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Genotype × environment interactions in transplanted clones of the massive corals *Favia speciosa* and *Diploastrea heliopora*

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ABSTRACT: Environment-dependent variation in the morphological, physiological, or behavioural expression of a genotype is termed phenotypic plasticity. To test for small-scale morphological plasticity in the Indo-Pacific massive corals *Favia speciosa* (Dana, 1846) and *Diploastrea heliopora* (Lamark, 1816), fragments (clone-mates) from 12 colonies of each species were reciprocally transplanted among 6 new habitats located within 2 environmental gradients: a depth cline and a nearshore-to-offshore gradient in sedimentation rates and total suspended solids (TSS). After 7 mo, all fragments were collected, cleared of tissue, and 10 morphometric characters extracted from randomly chosen corallites. Reaction norms, analysis of variance, and canonical discriminant analysis describe environment-induced changes in corallite architecture. These changes are more pronounced in the depth cline than along the sediment gradient. Similarity of response is suggested by exploratory factor analysis where, for both species, size attributes dominate the first factor, antisymmetry the second, and corallite exsertion the third. Highly significant genotype × environment interactions for *F. speciosa* indicate that, for this species, genotypes vary in the level of plasticity expressed. Light and TSS emerge as the primary correlates influencing morphological change, although other parameters might act additively, synergystically or antagonistically with them. In shallow waters, increased corallite exsertion may enhance light capture or, alternatively, protect the central (oral disc) area of each polyp from harmful UV radiation. Morphological variability, combined with environment-induced changes in pigmentation, could impede accurate identification of these taxa.

KEY WORDS: Phenotypic plasticity · Small-scale coral morphology · Corallite · Sedimentation · Total suspended solids · Light · Depth · Singapore

INTRODUCTION

The coral reef environment is extremely heterogeneous; within small temporal and spatial scales a large range of light regimes, hydraulic energy, sedimentation rates, and food availability may be encountered (Huston 1985a). This unpredictable environment makes adaptation difficult for the sessile reef organism. Corals can employ various strategies to improve their fitness, depending on factors including extent of larval dispersal, population size, and degree of variation in the environment (Warner 1997, Scheiner 1998). One alternative is to spawn numerous offspring with high levels of genetic differentiation so that at least some individuals will be suited to the local environment in which they settle (Lloyd 1984). Another option is to produce offspring with a fixed generalist genotype with traits that incur high mean fitness when averaged over the dispersal range of the larvae (Warner 1997). Under certain conditions, selection might encourage specialisation (Van Tienderen 1991, Whitlock 1996). Finally, phenotypic plasticity may evolve, enabling individuals to adjust (within limitations) to whatever environment they encounter (Bradshaw 1965, Schlichting 1986).

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Phenotypic plasticity is a broad term that encompasses an organism's morphological, physiological and behavioural responses to the environment (West-Eberhard 1989, Scheiner 1993, Silvertown 1998). Typical responses include acclimation, short-term reversible changes, and irreversible changes during development (Hoffmann & Parsons 1991). Plasticity of an individual or population can be summarised by a reaction norm — a graphical representation of how phenotypes differ in relation to their environment (Stearns 1989). Some phenotypic plasticity is clearly adaptive (Dodson 1989, Scharloo 1989, Newman 1992); however this is difficult to demonstrate empirically (Newman 1992, Dudley & Schmitt 1996). Common in terrestrial taxa, phenotypic plasticity has also been documented in a broad range of marine biota including fishes (Robinson & Wilson 1995, Turigan et al. 1995, Vanrooij et al. 1995), molluscs (Etter 1996, Trussell 1996), crustaceans (Lively 1986, Hazlett 1995, Mokady et al. 1999), echinoderms (Ebert 1996), sponges (Palumbi 1984), bryozoans (Harvell 1992, Okamura 1992) and corals (Foster 1979, Bruno & Edmunds 1997, Muko et al. 2000).

Since the 19th century, researchers have known that environment-related intraspecific variation occurs in coral colony form (Quelch 1886, Stephenson 1933) and corallite structure (Quelch 1886, Yonge 1936, Wijsman-Best 1974). Analogous to plants, this variation can be due to genetic differentiation (Willis & Ayre 1985, Ayre & Willis 1988), phenotypic plasticity (Foster 1977, Miller 1994, Bruno & Edmunds 1997, Muko et al. 2000) or both in synthesis (Foster 1979, Amaral 1994). As the majority of coral systematics is based upon morphological traits (Brakel 1977, Veron 2000), any plasticity of taxonomically important characters has far-reaching consequences. Debate continues as to whether the observed variation in corals should be attributed to fine-scale partitioning of species, widespread hybridisation, or extensive plasticity (Ayre & Willis 1988, Knowlton & Jackson 1994, Veron 1995, Stobart 2000). These issues are fundamental to modern hypotheses regarding the possible reticulate evolution of corals and other marine taxa (Veron 1995, Diekmann et al. 2001). Experiments on phenotypic plasticity should compliment those exploring phylogenetic relationships, leading to a better understanding of coral evolution and taxonomy.

Various physical parameters are thought to influence coral morphology. Light intensity decreases with increasing water depth and, as scleractinian corals host photosynthetic symbionts (zooxanthallae) that contribute to their energy budget, the average rate of calcification and growth also decreases with depth (Goreau 1959, Huston 1985b, Bosscher & Meesters 1993). Reduced light can affect whole colony form (Dustan 1975, Graus & Macintyre 1982) and possibly corallite structure (Wijsman-Best 1974). Similarly, wave action decreases with increasing depth (Roberts et al. 1975). Hydraulic energy can influence coral skeletal density (Scoffin et al. 1991) and gross morphology (Vosburgh 1977, Chappell 1980). Respiration and feeding are both affected by the interactions between coral colony morphology and water motion (Lasker 1976, Helmuth & Sebens 1993, Bruno & Edmunds 1998).

Sedimentation levels can also vary with depth, with higher rates occurring in shallow areas where wave action re-suspends benthic deposits (Huston 1985a). Sedimentation is the main physical variant between nearshore and offshore waters around Singapore. From 1962 to 1992 Singapore reclaimed 59.5 km^2 of land from the sea and continues to do so at a similar rate (Hilton & Manning 1995). These massive projects, combined with terrestrial run-off and the regular dredging of shipping lanes, have reduced the average visibility from 10 m in the 1960s to less than 2 m in 1996 (Chou 1996) and produced a sediment gradient with levels that decline with increasing distance from the mainland (Low & Chou 1994).

