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An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals

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Abstract

Previous research has demonstrated that the massive corals *Favia speciosa* (Dana, 1846) and *Diploastrea heliopora* (Lamark, 1816) are phenotypically plastic, i.e. the phenotype of these species can be altered by environmental conditions within their life span. Many researchers have suggested that light, water movement and/or sediment can affect coral morphology, but no work to date has attempted to separate these variables in a controlled aquarium experiment. To ascertain whether any of these three factors could induce morphological change in *F. speciosa* and *D. heliopora*, fragments (clone-mates) of both species were maintained in five aquarium tanks, representing: high water energy, high sedimentation, and three different light regimes. After 4 months, the architecture of 12 randomly chosen corallites from each fragment was measured. Reaction norms suggest a relationship between corallite morphology and light, but no consistent pattern could be detected for fragments kept in the sediment regime tank or the high water energy tank. Corallites expand, extend and deepen in high light conditions and possible functional explanations for this response are presented. However, more research is necessary to confirm that light is the primary controlling factor inducing small-scale morphological change in *F. speciosa* and *D. heliopora*.

Keywords: Phenotypic plasticity; Small-scale coral morphology; Light; Sediment; Hydraulic energy

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1. Introduction

The intraspecific morphological diversity that is typical of many scleractinian corals is familiar to taxonomists and reef ecologists alike (Stephenson and Stephenson, 1933; Lang, 1984; Veron, 1986). Various genetic and environmental factors contribute towards sustaining this variety (Veron, 1995; Bruno and Edmunds, 1997; Marfenin, 1997; Todd et al., 2001a) although their relative contribution, and significance, remains uncertain (Wijsman-Best, 1974; Brakel, 1977; Knowlton and Jackson, 1994; Miller and Benzie, 1997). Phenotypic plasticity, i.e. environment-dependent differences in a genotype's morphological, behavioural or physiological expression, is of particular relevance to corals as reefs worldwide appear to be undergoing changes that are possibly too rapid for the Scleractinia, with their long generation time and infrequent spawning, to adapt to through genetic change (Lasker and Coffroth, 1999).

In the heterogeneous reef environment, numerous factors can influence the morphology and physiology of a coral (Huston, 1985; Veron, 1995). Relationships have been described between coral form and light (Wijsman-Best, 1974; Dustan, 1975; Jaubert, 1977, Graus and Macintyre, 1982), water movement (Vosberg, 1977; Chappell, 1980; Riegl et al., 1996) and sediment rates (Hubbard and Pocock, 1972; Lasker, 1980; Dodge, 1982; Stafford-Smith, 1993; Riegl, 1995). These interactions can usually be correlated to coral metabolism. For example, the capacity of a colony to capture light is important to photosynthesis (Jaubert, 1977; Nakamori, 1988), mass transfer is linked to water movement (Helmuth and Sebens, 1993; Bruno and Edmunds, 1998), and sediment shedding increases respiration (Lasker, 1976, 1981; Rogers, 1979; Abdel-Salam and Porter, 1988; Riegl and Branch, 1995; Telesnicki and Goldberg, 1995).

Most of the reports regarding intraspecific variation in corals are correlatory, rather than studies of environmentally induced change. Only a few experiments have successfully demonstrated phenotypic plasticity, usually by moving whole colonies to new environments and recording morphological change with time (Foster, 1979; Graus and Macintyre, 1982; Willis, 1985; Miller, 1994). More recent studies have reciprocally transplanted colony fragments, i.e. clone-mates, to identify among-genotype variation for plasticity (Bruno and Edmunds, 1997; Raymundo, 2001; Todd et al., 2002a,b, in review). Many researchers have suggested physical factors that could induce change in coral morphology, including those mentioned in the previous paragraph, but no work to date has attempted to separate these variables in a controlled aquarium experiment.

Todd et al. (2002a,b, in review) established that the two massive corals *Favia speciosa* (Dana, 1846) and *Diploastrea heliopora* (Lamark, 1816) were phenotypically plastic and, through a process of elimination, concluded light was the probable controlling factor. The present study was originally conceived as a small follow-up experiment to this initial research, but it can equally be considered a pilot for further work. To ascertain whether light, sediment, and/or water movement could induce morphological change in these two species, fragments of *F. speciosa* and *D. heliopora* were collected from three reefs in Singapore's southern waters and maintained in five aquarium tanks, representing: high water energy, high sedimentation and three different light regimes. After 124 days and the removal of tissue, nine morphometric characters

from 12 randomly chosen corallites were extracted from each fragment and analysed for among-treatment differences.

2. Method

2.1. Study species, collection sites and sampling method

In previous research (Todd et al., 2000, 2001a,b, 2002a,b, in review), *F. speciosa* and *D. heliopora* were chosen as study species for three primary reasons: (1) they are common around Singapore; (2) they possess large and distinctive ployps (plocoid); and (3) they represent phenotypically variable and invariable Faviids (*F. speciosa* and *D. heliopora*, respectively). The same rationale applies to the present research, although the phenotypic stability of *D. heliopora* has recently been questioned (Todd et al., 2002a,b, in review). Colonies of *D. heliopora*, usually found in shallow water or near the reef crest, are typically very large (>1 m diameter) and dense (Veron, 2000), whereas *F. speciosa* colonies are smaller (< 1 m diameter) and inhabit a slightly deeper zone (between 3 and 6 m below mean sea level).

