechanical vulnerability. *Acropora hyacinthus* and, to a lesser degree, *Acropora gemmifera* appeared to reach a mechanical threshold as MPS increased with colony size. The possible existence of a mechanical threshold, which was likely shaped by gradients in the external physical environment (i.e., substrate strength and maximum water velocity), warrants further investigation of the magnitude and frequency of the hydrodynamic regimes by which it is maintained.

3.4.1 Biomechanical differences between the study species

The magnitude of the differences in mechanical vulnerability found between the three study species was far greater than initial expectations and indicated a clear distinction between species to potential mechanical dislodgement of colonies during hydrodynamic disturbances (Fig. 3.2). *Acropora palifera* was found to be mechanically superior to the other study species, as is indicted by the low levels of MPS relative to the other species. These low levels of MPS were the consequence of a characteristically large basal attachment and the distribution of this species' projected area close to the substrate (i.e., a low centre of gravity). These characteristics minimised bending moments and, therefore, the stress transmitted to the substrate (Eq. 3.3). On average, the levels of MPS in colonies of *Acropora palifera* were 3-times less than those of *Acropora gemmifera* and 6-times less than those of *Acropora hyacinthus*. As a further illustration of these inter-specific differences, the average colony of *Acropora palifera* would have to interact with an unrealistic water velocity of 12.2ms^{-1} to register an MPS equal to that of the average colony of *Acropora hyacinthus* at a realistic water velocity of 5ms^{-1} (Eq. 3.2; Denny 1999).

The highest levels of MPS were found in *Acropora hyacinthus* for two reasons. First, colonies of *Acropora hyacinthus* are “top-heavy,” that is, the projected area of colonies is distributed away from the substrate. Because force is directly proportional to projected area (for a standard flow velocity; Eq. 3.2) and the bending moment is equal to force multiplied by distance from the substrate (see Fig. 3.1), the bending moment for a colony of *Acropora hyacinthus* will be high compared to a similar-sized colony of the other two species. Secondly, because stress is equal to force divided by the area over which it acts, the small area of basal attachment—a consequence of distributing projected area away from the substrate—provides little material to mediate the bending moments, thus resulting in high levels of MPS. MPS in colonies of *Acropora gemmifera* were intermediate to the other species, but, on average, were closer to those of *Acropora hyacinthus* than those of *Acropora palifera*. The distribution of projected area of *Acropora gemmifera* colonies was geometrically more isometric, and consequently bending moments in these colonies were reduced (Fig. 3.3). In addition, the basal attachment area in colonies of *Acropora gemmifera* is greater than for *Acropora hyacinthus*, and therefore internal stress is more effectively diluted.

To compare differences in predicted survival probability of colonies, estimates of substrate strength and maximum water velocity are required (Chapter 2). The former was estimated over a spatial gradient on the study reef at Lizard Island in the previous chapter. Previous studies of reef-scale hydrodynamics, however, focus primarily on mean water transport over reef (e.g., Massel 1989; Black and Gay 1990a,b) and thus no reliable estimates of the maximal water velocity on coral reef platforms were found in the literature. At this point, therefore, comparisons of colony vulnerability to hydrodynamic disturbance on the study reef are calculated as relative differences in the internal stress transmitted to the substrate for a given water velocity (i.e., the MPS).

3.4.2 Relationships between maximum predicted stress and colony size

Three distinct relationships between colony size and levels of MPS were revealed by this study (Fig. 3.3). Vertical colony growth and larger projected area increases interaction with the water column (Jackson 1979). Therefore, levels of internal stress were expected to increase in concert with colony size. This relationship was clearly demonstrated for *Acropora hyacinthus*, where larger colonies exhibited higher levels of MPS (Fig. 3.3c). Initial colony growth in this species is principally vertical, until a height is reached (approximately 10 to 30 centimetres above the substrate) at which growth becomes lateral at the top of the colony, while the central stalk ceases any significant growth (Stimson 1985; Baird and Hughes 2000). Therefore, increases in a colony's projected area cannot be mechanically countered by an increase in basal attachment area, and colonies inevitably become increasingly susceptible to dislodgement via bending stress.

A similar relationship between colony size and MPS was found for *Acropora gemmifera*, but with one important difference: 95% prediction intervals indicate that the lower bound to MPS remains fairly constant, while the upper bound increases. In other words, increased size does not necessarily appear to increase mechanical vulnerability. Field observations revealed that this species assumed a continuum of different morphologies at larger sizes. At one extreme, colonies raised themselves above the substrate with a stalk-like basal attachment that was smaller than the upper regions of the colony (similar to, but less extreme than, *Acropora hyacinthus* – upper right schematic in Fig. 3.3b). At the other extreme, colonies tended to spread over the substrate with a low profile and large attachment area (similar to colonies of *Acropora palifera* – lower right schematic in Fig. 3.3b). These observations can help explain the increased variation in MPS within larger colonies of this species, by suggesting that this species posses a higher level of mechanically significant morphological plasticity and, therefore, greater potential for large colonies to counter variable levels of hydrodynamic force.

In contrast to the other two focal species, *Acropora palifera* illustrated no obvious relationship between colony size and MPS. Growth in this species is the closest to isometric of the three study species. This result supports theoretical findings in Chapter 2 that mechanical integrity is independent of size if shape remains constant (Eq. 2.6). Although increases in size increase drag forces on a colony, the “bottom-heavy” growth form (projected area distributed closer to the substrate) reduces bending moments and a corresponding increase in basal area counters drag, thus together preventing any significant increase in internal stress.