The deleterious effects of increased sedimentation on coral reefs are well-documented (Rogers 1990, McClanahan & Obura 1997). Sediment settling on individual colonies interferes with both photosynthesis and respiration (Abdel-Salam & Porter 1989, Riegl & Branch 1995). Many corals have sediment-rejection mechanisms (Hubbard & Pocock 1972, Stafford-Smith 1993, Riegl 1995), the efficiency of which depends on colony form (Lasker 1980, Riegl et al. 1996), corallite morphology (Marshall & Orr 1931, Lasker 1980), and sediment size and type (Stafford-Smith 1993). Moreover, suspended sediment in the water column causes light to be diffracted (Rogers 1979, Telesnicki & Goldberg 1995) and light attenuation increases rapidly in turbid waters, an effect particularly apparent in Singapore where, even on a sunny day, it can be completely dark at 10 m depth (P. A. Todd pers. obs.).

The majority of previous tests for plasticity in corals have been conducted at the population level, i.e. whole colonies have been transplanted to new habitats and phenotypic change measured (Foster 1979, Graus & Macintyre 1982, Willis 1985). The drawback of this approach is that it is impossible to completely separate the effect of the environment from that of the different genotypes that individual colonies probably represent. More recent studies have successfully used coral fragments (clone-mates) to establish within-genotype plastic responses across a number of environments. Bruno & Edmunds (1997) confirmed small-scale morphological plasticity in the branching coral *Madracis mirabilis*, and Muko et al. (2000) demonstrated how explanate forms of *Porites sillimaniani* develop branches when exposed to high light intensities.

In the present experiment, colony fragments of 2 massive species of coral, *Favia speciosa* (Dana, 1846) and *Diploastrea heliopora* (Lamark, 1816), were reciprocally transplanted in 2 environmental gradients to the south of mainland Singapore. The first gradient was a depth cline, known to affect a number of physical parameters (Huston 1985a); the second gradient was a nearshore to offshore decrease in total suspended solids (TSS) and sedimentation rates (Low & Chou 1994). After 7 mo, all coral fragments were collected, cleared of tissue, and examined. The hypotheses tested were: (1) changes in small-scale morphology can be environmentally induced; (2) there exists among-genotype variation for the levels of plasticity expressed; (3) the patterns of induced morphological change are qualitatively similar for both species. In addition, the probable physical environmental parameters inducing change are explored and any functional value to the findings are discussed. This study marks the first case where 2 massive coral species have been simultaneously tested for plasticity using clone-mates.

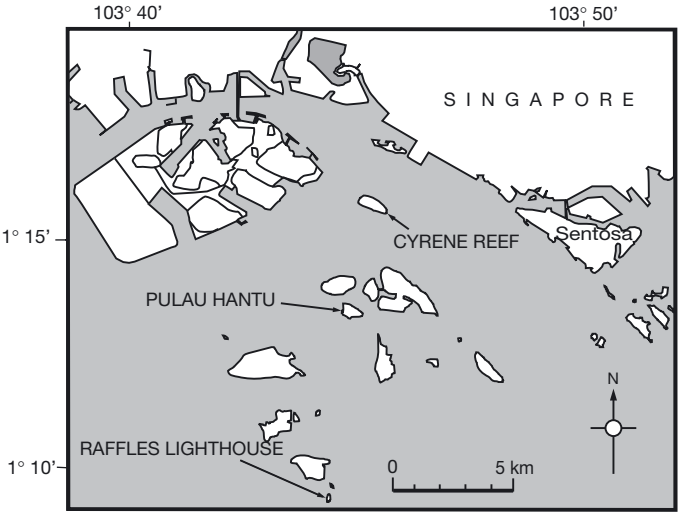

Fig. 1. Singapore's southern islands and the 3 reefs studied

MATERIALS AND METHODS

Study area. Singapore is situated 137 km north of the equator, near the southern tip of the Malaysian peninsular. Tides are semi-diurnal, with a mean range of 2.2 m and a maximum spring range of 3.7 m. Tidal currents can reach up to 4 knots in open channels, but no data are available for current speeds over the reefs themselves. Singapore experiences a mild SW monsoon from June to August and a wetter NE monsoon between November and February. Temporal sea surface temperatures (SST, mean 29.7°C) and salinity variations (mean 30.6 ppt) in Singapore Strait (an area encompassing the research area of the present experiment) are small: during a 3 yr study SST ranged from 28.3 to 31.2°C and salinity ranged from 28.7 to 32.2 ppt (Gin et al. 2000). Mean levels of total nitrogen, phosphorus and TSS were 0.55, 0.0016, and 15 mg l^{-1}, respectively (Gin et al. 2000). Although the water column is well mixed (Chuang 1977), the coast of Singapore is a low-energy environment with maximum wave heights of 0.4 m during the NE monsoon, receding to 0.1–0.2 m throughout the rest of the year (Pitts 1992).

Site (Fig. 1). ***Cyrene Reef (01° 15.240' N, 103° 45.524' E):*** shallow station (CR-S), 2.2 m below mean sea level (BMSL); deep station (CR-D), 7.6 m BMSL.

Completely submerged at high tide, Cyrene is a large patch reef situated at the division of 2 shipping fairways. The sediment produced by continual dredging of the shipping lanes severely impacts the reefs and live coral cover is low (Chou 1988, 1996). Shore-based building projects, and the outflow from 2 rivers only 4 km away, also contribute sediment loads (Goh & Chou 1992).

Pulau Hantu (01° 13.635' N, 103° 44.797' E): Shallow station (PH-S), 2.3 m BMSL; deep station (PH-D), 8.9 m BMSL.

Pulau Hantu was originally a small islet with a wide fringing-reef; however, most of the reef flat was reclaimed in 1974, leaving only the reef slopes intact. The remaining reef survived the reclamation project, but it is still subject to sedimentation from similar work and dredging in the vicinity. Located 7 km offshore and bounded by other islands, the reef is not affected by shore-based construction and has the calmest waters of the 3 study sites.

Raffles Lighthouse (Pulau Satumu) (01° 0.477' N, 103° 44.495' E): Shallow station (RL-S), 2.4 m BMSL; deep station (RL-D), 7.0 m BMSL.

Raffles Lighthouse is situated 13 km from the mainland, at the limit of Singapore's territorial waters. With open sea to the south, this site generally has the best underwater visibility, although turbulence originating from a major shipping fairway, 2 km to the south, sporadically disturbs bottom sediments.

Study species. *Favia speciosa* is a common faviid around Singapore. Its distinctive polyps have bright green oral discs surrounded by brown tissue. Corallites are large, roughly circular, and become compacted and irregular in shallow water (Veron 2000). Septa are thin and uniform, the columella well formed. *F. speciosa* is known to morphologically vary among reefs (Wijsman-Best 1974, Todd et al. 2001) and with depth (Wijsman-Best 1974, Veron 2000).