For this experiment, one colony of each species was sampled from the westward slopes of three reefs; Cyrene Reef (4 km offshore), Pulau Hantu (7 km offshore) and Raffles Lighthouse (13.5 km offshore). The large distance between these populations reduced the possibility of the colonies sharing similar genotypes (Miller, 1994). Maps and full site descriptions can be found in Todd et al. (2001a) and Todd et al. (in review). Six palm-sized fragments (mean = 50.3 cm^2, S.E. = 1.9) were removed from the seaward facing side of each colony. To test whether any change in morphology would occur during the experimental period to fragments left in their natural habitat, control fragments, made up of one fragment from each colony, were left on the three reefs. The control fragments were glued in situ (underwater epoxy cement) to plastic platforms and fixed to stakes driven into the reef substrate near their parent colonies. The remaining fragments were quickly transported (within 3 h) to the aquarium in shaded 50 l containers filled, and frequently replenished, with seawater.

2.2. Aquarium and treatments

The aquarium, part of Raffles Marina Research Station, is situated on the west coast of Singapore, 10–15 km from the sampling sites. The water system is flow-through, with fresh filtered (20 μm) seawater pumped from outside the marina seawalls. The aquarium facility is outdoors, but roofed with clear corrugated plastic and a single layer of nursery netting that blocks approximately 75% of ultra-violet (UV) and photosynthetically active radiation (PAR, 400–700 nm).

To determine coral growth during the experiment, the fragments were stained with Alizarin Red S. All samples were individually enclosed in 5 l clear plastic bags, injected with alizarin concentrate to produce a solution of 8–10 mg l^{-1}, and left for 16–18 h (Lamberts, 1974; Le Tissier, 1988). To reduce stress, the fragments were kept in holding tanks for 2 weeks prior to the alizarin treatment, and for another 2 weeks after the staining.

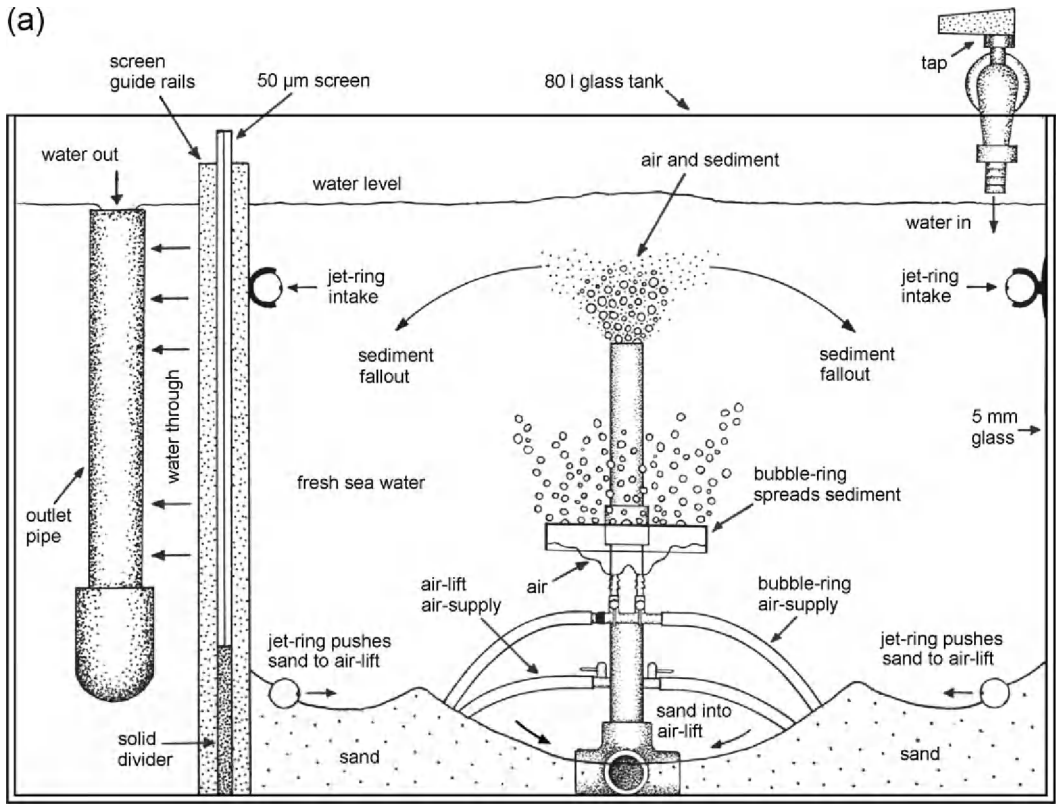

Fig. 1. The sediment regime (SR) tank. (a) Side view depicting the airlift and 'bubble-ring' device. For simplicity, the coral fragments have been omitted. (b) Top view illustrating the arrangement of coral fragments and the design of the 'jet-ring'.