These three relationships between size and mechanical vulnerability indicate three different means by which the size-structure of coral populations may potentially be altered during a hydrodynamic disturbance. The first of these, in which shape remains similar as a colony grows and mechanical vulnerability is theoretically independent of size (illustrated by *Acropora palifera*, Fig. 3.3a), indicates that as maximum water velocity increases, the likelihood of colony dislodgement is equal for any size (Fig. 3.5a). The second of these, in which MPS potentially, but not necessarily, increases with size (illustrated by *Acropora gemmifera*, Fig. 3.3b), indicates that larger colonies are more likely to be dislodged, but that large colonies will potentially remain in the population (Fig. 3.5b). The third of these, in which MPS is correlated with colony size (illustrated by *Acropora hyacinthus*, Fig. 3.3c), indicates that the probability of dislodgement is indirectly a function of size, and that the larger subset of colonies in the population will likely be removed first during a hydrodynamic disturbance (Fig. 3.5c).

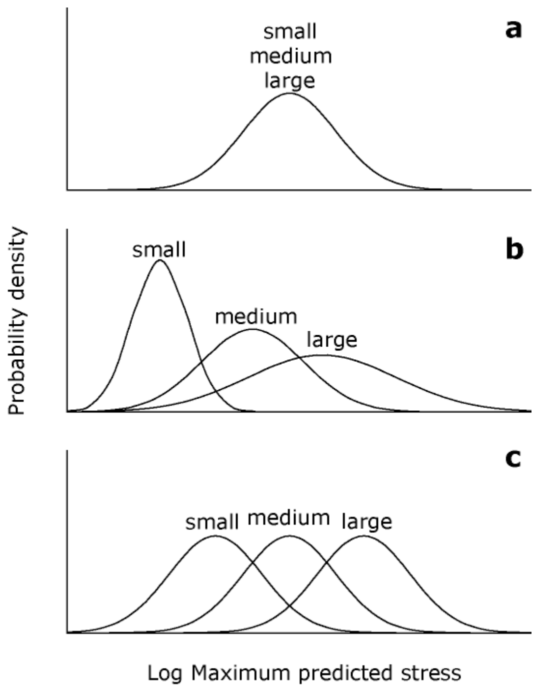

Fig. 3.5: a) Schematic of the probability density distributions of log-transformed MPS levels for three discrete colony size-classes (small, medium and large) of populations representing the three study species. a) MPS is independent of colony size and the three size-classes overlap illustrating that, as hydrodynamic disturbance removes higher MPS colonies, the abundances of all size-classes are affected similarly (e.g., *Acropora palifera*). b) MPS levels are potentially, but not necessarily, a function of colony size illustrating that larger colonies may be removed more frequently but, even after the strongest hydrodynamic disturbance, some existing large colonies will likely remain in the population (e.g., *Acropora gemmifera*). c) MPS is an indirect function of colony size, illustrating a hierarchical likelihood of larger colonies being removed from the population (e.g., *Acropora hyacinthus*).

3.4.3 Maximum predicted stress and distance over the reef

This study identified a clear mechanical threshold over the reef transect that was elucidated by MPS levels of mechanically vulnerable *Acropora hyacinthus* colonies living at various distances from the crest (Fig. 3.4c). The upper bound of MPS levels appeared to closely mirror the expected decay in water velocity across the reef as a function of wave attenuation (Black 1978; Symonds et al. 1995). However, no information on gradients of maximum water velocity caused by wave attenuation nor the recurrence of elevated hydrodynamic events could be located in the literature. Therefore, the results presented in this chapter should be investigated further by modelling the magnitude and return times of maximum water velocity spatially over the reef. This procedure is the focus of the following chapter.

In contrast to *Acropora hyacinthus*, the populations of *Acropora gemmifera* and *Acropora palifera* showed no signs of mechanical truncation and, due to characteristically lower MPS levels in these species, may not have been subjected to a recent hydrodynamic event that significantly affected their population structure. However, colonies of *Acropora gemmifera* did show signs of a constrained upper bound to MPS towards the reef crest (Fig. 3.4b). Despite this constraint, no firm evidence was found of a truncated distribution of MPS levels. I offer two possible explanations for the pattern of MPS levels exhibited by *Acropora gemmifera* over the reef. Firstly, the last mechanically significant hydrodynamic event that shaped this population may have occurred long enough ago that obvious signs of truncation have been obscured through subsequent colony growth. Secondly, colony growth of this species may be morphologically responsive to different levels of water motion and, given sufficient time, may grow into sturdy morphologies in more exposed habitats (for examples of this plasticity in corals see Graus et al. 1977; Veron 1993; Kaandorp 1999).

The procedure described above for quantifying a coral colony’s mechanical vulnerability allows comparisons to be made between the implicit differences in the maximum stress that various coral morphologies can exert upon the substrate under similar flow regimes. Because the spatial variability of substrate strength on the study reef has been previously measured (Chapter 2), the next step to estimating coral mortality due to hydrodynamic disturbance is to estimate the frequency and magnitude of maximum levels of water velocity over the reef. Given this information, the potential exists to estimate species-, size-, and location-specific mortality rates of coral colonies. Accurate estimates of coral mortality, in turn, may provide us with a useful tool for modelling coral reef community dynamics under current and projected future climatic conditions.