Diploastrea heliopora has the longest fossil record (as recognisably the same species) of all the faviids.

Widespread in the Indo-Pacific, its dome form can grow to over 2 m high and more than 7 m in diameter (Veron et al. 1977). Thick septa that taper towards the columella are interspersed with fine ones; the columella is large and distinct (Wood 1983). In contrast to *Favia speciosa*, it is easy to identify due to its lack of variability (Veron 2000).

For this experiment, specimens of *Favia speciosa* (independently identified by J. E. N. Veron) were collected from between 4 and 7 m BMSL, where it is most common. Around Singapore, *Diploastrea heliopora* (identified by the authors) is restricted to the reef flat and reef crest, and so samples were gathered from no deeper than 3 m BMSL. Because a comparable, environment-induced, response in 2 similar corals would be of less interest than an analogous response from quite different species, these 2 taxa were purposely chosen to contrast what were considered to be morphologically variable and invariable faviids (Veron 2000).

Experimental design. Fragments of *Favia speciosa* and *Diploastrea heliopora* were reciprocally transplanted across the 6 stations described previously (3 reefs × 2 depths) to test the 3 hypotheses outlined in the introduction. We randomly sampled 4 colonies of both species (each colony spaced >30 m apart) from west-facing, 200 m sections of the 3 reefs (a total of 12 colonies for each species). From every colony, 6 fragments (clone-mates) were chiselled from the seaward-facing side and randomly distributed throughout the 6 stations (1 at each). Thus, there were 12 fragments of *F. speciosa* and 12 fragments of *D. heliopora* at every station. Transportation of fragments among sites was performed within 1 h, during which time the pieces were held in large containers filled, and frequently replenished, with fresh seawater. The entire operation took 2 wk with all fragments in place by 9 May 2000.

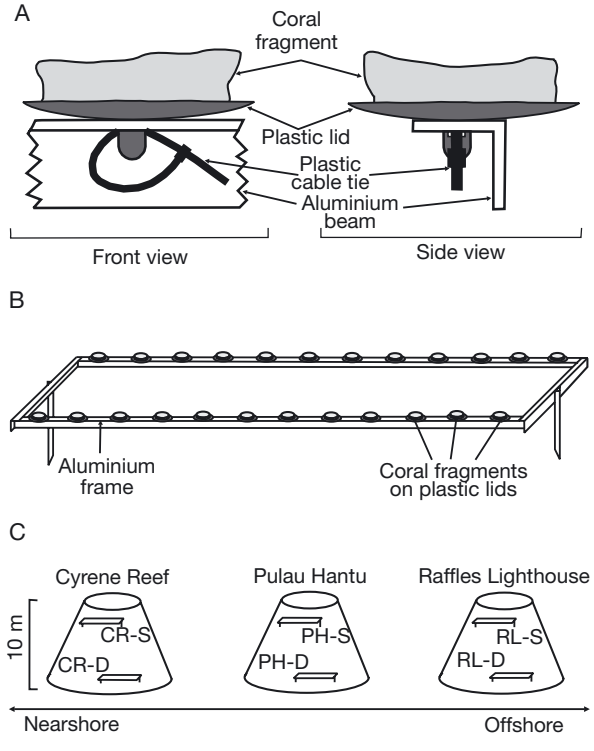

Fig. 2. (A) Attachment of coral fragments; (B) design of the aluminum racks; (C) position of racks at the 6 stations. CR-S: Cyrene Reef—shallow; CR-D: Cyrene Reef—deep; PH-S: Pulau Hantu—shallow; PH-D: Pulau Hantu—deep; RL-S: Raffles Lighthouse—shallow; RL-D: Raffles Lighthouse—deep

At inception, the *Favia speciosa* fragments had a mean living surface area of 49.8 cm^2 (SE = 1.8 cm^2), whereas those of *Diploastrea heliopora* were slightly larger at 53.5 cm^2 (SE = 1.7 cm^2). Each was glued to a 110 mm diameter plastic lid with underwater epoxy (Expogrout putty, Fosroc, Malaysia). At each station, 24 fragments (12 of each species) were attached to rectangular racks made from 2 parallel 2.4 m aluminium beams fixed 0.5 m apart by connecting sections (Fig. 2). Metal stakes driven into the reef substrate held the racks in line with the reef slope at a height of ~0.45 m. The fragments were arranged in a sequential order because of logistical problems associated with 2 simultaneous, photography-based, experiments. These other experiments (Todd et al. 2002a,b) required the fragments to be in an order that would obviate the need to identify every piece separately, in the field, before each photograph. It was anticipated that the fragments from each island that were left at their 'home' stations would act as controls; however, due to slight discrepancies between the depths of the parent colonies and the stations, this approach proved unsatisfactory.

The fragments were checked approximately every 10 d; sediment and algae were carefully removed from the surrounding surfaces with nylon brushes and any necessary repairs conducted. An estimate of tissue loss, relative to upper surface area, was made for each species at each station 1 wk before the corals were recovered, and was categorised as minimal (0 to 10%), moderate (10 to 50%), and severe (>50%). On 7 December 2000 (214 d from commencement) the fragments were collected, cleared of tissue with 3% sodium hypochlorite, rinsed with freshwater, and oven-dried overnight at 50°C.

Morphometrics. Morphometric characters were measured from projected slides, digitised images, and directly from cleaned skeletons (Fig. 3). The characters were selected based on their taxonomic importance, ease of extraction, and intraspecific variability (Wijsman-Best 1974, Brakel 1977, Veron 2000). Two 2:1 macro images were taken of each coral fragment with an SLR camera loaded with colour-slide film (ASA 50) in outdoor ambient light; the developed transparencies were scanned at 400 dots per inch. From each pair of

images, all suitable corallites were identified (those that were mature, perpendicular to the camera, away from the growing edge and in sharp focus) and individually numbered. Using random-number tables, 6 of these corallites were chosen for measuring. Calice maximum diameter (CDmax), calice minimum diameter (CDmin), maximum septa length (SL), median septa width at mid-point (SW), nearest neighbouring calice (NNC), and septa number (SN) were all measured with digital vernier calipers (±0.01 mm) from slide images projected to 10× actual size. Calice area (CA) and columella area (CoA) of the same corallites were measured using SigmaScan (Version 1.20.09) image-analysis software (Jandel Scientific) applied to the scanned slides. Corallite depth (CDTH) and fragment rugosity (R, calculated by averaging height readings of haphazardly chosen corallites; 1 reading 5 cm^{-2} of surface area) were measured directly from the fragment skeletons, again with digital vernier calipers (±0.01 mm). The number of corallites per unit area (CPUA) was the mean number of complete corallites within a 4 × 4 cm square window haphazardly placed on each fragment 3 times. The surface area (±5 cm^2) of each fragment was estimated with a 1 cm^2 grid; if the fragments had developed buds, their number was noted. By subtracting CDmin from CDmax an index of antisymmetry (AS) was derived.