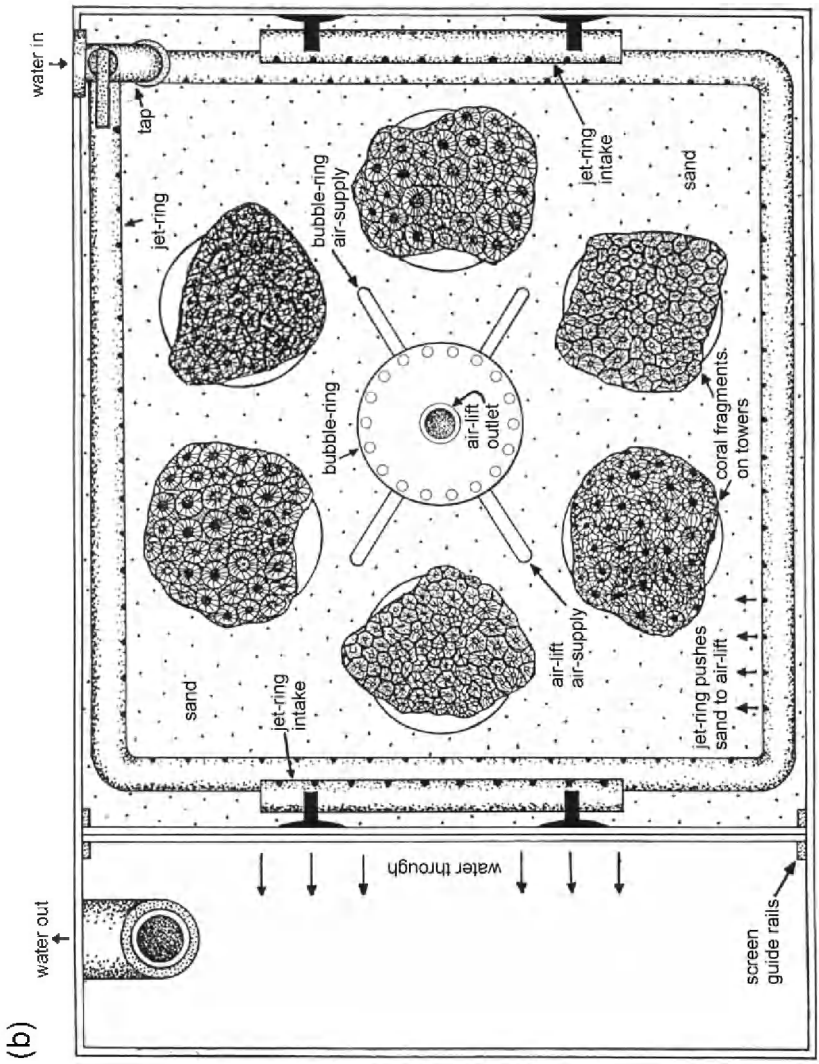

Fig. 1 (*continued*).

Five glass tanks (60 × 40 × 38 cm, holding approximately 80 l), were modified to reproduce five aspects of the reef environment, i.e. high light (HL), medium light (ML), low light (LL), medium light with a sediment regime (SR) and medium light with high hydraulic energy (HE). Every tank had a flow-through rate of 2 l min^{-1} and was lightly aerated. On the reef there would have been planktonic food available to these corals, therefore, approximately 500 l of unfiltered seawater was pumped into the set of tanks four times every night (between 20:00 and 6:00 h).

To create the sediment regime, a tank was filled 5 cm deep with a blend of 5% coarse sand, 45% medium sand, 45% fine sand and 5% very fine sand (90% quartz and 10% carbonate material). Finer sediments were excluded as these would have clouded the water and reduced light penetration, thereby introducing a confounding

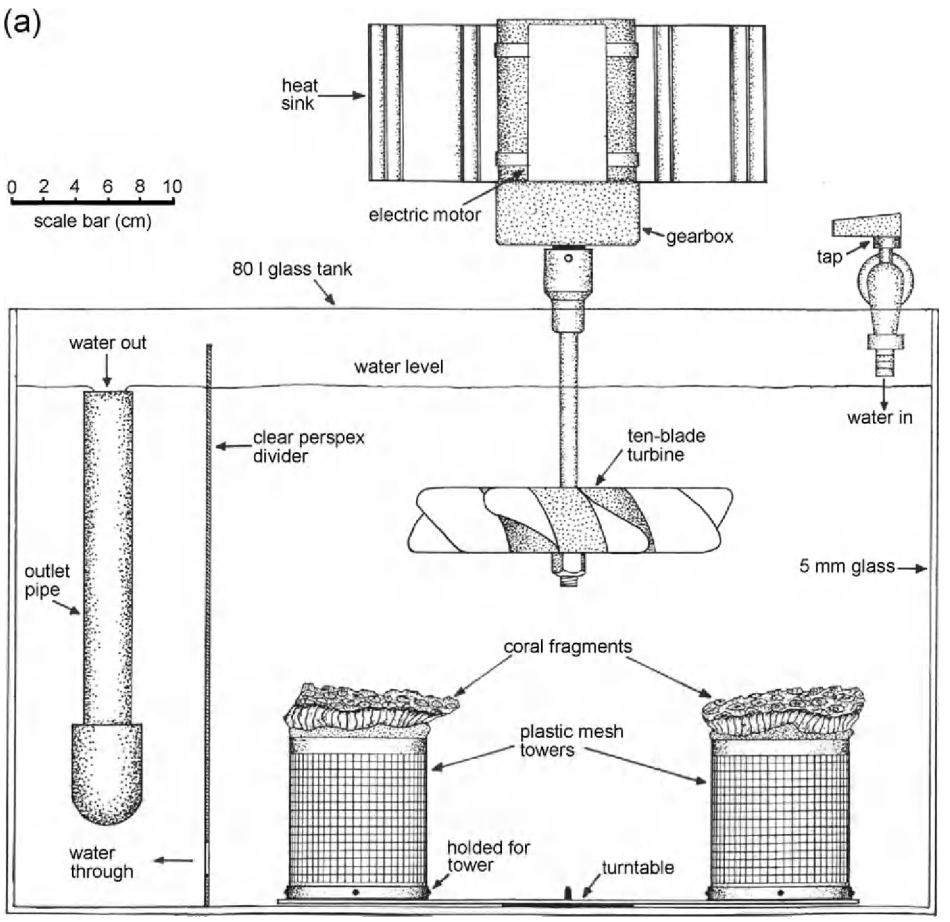

Fig. 2. The hydraulic energy (HE) tank. (a) Side view shows the position the turbine relative to the corals. The scale bar is also applicable to Fig. 1. (b) Top view. For simplicity, the structure supporting the motor in not included in (a) or (b).

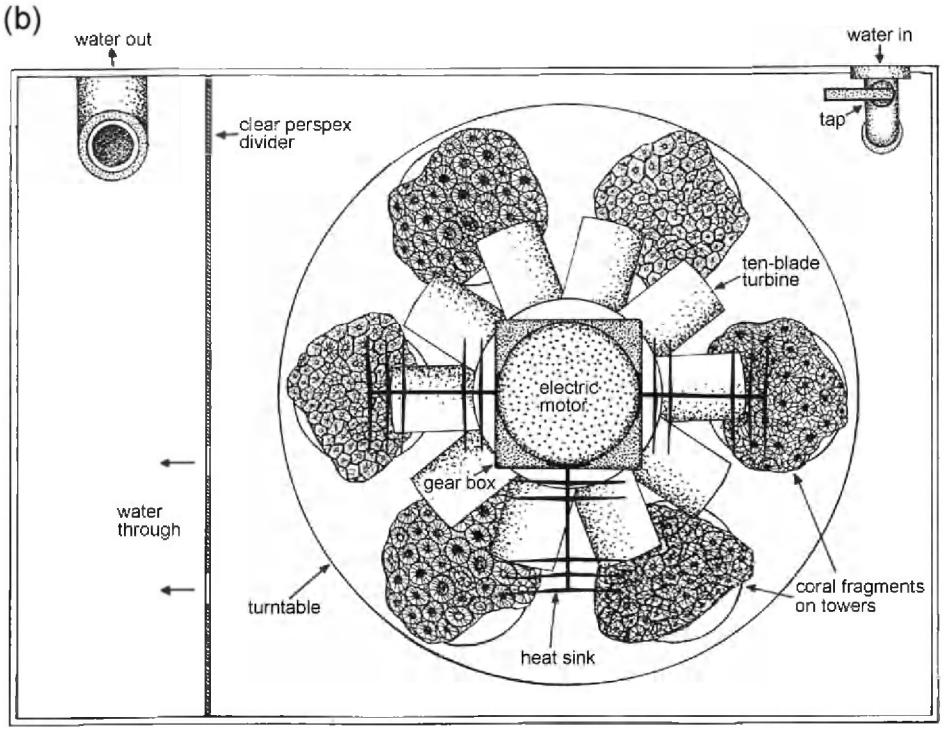

Fig. 2 (*continued*).

factor. As the water system was flow-through, a divider made of 50-μm nylon mesh in a plastic frame was fitted across one end of the tank, near the outflow, to trap particles. An airlift design, adapted from Riegl (1995), was used to draw up sand from the middle of the tank and eject it into the water body (Fig. 1). To ensure that the airlift was constantly supplied with sediment, water was pumped through a ring of inward facing jets fitted to the perimeter of the tank. This 'jet-ring' gently pushed the sand back towards the airlift intake. Whereas Riegl (1995) utilised an upturned perforated funnel to spread the sediment emerging from the top of the lift, here, a 'bubble-ring' device, that efficiently scattered the sand throughout the tank, was fabricated (Fig. 1). Because the sediment rate produced by the airlift was greater than the rate the corals could clear themselves, the regime would have eventually smothered the fragments. To circumvent this, a timer was included so that the lift operated only for 1–5 min periods, haphazardly triggered four times throughout any 24-h period. Based on sediment traps placed in the tank, an average rate of 20 mg cm^2 day^{-1} (S.E. = 2.7) was achieved. This rate was similar to the more impacted sites around Singapore (Low and Chou, 1994), although the regime itself was sporadic as opposed to continuous. No sediment was introduced into any other treatment other than the SR tank.

Six fragments, one of each genotype, were selected using random number tables. These were then fixed with underwater epoxy to 10 cm high cylindrical 'towers' made of rigid plastic mesh. The mesh size was large enough to allow sand to easily flow through the cylinders. The fragments on towers were equidistantly embedded in the sediment in a hexagonal pattern (Fig. 1b). For consistency, the tower design and hexagonal arrangement was used for all the treatments, with fragments assigned their positions within the pattern using random number tables (with the proviso that the two species be placed alternately). The remaining tanks had turntables and jigs to hold the fragments at a fixed distance from each other (Fig. 2). Approximately every 10 days, the coral pieces were moved one position (60°) clockwise and their orientation to the centre of the tank was haphazardly altered.

Most water motion around Singapore is in the form of tidal currents rather than wave action, so, instead of building a paddle apparatus (sensu Stambler et al., 1991), a turbine-based method was used to create hydraulic energy (Fig. 2). The 10-blade turbine, driven by an electric motor via a gearbox, rotated at a mean of speed 81 rpm. At this rate, the outer edge of the turbine blade was travelling at 0.93 m s^{-1} (1.81 knots) and, assuming no friction, the water speed over the fragments would have been between 0.68 (1.32 knots) and 1.53 m s^{-1} (2.97 knots). However, water friction, turbulence caused by the fragments on towers, and interference from the sides of the tank, all reduced this speed. Although currents around the sampling sites reached a maximum of 3.7 knots during the study period, they were more commonly between 1 and 2 knots (Marine and Port Authority of Singapore, 2001). Furthermore, the reef itself was liable to reduce current speeds by up to 30% (Roberts et al., 1975). Although all five tanks were aerated and had seawater flowing through them, the water movement created by these actions was minimal.