Environmental measurements. Approximately every 10 d, 1.5 l of seawater was sampled near (<20 m laterally) the 6 stations. Samples were filtered (0.45 µm, oven-dried, nylon membranes) and rinsed with deionised water (to remove salts). To determine total suspended solids (TSS), filter discs were dried at 103°C for 1 h before being re-weighed (APHA 1995).

Sedimentation was calculated from particulate matter collected in sediment traps based on the method described by English et al. (1997) and previously used in Singapore by Low & Chou (1994). Traps measuring 5 cm in diameter × 11.5 cm deep were arranged in sets of 3 and fixed to the aluminium frames at the same height of the coral fragments (~0.45 m above the substrate). The traps were collected and replaced approximately every month. Contents of all traps were left to stand for 24 h before decanting excess water. The remaining ~200 ml of slurry was dried overnight at 60°C before weighing. An estimated salt content of 30 g l^{-1} was deducted from the final weights.

Measurements of photosynthetically active radiation (PAR) were taken only once, on a sunny day, to confirm that there was a reduction in light with depth. A profiling reflectance radiometer (PRR600 and 61, Biospherical Instruments) was lowered to 10 m a total of 6 times at Raffles Lighthouse and the changes in PAR continually logged. From the mean readings, percentage of surface PAR was calculated for depths equivalent to the 6 stations. This enabled comparisons to be made among stations without having to account for varying levels of TSS.

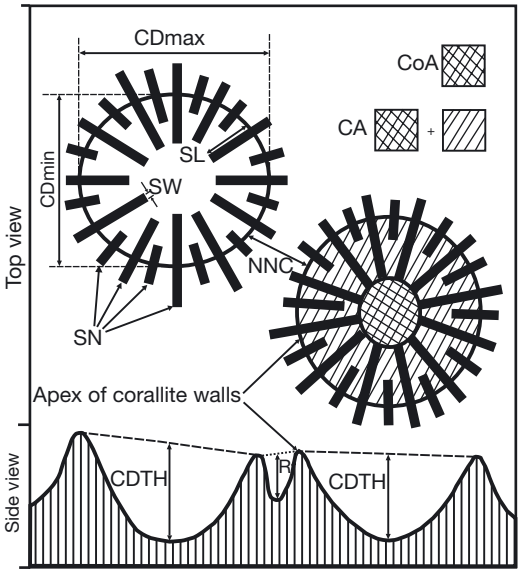

Fig. 3. *Favia speciosa* and *Diploastrea heliopora*. Morphometric characters extracted for analysis (see 'Materials and methods' for details). Abbreviations are explained in legend to Table 1. (Reprinted from J Exp Mar Biol Ecol, 299, Todd PA, Sidle RC, Lewin-Koh NJI, An aquarium experiment for identifying physical factors inducing morphological change in two massive scleractinian corals, p 97–113, Copyright [2004], with permission from Elsevier)

Multivariate statistics. To reduce the dimensionality of the data, a principle-components exploratory factor analysis (EFA) was performed on the 10 corallite-level characters (4320 measures for each species). EFA is similar to principle-components analysis (PCA) except that it identifies eigenvectors that maximise the amount of *common* variance that is explained rather than the total variance (Grimm & Yarnold 1995). Kolmogorov-Smirnov tests (Sokal & Rohlf 1995) on individual characters indicated normal distributions, and scatterplots for all pair-wise combinations described fundamentally linear relationships (Grimm & Yarnold 1995). Box-and-whisker plots of means and variances for each character were compared and found acceptable. A varimax (orthogonal) rotation was carried out to simplify the structure and provide more readily interpretable factors.

Whereas EFA is able to extract eigenvectors that explain common variance, canonical discriminant function analysis (CDA) is efficient at differentiating predetermined populations (Sokal & Rohlf 1995). As the experiment was divided into well-defined entities (the 6 stations), a complete (non-stepwise) CDA was performed on character means and fragment-level

measures, including corallites per unit area (CPUA) and rugosity (R). To prevent size dominating and distorting the variance/co-variance matrix, residuals from corallite-level characters regressed against CA were inserted as shape variables in the analysis. Normality and homogeneity of variance were tested as previously described. Based upon '*F* to remove' results, the characters that contributed least to group separation were eliminated.

After testing for normality and homogeneity of variance with Kolmogorov-Smirnov and Levene's tests, the loading scores for each corallite upon the first 3 factors of the EFAs were used as the response variables in 6 separate analyses of variance (ANOVAs) to determine any morphometric differences among depths, reefs, genotypes, depths × genotypes, and reefs × genotypes. In the ANOVAs, the unit of measurement was the corallite (a repeated measure), which was nested within genotype. Genotype, reef, and depth were crossed and all were treated as fixed effects. Fixed effects were assumed for reefs as these were chosen for their different sedimentation levels; depths were predetermined to represent alternate light levels and therefore also fixed. Ideally, genotype would have been treated as a random effect; however, due to lack of replication (and thus reduced degrees of freedom), a mixed model with genotype as a random effect would have meant the genotype × environment interaction was impossible to calculate. Treating genotype as a fixed effect reduces the level of inference that can be made regarding the genotype population not tested in this experiment. The within-genotype, among-corallite, effects were not of interest and have been excluded from the results table (see Table 4). The analysis was exploratory, the extracted EFA axes were orthogonal (uncorrelated), and the tests thus independent; therefore, Bonferroni corrections for the nominal Alpha were not used. All the analyses mentioned in the previous 4 paragraphs were conducted on PC-ORD 4 (mjm Software), Systat 8.0 (SPSS), Statistica 5.1 (StatSoft), and SAS (SAS Statistical Institute).