Irradiance was measured at points equivalent to fragment positions with a LI-COR LI-1400 light meter on both sunny and cloudy days. Light was prevented from entering the back, sides and top of the low light tank, and the front was covered in a single layer of nursery netting. This reduced light levels to 1.1% (S.E. = 0.11%) outdoor PAR. The high light tank, with no barrier to full sunlight other than the roof of the aquarium, had light levels of 17.2% (S.E. = 0.89%) outdoor PAR. The medium light (the control), hydraulic energy, and sediment regime tanks were covered with layers of netting to produce a light regime of 6.2% (S.E. = 0.38%) outdoor PAR. The high and low light tanks experienced PAR levels similar to those found at 2.5 and 7.7 m depth around Raffles Lighthouse, the sampling site least affected by sediment (Todd et al., in review).

2.3. Morphometric analysis

After 124 days the fragments were removed, soaked for 48 h in a 3% sodium hypochlorite solution, rinsed with fresh water and oven dried overnight. Two 2:1 images of every fragment were taken with a SLR camera and the resultant slides digitised (at 450 dpi). Twelve corallites, mature and perpendicular to camera, were randomly chosen from each pair of images using random number tables. From each corallite, nine morphometric characters were measured (Fig. 3). The characters were selected based on their taxonomic importance, ease of extraction (those that could be measured with the greatest precision),

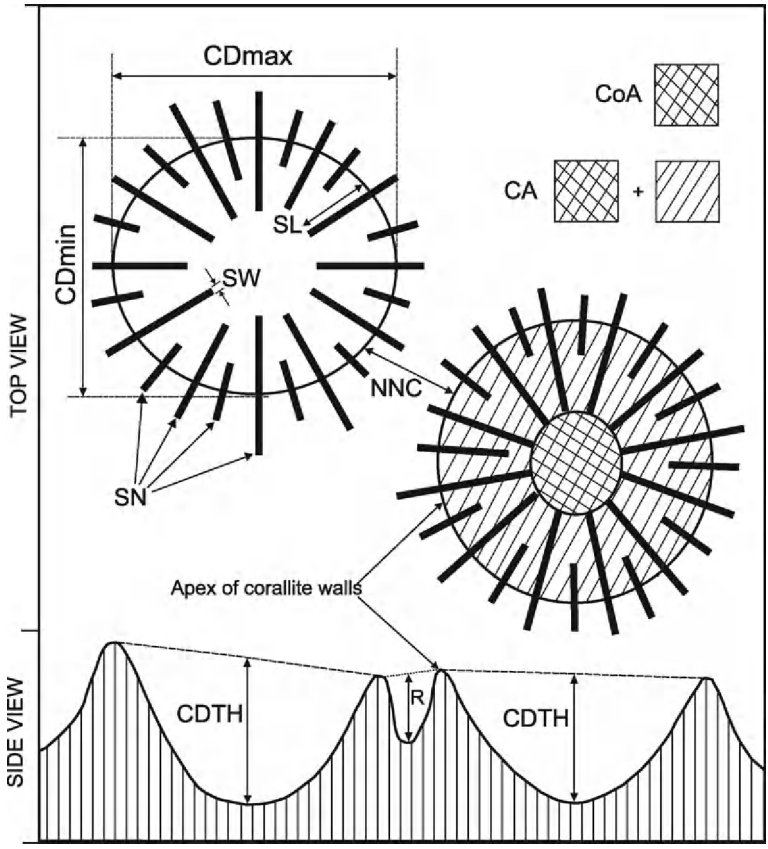

Fig. 3. A diagrammatic representation of the skeletal morphometric characters extracted.

and intraspecific variability (Wijsman-Best, 1974; Brakel, 1977; Veron, 2000). Two fragment-scale readings were also taken (Table 1). Altogether, six readings were from slides projected to 10 × actual size, two from the digitised images (using SigmaScan software) and three directly from the cleaned skeletons (Table 1). These three techniques were used simultaneously to ensure that all readings came from the same corallites. The number of corallites per unit area (CPUA) was the number of whole corallites in a 4 × 4 cm frame averaged over three readings. Rugosity (R) was the average height of haphazardly chosen corallites with one reading taken for every 5 cm^2 of surface area. More details of the measuring process can be found in Todd et al. (in review).

2.4. Statistical analysis

After testing all corallite-level character measurements for multivariate normality (Kolmogorov-Smirnov tests followed by examination of scatterplots for all pair-wise combinations) and homogeniety of variance (Box's *M*-test) a principle components analysis (PCA) was conducted on the complete (both species), untransformed data set

Table 1
Morphometric characters extracted and measurement methods

Abbreviation	Character	Measurement method
CDmax	Calice maximum diameter	Projected slide-vernier calipers
CDmin	Calice minimum diameter	Projected slide-vernier calipers
SL	Septa length	Projected slide-vernier calipers
SW	Median septa width at mid point	Projected slide-vernier calipers
NNC	Nearest neighbouring calice	Projected slide-vernier calipers
SN	Septa number	Projected slide-count
CA	Calice area	Analysis of computer images
CoA	Columella area	Analysis of computer images
CDTH	Calice depth	Actual skeleton-vernier calipers
R	Rugosity	Actual skeleton-vernier calipers
CPUA	Corallites per unit area	Actual skeleton-count
AS	Antisymmetry—CD_{max} minus CD_{min}	Projected slide-vernier calipers