Table 1. *Favia speciosa* and *Diploastrea heliopora*. Character means and standard errors at each station. Characters: CA: calice area; CoA: columella area; CDTH: corallite depth; CDmax: calice maximum diameter; CDmin: calice minimum diameter; CPUA: corallites per unit area; NNC: nearest neighbouring calice; SN: septa number; SL: maximum septa length; SW: median septa width; R: rugosity; AS: antisymmetry. Stations: CR-S: Cyrene Reef—shallow; CR-D: Cyrene Reef—deep; PH-S: Pulau Hantu—shallow; PH-D: Pulau Hantu—deep; RL-S: Raffles Lighthouse—shallow; RL-D: Raffles Lighthouse—deep

Character	Stations					
	CR-S	CR-D	PH-S	PH-D	RL-S	RL-D
F. speciosa						
CA (mm^2)	58.89 ± 1.87	48.77 ± 1.57	59.81 ± 1.35	49.19 ± 1.64	57.57 ± 1.27	50.60 ± 1.85
CoA (mm^2)	6.56 ± 0.19	4.82 ± 0.15	6.40 ± 0.15	4.59 ± 0.17	5.04 ± 0.10	4.71 ± 0.18
CDTH (mm)	4.01 ± 0.12	2.72 ± 0.09	5.47 ± 0.10	3.02 ± 0.12	5.13 ± 0.11	2.79 ± 0.08
CDmax (mm)	9.88 ± 0.14	8.33 ± 0.17	9.60 ± 0.13	8.33 ± 0.16	9.55 ± 0.13	8.69 ± 0.17
CDmin (mm)	7.63 ± 0.16	6.53 ± 0.11	7.39 ± 0.12	6.88 ± 0.12	7.16 ± 0.12	6.95 ± 0.13
CPUA (count)	8.67 ± 0.68	8.67 ± 0.47	8.50 ± 0.38	9.33 ± 0.53	9.67 ± 0.56	9.17 ± 0.30
NNC (mm)	2.70 ± 0.09	3.25 ± 0.08	2.32 ± 0.05	3.26 ± 0.09	2.16 ± 0.06	2.84 ± 0.06
SN (count)	34.76 ± 0.59	30.58 ± 0.57	32.71 ± 0.53	29.14 ± 0.46	32.56 ± 0.46	28.89 ± 0.40
SL (mm)	3.80 ± 0.08	3.42 ± 0.08	3.66 ± 0.07	3.25 ± 0.07	3.70 ± 0.07	3.48 ± 0.08
SW (mm)	0.25 ± 0.01	0.21 ± 0.01	0.23 ± 0.01	0.20 ± 0.00	0.24 ± 0.01	0.20 ± 0.00
R (mm)	2.38 ± 0.15	1.69 ± 0.14	2.91 ± 0.19	1.72 ± 0.15	3.42 ± 0.21	1.73 ± 0.13
AS (index)	2.25 ± 0.15	1.80 ± 0.12	2.21 ± 0.15	1.45 ± 0.11	2.39 ± 0.14	1.73 ± 0.12
Buds	1.83 ± 0.35	0	5.08 ± 1.31	0	4.42 ± 0.87	0
D. heliopora						
CA (mm^2)	56.10 ± 1.42	57.37 ± 1.26	55.65 ± 1.34	57.19 ± 1.22	54.03 ± 1.26	57.02 ± 1.26
CoA (mm^2)	10.44 ± 0.27	9.91 ± 0.26	10.95 ± 0.28	9.92 ± 0.22	9.49 ± 0.26	9.88 ± 0.24
CDTH (mm)	1.96 ± 0.04	1.93 ± 0.05	2.26 ± 0.04	1.96 ± 0.04	2.22 ± 0.05	1.72 ± 0.04
CDmax (mm)	8.68 ± 0.12	8.83 ± 0.11	8.88 ± 0.13	8.92 ± 0.12	8.73 ± 0.12	9.21 ± 0.13
CDmin (mm)	7.29 ± 0.11	7.58 ± 0.10	7.45 ± 0.10	7.74 ± 0.10	7.55 ± 0.11	7.83 ± 0.11
CPUA (count)	10.83 ± 0.67	11.17 ± 0.69	11.17 ± 0.81	10.83 ± 0.65	10.75 ± 0.94	9.92 ± 0.36
NNC (mm)	1.91 ± 0.08	1.70 ± 0.06	1.91 ± 0.08	1.86 ± 0.09	2.28 ± 0.10	1.82 ± 0.06
SN (count)	22.88 ± 0.25	22.32 ± 0.22	22.69 ± 0.25	22.36 ± 0.26	23.11 ± 0.27	22.58 ± 0.24
SL (mm)	3.02 ± 0.05	3.09 ± 0.05	2.87 ± 0.06	3.10 ± 0.06	3.06 ± 0.06	3.32 ± 0.05
SW (mm)	0.40 ± 0.01	0.37 ± 0.01	0.41 ± 0.01	0.36 ± 0.01	0.41 ± 0.01	0.39 ± 0.01
R (mm)	1.77 ± 0.12	1.42 ± 0.15	1.85 ± 0.12	1.35 ± 0.17	1.69 ± 0.12	1.23 ± 0.08
AS (index)	1.39 ± 0.11	1.25 ± 0.08	1.42 ± 0.10	1.18 ± 0.09	1.18 ± 0.08	1.39 ± 0.09
Buds	7.00 ± 2.55	0	10.75 ± 2.70	0	16.92 ± 4.10	0.08 ± 0.08

RESULTS

All 144 coral fragments were successfully retrieved from the study sites; 3 fragments that showed signs of imminent mortality were collected 2 to 3 mo early, but remain in the analysis. Reduction of tissue cover was minimal for both species at all stations except Cyrene Reef deep (CR-D) and Pulau Hantu deep (PH-D), where tissue loss was moderate for *Diploastrea heliopora*, and severe for *Favia speciosa*. At the deep stations, the green oral discs of *F. speciosa* lost their vivid colour while the tissue of *D. heliopora* turned almost translucent (Todd et al. 2002a). Some fragments of *F. speciosa* exhibited slight bleaching at the shallow stations, resulting in their brown-pigmented areas turning yellow (Todd et al. 2002a).

Station-level means and standard errors for all character measures are presented in Table 1. No morphometric characters were significantly correlated with fragment size. The most salient features of the summarised data for *Favia speciosa* (Table 1) are the differences in calice and columella sizes (CA, CoA, CDmax and CDmin), skeletal topography (CDTH and R), septa features (SL, SW and SN), and corallite 'packing' (CPUA, NNC and AS), between deep and shallow stations. Differences among reefs, and especially among the deep stations, are less apparent. *Diploastrea heliopora* shows less morphological variation than *Favia speciosa* and, although similar patterns are discernible (Table 1), variation is not necessarily greater between depths than it is among reefs.

Only one bud was found on a fragment from the deep stations. At the shallow stations, 34 out of 36 *Favia speciosa*, and 30 out of 36 *Diploastrea heliopora* fragments developed buds. All genotypes developed buds at at least 1 station (Todd et al. 2002b).

The reaction norms in Fig. 4B illustrate noise characteristic of the *Diploastrea heliopora* data; patterns are easier to distinguish in the *Favia speciosa* plots (Fig. 4A). The vertical fluctuations denote change in morphology with depth and are apparent for both species. Trends within the nearshore to offshore gradient (left to right, Fig. 4) are difficult to identify. Plots for individual genotypes cross, possibly indicating G × E interactions. Origin of population appears to have no effect on genotype responses, a result similar to that of Bruno & Edmunds (1997).

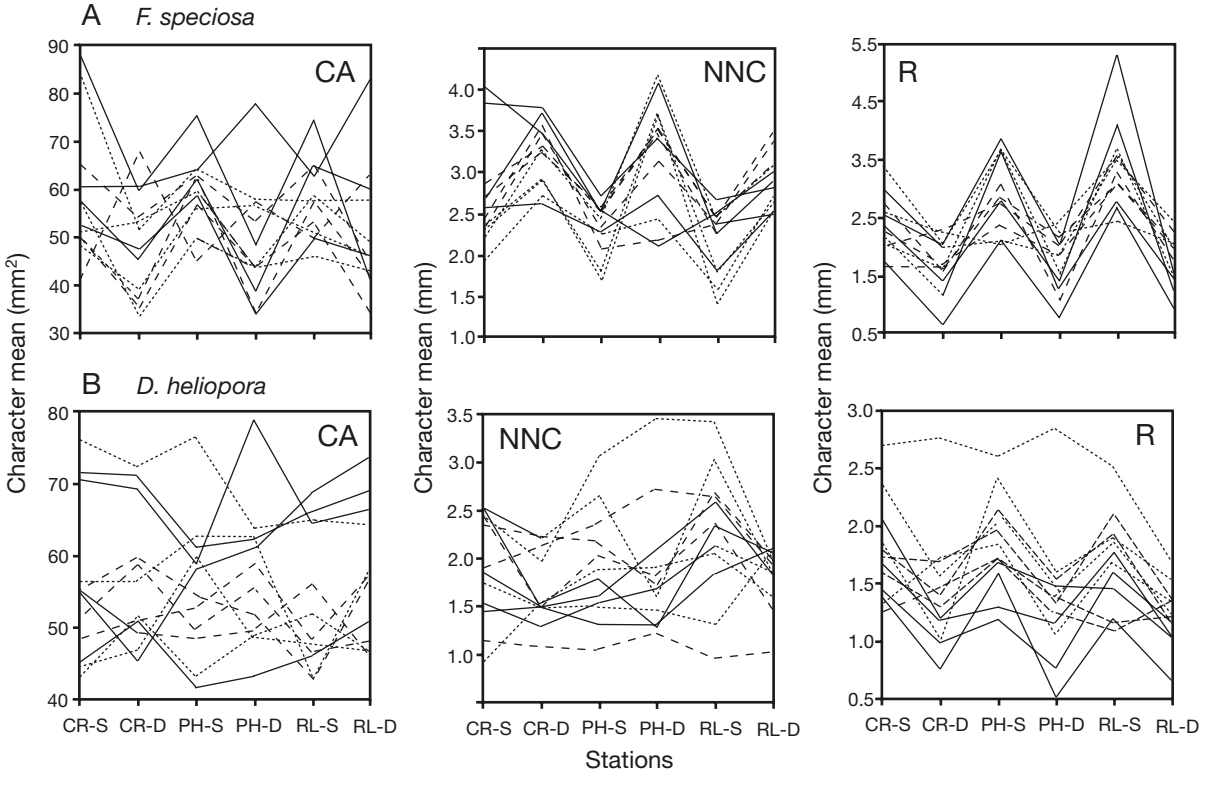

Fig. 4. *Favia speciosa* and *Diploastrea heliopora*. Reaction norms. Different lines show population origin. (—) Cyrene Reef; (– – –) Pulau Hantu, (-----) Raffles Lighthouse. Stations on the *x*-axis are ordered along nearshore to offshore sediment gradient, and alternate between shallow and deep. Station abbreviations as in Fig. 2, character abbreviations as in Table 1

Multivariate results

The exploratory factor analysis (EFA) successfully identified 3 factors and, if loading scores >0.65 are interpreted as defining the factors, a pattern emerges (Table 2). For both *Favia speciosa* and *Diploastrea heliopora*, calice size dominates Factor 1, as exemplified by high loadings for CA, CoA, CDmax, CDmin, and SL. Factor 2 represents antisymmetry (AS), with scores >0.9 for each species. NNC and CDTH are most important on Factor 3, reflecting corallite packing and exsertion.

Canonical discriminant function analysis (CDA) confirmed that morphological differences between stations are more pronounced for *Favia speciosa*, though Wilk's lambda statistics for both species are highly significant (*F. speciosa* $\lambda = 0.0292$, $p < 0.001$, *Diploastrea heliopora* $\lambda = 0.1931$, $p < 0.001$). For both species, the shallow stations group towards the negative region of the first canonical variable (CV 1); the deep stations group towards the positive (Fig. 5). The separation of deep and shallow is almost complete for *F. speciosa*, whereas there is considerable overlap for *D. heliopora*. CA, AS, NNC, R and CDTH had the greatest effect on group separation (Table 3) whereas SN, SL and CDmin had the least and were removed from the analysis.

For both *Favia speciosa* and *Diploastrea heliopora*, highly significant differences between EFA loadings on Factors 1, 2, and 3 were found among genotypes (ANOVA results, Table 4). For *F. speciosa*, highly significant differences for loading scores on Factors 1, 2 and 3 in the depth cline, and for loadings on Factor 3 among reefs, are also found (Table 4). For *D. heliopora*, only EFA loadings on Factor 3 were significantly different in the depth cline. The only significant interaction was genotype × depth for loading scores on *F. speciosa* Factor 1.