(Grimm and Yarnold, 1995). The loading scores for each corallite upon the first two principle components were used as the response variables in two separate analyses of variance (ANOVAs) to determine any morphometric differences among species, treatments and, and treatments × species. In the ANOVAs, the unit of measurement was the corallites (a repeated measure), which was nested within fragment, and fragment was nested within species; we assumed fixed effects. The within-fragment, among-corallite, effects were not of interest and have been excluded from the results table (Table 3). The analysis was exploratory, the extracted PCA axes were orthogonal (and therefore uncorrelated), and only two independent tests were conducted; therefore Bonferroni corrections for the nominal Alpha were not used. The species-level means for each tank were also calculated from the PC 1 and PC 2 loading scores and plotted as reaction norms Analyses were conducted on PC-ORD 4 (mjm Software), Statistica 5.1 (StatSoft) and SAS (SAS Statistical Institute).

3. Results

This experiment was designed to run for 7 months; a period similar to that used by Todd et al. (2002a,b, in review). Unfortunately, because the pump supplying the entire aquarium facility with seawater failed, the study was terminated after only 4 months. All corals in the aquarium tanks survived, although a few specimens exhibited some minor bleaching. However, of the six controls left at the sampling sites (three fragments from each of the two species), three fragments were lost. As the number of field controls was already very low, that section of the experiment has been omitted from the results. When the coral skeletons were cut laterally, the alizarin stain line was visible, but growth above the line was small (1–3 mm) and too variable within fragments to measure with either accuracy or precision.

For each species, the corallite morphometric data has been pooled, and reaction norms for character means and standard deviations plotted (Fig. 4). As septa number (SN), coralllite depth (CDTH), and septa width (SW) are within-corallite measurements they are

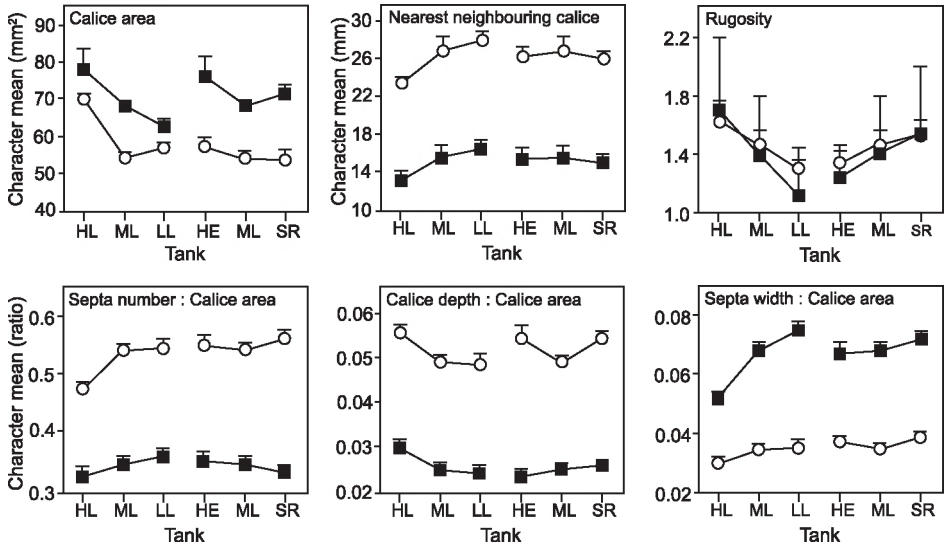

Fig. 4. Reaction norms for character means and standard errors grouped by species and tank; ■ = *D. heliopora*, ○ = *F. speciosa*. To aid interpretation, the medium light (ML) results are plotted twice on each graph, once between the high light (HL) and low light (LL) results and again between the high energy (HE) and sediment regime (SR) results, where it represents a control. The standard errors for R are large because they are based on whole fragment means ($n = 3$). All data come from a single experiment and analysis.

presented as ratios to calice area (CA). For ease of interpretation, the medium light (ML) results are plotted twice on each graph, once between the high (HL) and low light (LL) results, and again between the high energy (HE) and sediment regime (SR) results, where it represents a control. No trends could be discerned for corallites per unit area (CPUA) or for the ratios columella area (CoA)/calice area, septa length (SL)/calice area and antisymmetry (AS)/calice area. The data for these characters were similarly erratic in Todd et al. (submitted for publication) and are probably unreliable as indicators of morphological change. Although the readings for CPUA, CoA, SL, and AS are used in the PCA (Table 2), they are not presented as graphs.

Table 2
PCA Eigenvalues for each character and the percentage of variance accounted for by the first two PCA axes.

Character	PC 1	PC 2
CA	− 0.6830	− 0.2747
CD_{max}	− 0.5542	0.1524
CD_{min}	− 0.4132	0.0153
CoA	− 0.0859	− 0.0731
NNC	0.1126	− 0.8427
CDTH	− 0.0001	0.0529
SN	− 0.0234	− 0.4206
SL	− 0.1830	0.0144
SW	− 0.3850	0.0750
Variance captured	76.1%	8.6%

The reaction norms are more easily interpreted by first looking at the high light, medium light and low light tanks as a group (Fig. 4). For both species, a gradient of light-related morphological change can be discerned for rugosity (R), nearest neighbouring

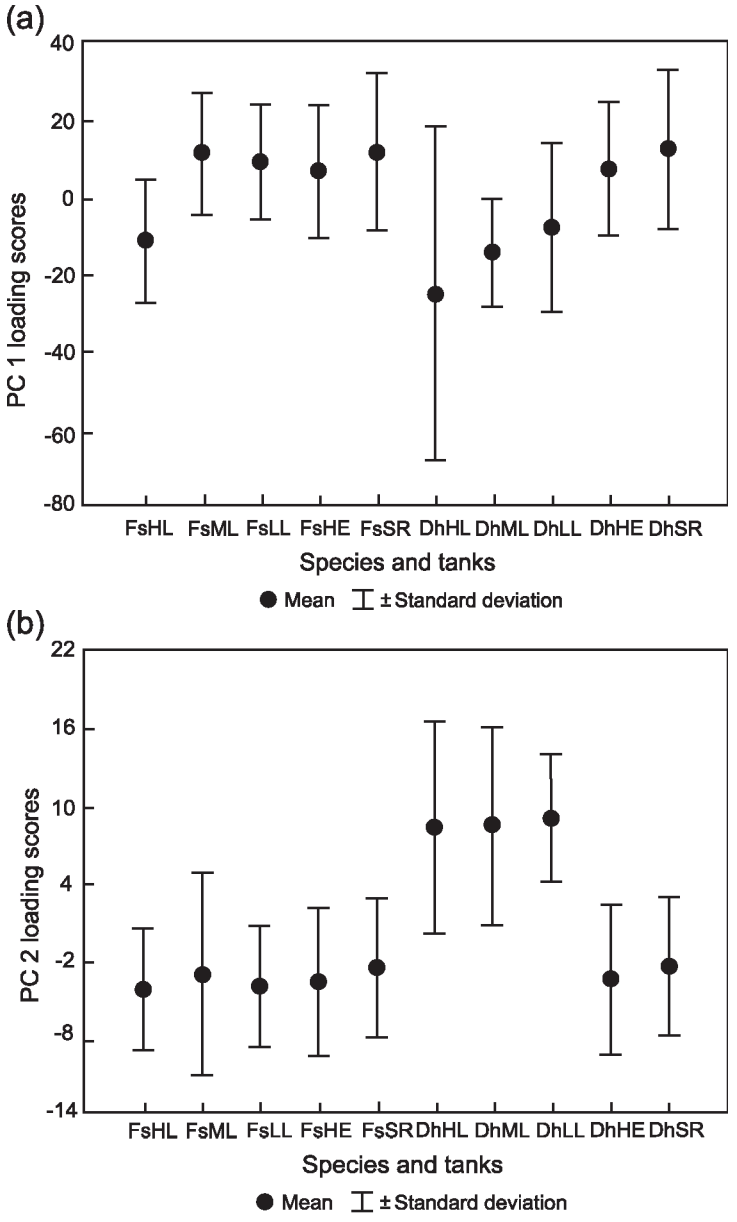

Fig. 5. The dimensionality of the morphometric data were reduced with PCA. Presented are reaction norms using the loading scores on (a) the first, and (b) the second principle components. Fs = *F. speciosa*, Dh = *D. heliopora*, HL = high light, ML = medium light, LL = low light, HE = high energy, SR = sediment regime.

Table 3
ANOVAs performed on PC 1 and PC 2 loading scores

Factor	*df*	PC 1				PC 2			
		ss	ms	*F* value	*P*	ss	ms	*F* value	*P*
Tank	4	15,833	3958	1.07	0.4041	175	43	0.17	0.9488
Species	1	50,807	50,807	13.72	<0.01	11,263	11,263	44.64	<0.001
Fragment (Species)	4	76,895	19,223	5.19	<0.01	1866	466	1.85	0.1687
Tank × Species	4	3959	989	0.27	0.895	178	44	0.18	0.9471
Error	16	59,256	3703			4037	252		

Parentheses indicate nesting.

calice (NNC), and the ratios SN/CA, CDTH/CA and SW/CA. For CA, the gradient among tanks exists for *D. heliopora*, and there is a difference between high and low light for *F. Speciosa*. Calice area, depth and rugosity all increase in high light indicating corallite expansion and extension, whereas NNC decreases, signifying tighter corallite packing. The standard errors for R are large because they are based on whole fragment means ($n=3$).

Differences between the high-energy tank, the sediment regime tank and the medium light control are small for most character means. For both species, R increases in the sediment regime tank and decreases in the high-energy tank. For *F. speciosa*, CDTH/CA increases in both the high-energy tank and the sediment regime tank relative to the control. No trends are discernible for NNC, SN/CA, and SW/CA.

The PCA reduced the dimensionality of the data, enabling differences in fragment morphology among tanks to be compared more easily. The reaction norms for species means and variances derived from PC 1 loading scores (Fig. 5a), mirror those of CA (Fig. 4). This relationship, and the PC loading scores of calice maximum diameter (CDmax) and calice minimum diameter (CDmin), strongly suggest that PC 1 is dominated by calice size (Table 2). For *F. speciosa*, the species means and variances from PC 2 do not reveal any pattern, but those for *D. heliopora* describe a separation of the light regime tanks from the high energy and sediment regime treatments (Fig. 5b). The reaction norms in Fig. 5 suggest that, for PC 1, responses for *F. speciosa* in the high light tank are different from the other four treatments, and that for PC 2, *D. heliopora* high light, medium light and low light are different from all other groups. However, the ANOVA results only indicate significant differences between species (Table 3).