Table 2. *Favia speciosa* and *Diploastrea heliopora*. Loading scores for each character upon factors extracted by exploratory factor analysis (EFA). Scores over 0.65 have been highlighted to illustrate similarities between *F. speciosa* and *D. heliopora*

Character	Factor 1	Factor 2	Factor 3
F. speciosa			
CA	0.945	0.125	0.050
CoA	0.722	0.169	0.258
CDmax	0.818	0.500	0.155
CDmin	0.899	−0.363	0.026
SL	0.798	0.398	−0.019
SN	0.719	0.203	0.168
SW	0.166	−0.133	0.428
CDTH	0.321	0.156	0.739
NNC	0.077	−0.197	−0.809
AS	0.121	0.959	0.163
Proportion of total	0.420	0.163	0.153
D. heliopora			
CA	0.901	0.179	0.173
CoA	0.733	0.059	0.210
CDmax	0.836	0.467	0.104
CDmin	0.864	−0.268	0.152
SL	0.731	0.423	−0.067
SN	0.388	0.173	0.668
SW	0.672	−0.251	−0.215
CDTH	0.060	−0.009	0.676
NNC	0.041	−0.420	0.652
AS	0.109	0.919	−0.036
Proportion of total	0.395	0.162	0.149

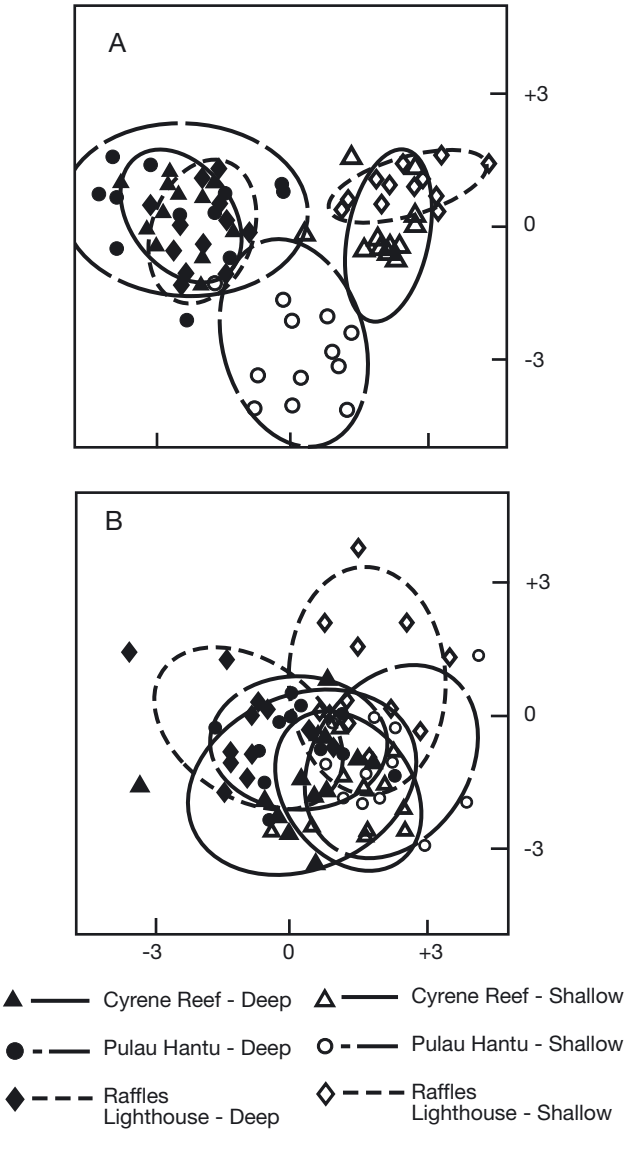

Fig. 5. (A) *Favia speciosa* and (B) *Diploastrea heliopora*. Canonical discriminant analysis (CDA) plots. For *F. speciosa*, shallow stations almost completely separate from deep stations

Table 3. *Favia speciosa* and *Diploastrea heliopora*. Loading scores for each character upon canonical variates extracted by canonical discriminant analysis (CDA). Character abbreviations as in Table 1

Character	Canonical variates		
	CV 1	CV 2	CV 3
F. speciosa			
CA	0.528	0.372	0.321
CoA	0.048	0.228	−0.111
CDmax	−0.328	−0.213	−0.225
SW	−0.327	0.169	0.025
CDTH	−0.328	−0.213	−0.225
NNC	−1.417	−0.360	−0.195
AS	0.099	−0.632	−0.185
CPUA	−0.252	−0.033	−0.428
R	0.638	−0.277	−0.751
D. heliopora			
CA	1.023	0.355	0.012
CoA	−0.057	0.122	−0.150
CDmax	0.147	−0.184	−0.230
SW	−0.150	−0.189	−0.058
CDTH	−0.557	−0.392	0.230
NNC	0.619	2.053	−0.535
AS	−0.369	0.142	−0.094
CPUA	0.319	0.048	−0.181
R	0.604	−2.270	−0.535

Environmental measurements

Total suspended solids (TSS) are significantly higher at CR-D than at the other stations (Table 5). Overall, levels are greatest at Cyrene Reef (shallow = 12.99 mg l^{-1}, deep = 15.63 mg l^{-1}), the site closest to Singapore's mainland, and are considered 'high' (Rogers 1990). However, the results for CR-S and the remaining 4 stations are not significantly different from each other,

Table 5. ANOVAs for total suspended solids (TSS). Only TSS levels at Cyrene Reef (deep) were significantly different (highlighted numbers) from the other stations (ANOVA and Tukey tests). Station abbreviations as in Table 1

TSS ANOVA

	Effect df	Effect MS	*F*	p-level
Stations	5	<0.001	3.31	< 0.01

Tukey HSD test

	CR-S	CR-D	PH-S	PH-D	RL-S
CR-D	0.761				
PH-S	0.420	0.021			
PH-D	0.991	0.388	0.790		
RL-S	0.443	0.023	1.000	0.810	
RL-D	0.557	0.038	1.000	0.890	1.000

with means ranging from 9.3 to 11.83 mg l^{-1} (Fig. 6). There is a slight trend of elevated levels of suspended solids at the deeper stations.

Sedimentation rates are also summarised in Fig. 6. Not all sets of traps were recovered, as indicated by the numbers on the bars. The data are too coarse to detect any significant differences between stations but, as with TSS, a general pattern of decreasing sedimentation with increasing distance from shore is discernible. These results corroborate a similar trend identified by Low & Chou (1994). Additionally, the shallow stations appear to have higher sediment levels than the deeper stations. Mean rates for all sites, other than RL-S, fall within Rogers' (1990) definition of 'high' sedimentation, i.e. >10 mg cm^2 d^{-1}.