4. Discussion

The apparatus designed to create high water energy and sedimentation, although technologically simple, performed well. The turbine ran continually for the duration of the experiment and, due to a lack of moving parts, the sediment regime tank only required minor maintenance. Although the trends are not strong, some indication of morphological change is suggested, with corals maintained in the high light tank altering the most. As the responses were among coral clones, they must be attributed to the environmental variables rather than genetic factors.

D. heliopora and *F. speciosa*, within the limitations of their interspecific differences in morphology (both corals are plocoid, but the skeleton of *D. heliopora* is more dense), are known to respond in corresponding ways to new environments (Todd et al. 2002a,b, in review). A similar association is apparent in this study, as illustrated by Figs. 4 and 5a, and increases the probability that the observed trends are real. The reaction norms for PC 1, CA, NNC, R, SN/CA, CDTH/CA, and SW/CA, depict a relationship between morphology and light. Character size tends to increase with increasing light, except for NNC where the opposite is true. NNC is a measure of corallite expansion and is therefore expected to decrease as CA increases. Todd et al. (2002a,b, in review) found very similar results, with the fragments transplanted to shallow and deep sites in those studies responding in an analogous way to those maintained in the high and low light tanks of this experiment.

The reaction norms of character means, by definition, describe size. The first principle component of a PCA, performed on morphometric data, can also correspond to size, especially when this supposition is supported by the raw data (Thorpe, 1976; Todd et al., 2001a,b). Ratios of characters to a standard dimension (CA in this case) and the second principle component of a PCA can, arguably, be considered indicators of shape (Spivey, 1988; Bookstein, 1989). Therefore, some correlation between PC 1 and corallite size, and PC 2 and the character ratios, may be expected. Although the PC 1 reaction norms for *D. heliopora* and *F. speciosa* exactly mirror those for the CA means, none of the ratio plots are comparable to the PC 2 reaction norms (Figs. 4 and 5a). SN:CA, CDTH:CA, and SW:CA all suggest a light-related trend (Fig. 4), whereas PC 2 indicates no pattern among tanks for *F. speciosa*, and a separation of the light regime tanks from the high energy and sediment regime treatments for *D. helipora* (Fig. 5b). In this particular case, the ratio data might be more reliable as PC 2 only explains 8.6% of the total variation.

No clear pattern emerges from the reaction norms, with the possible exception of those based on PC 2, for specimens kept in the high energy and sediment regime tanks (Figs. 4 and 5). It is conceivable that the fragments in these treatments could not acquire sufficient energy to morphologically change within the 4-month experiment. Dodge (1982) observed growth reduction in colonies of *M. annularis* treated with drilling mud and noted how this may further reduce the coral's capacity to improve its shedding ability. Moreover, in the high energy tank of the present study, the corals might have had difficulty keeping their polyps extended, thus impairing their feeding ability (Hubbard, 1974; Sebens and Johnson, 1991).

Although this study was exploratory, both in terms of treatments and analysis, the methods could be developed for a more thorough investigation into the environmental factors inducing morphological change in scleractinian corals. The aquarium experiment was constrained by small sample size and reduced running time, and future efforts would need to address these problems. Differences in original corallite architecture also hindered identification of trends; intercolonial morphological variation is found in both species and, unless morphological responses to treatments are large, this initial variation will persist. Additional treatment permutations should be tested, for example, high light with a sediment regime, and high light with high hydraulic energy. Although the apparatus for creating high water energy and the sediment regime operated satisfactorily, it is difficult to determine how effectively these devices mimicked the reef environment.

It would be speculative to predict exactly how corals may plastically respond to anthropogenic impacts such as increased sedimentation and global climate change, but

the results presented here, and those from previous work (e.g. Foster, 1979; Bruno and Edmunds, 1997; Muko et al., 2000; Todd et al., 2002a,b, in review), suggest corals may be able to acclimatise to chronic stresses in relatively short time periods. However, morphological plastic responses are unlikely to help corals survive acute impacts such as storms or destructive fishing practices. Other consequences of phenotypic plasticity in corals are less ambiguous. For instance, coral systematics is still primarily based on morphological traits (Brakel, 1977; Veron, 2000) and plasticity of taxonomically important traits can only confound the, already difficult, task of coral identification. The interaction between genotype (or at least species) and environment needs to be quantified if morphological variable taxa are to be accurately classified.

Plastic corals can justifiably be considered generalists (Whitlock, 1996) and may be expected to have a wider distribution that less plastic corals. Thus, interspecific variation in plasticity will probably have an effect on a reef community (Foster, 1979), but this relationship has not yet been explored. Neither the role, nor mechanism, of plasticity in corals is understood, with little or no evidence of the evolutionary costs or limits that have been described in other, mostly terrestrial, plastic taxa (e.g. Newman, 1992; DeWitt, 1998). Demonstrating that a plastic response is beneficial to a coral is plagued with difficulties, mostly arising from their complex life histories (Foster, 1979; Bruno and Edmunds, 1997; Muko et al., 2000), but it is still possible to infer potential advantages. For example, Todd et al. (2002a) and Todd et al. (in review) postulate that the light-related expansion, deepening, and extension of corallites might have a functional explanation. They suggest that the increase in polyp surface area may enhance the light capturing ability of the coral in shallow waters characterised by surfeit light. Alternatively, the shading caused by the deepening of the calice might protect the tissue of the oral disc area from high levels of ultra-violet radiation. More research is necessary to support these hypotheses, and to confirm that light is the primary factor inducing small-scale morphological change in *F. speciosa* and *D. heliopora*.

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