Irradiance is inversely related to depth, with (extrapolated) <0.6% surface PAR reaching the depth of the

Table 4. *Favia speciosa* and *Diploastrea heliopora*. ANOVAs using loading scores from EFA Factors 1, 2 and 3 as traits; *F. speciosa* and *D. heliopora*. ***p < 0.001, **p < 0.01, *p < 0.05

Parameter	df	Factor 1		Factor 2		Factor 3	
		MS	*F*	MS	*F*	MS	*F*
F. speciosa							
Depth (D)	1	44.478	28.63***	4.091	3.15**	218.887	190.63***
Reef (R)	2	2.045	1.32	1.743	1.34	9.348	8.14***
Genotype (G)	11	6.886	4.43***	4.027	3.10***	3.557	3.10***
D × G	11	7.764	5.00***	1.088	0.87	1.601	1.39
R × G	22	2.095	1.35	1.125	0.87	1.264	1.10
Residuals	24	1.553		1.298		1.148	
D. heliopora							
Depth (D)	1	2.675	1.59	1.237	0.66	31.163	25.12***
Reef (R)	2	0.668	0.40	0.597	0.32	1.884	1.52
Genotype (G)	11	20.501	12.15***	6.288	3.37***	15.833	12.76***
D × G	11	1.750	1.02	1.126	0.60	1.749	1.41
R × G	22	2.084	1.23	1.447	0.78	1.862	1.50
Residuals	24	1.688		0.739		0.360	

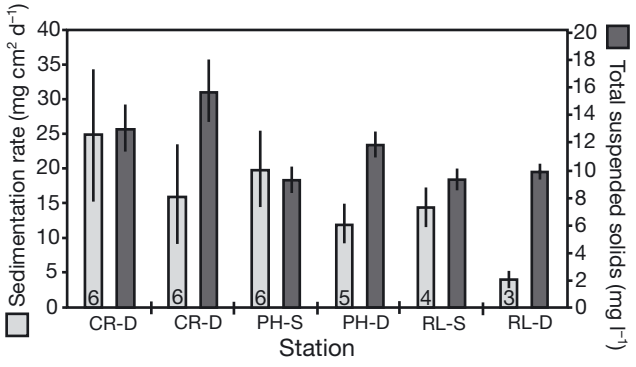

Fig. 6. Mean (±SE) sedimentation rates and total suspended solids (TSS) at all 6 stations. For sedimentation rates, number of successful sampling occasions are indicated within the bars. Station abbreviations as in Fig. 2

Table 6. Percent surface photosynthetically active radiation (PAR) reaching depth at 6 stations. Results extrapolated from readings at Raffles Lighthouse, and therefore not affected by differences in total suspended solids (TSS) levels among stations. BMSL: below mean sea level; station abbreviations as in Table 1

Station	Depth BMSL (m)	PAR	SE
CR-S	2.2	20.60	0.77
CR-D	7.6	1.13	0.04
PH-S	2.3	19.29	0.75
PH-D	8.9	0.58	0.02
RL-S	2.4	18.48	0.64
RL-D	7.0	1.55	0.06

deepest station (PH-D = 8.9 m) compared to (extrapolated) >20% penetrating to the depth, of the shallow station at Cyrene Reef (2.2 m). As all the light data were collected from Raffles Lighthouse on a day with good underwater visibility (~4 m), the results are biased towards higher levels of PAR than might actually be expected, especially for Cyrene Reef, where high TSS conditions were prevalent (Table 6).

DISCUSSION

This study has established that fragments of massive corals can be used in transplant experiments with little mortality, and that corallite-level morphology is able to change in relatively short time periods. Small-scale morphological variation in the test specimens of *Favia speciosa* and *Diploastrea heliopora* is related to environmental variables and phenotypic plasticity has been demonstrated in a number of ways. For both species, corallite characters fluctuate in size among environments, with increases most apparent at the shallow stations (Table 1). Reaction norms graphically illustrate clonal differences in levels of plasticity expressed (Fig. 4). CDA analyses all traits simultaneously, and describes group separation between depths and among the shallow stations. EFA reduces the dimensionality of the data, establishes the underlying factors; ANOVAs based on EFA loading scores show significant changes in morphology between shallow- and deep-transplanted genotypes.

Comparison of responses between species

The corallite morphology of *Favia speciosa* alters more dramatically in the test environments than the morphology of *Diploastrea heliopora*. From the tables of means (Table 1) and the reaction norms (Fig. 4) it is difficult to ascertain whether the 2 species are changing in the same direction. Although the group separation identified by CDA is strongest for *F. speciosa*, the separation for *D. heliopora* follows a comparable, if much reduced, trend in response to depth (Fig. 6). Similarity of response is also suggested by the factors extracted through EFA where, for both species, size dominates the first component, antisymmetry the second, and exsertion the third (Table 2).

The highly significant among-genotype differences for *Favia speciosa* and *Diploastrea heliopora* are to be expected, and probably reflect the initial (pre-experiment) variation among fragments (Table 4). Whereas size characters (EFA Factor 1), antisymmetry (EFA Factor 2), and corallite exsertion (EFA Factor 3) vary significantly in the depth cline for *F. speciosa*, only corallite exsertion (EFA Factor 3) varies significantly between deep and shallow for *D. heliopora*. Variation in calice symmetry is a consequence of corallite packing and is not related to developmental stability (Todd et al. 2000). The highly significant genotype × depth interaction for *F. speciosa* size-characters (EFA Factor 1) indicates that the 12 genotypes do not respond to local environmental conditions in exactly the same way. The results verify what can be seen graphically in the reaction norms (Fig. 4A), and signifies the existence of genetic variation for phenotypic plasticity, a prerequisite if natural selection is to act upon it (Bradshaw 1965, Via & Lande 1985).

As mentioned in 'Materials and methods', the test species have relatively similar large- and small-scale morphologies, but *Diploastrea heliopora* is more phenotypically stable (Veron 2000) and its skeleton tends to be denser. Particularly important are the differences in corallite spacing; although both species are massive and have large corallites, those of *D. heliopora* are more tightly packed and the inter-calice areas are less porous. This probably explains why, for *D. heliopora*,

significant differences between shallow and deep stations are only apparent for loading scores on EFA Factor 3, as these relate to corallite exsertion and topography. Due to the tight packing of *D. heliopora* corallites, they are mechanically constrained from lateral expansion (unlike those of *Favia speciosa*).

Plasticity of budding is particularly evident for both species, and important because it represents a mode of reproduction. Buds were produced by many fragments at all 3 shallow stations, but only 1 appeared on a deep fragment. After taking into account differences in total surface area and polyp numbers, *Diploastrea heliopora* produced >60% more buds than *Favia speciosa* (Table 1).

Favia speciosa persists at a greater range of depths, and has been shown here to be more phenotypically plastic, than *Diploastrea heliopora*; thus it superficially appears to be more of a generalist, and as such may be expected to survive better in novel environments (Whitlock 1996). However, *D. heliopora*, usually restricted to shallow water, experienced less tissue loss at the deep stations CR-D and PH-D than *F. speciosa*. *D. heliopora* may be augmenting photosynthesis by feeding (Lewis 1977, Anthony & Fabricius 2000); its zooxanthellae could have acclimatised to the low light levels (Schlichter & Fricke 1991, Titlyanov 1991), or other, unknown, mechanisms might be aiding homeostasis. Regardless of the process, *D. heliopora* remained healthier than *F. speciosa* in deeper water, suggesting that a broader habitat range and higher levels of morphological plasticity do not necessarily equate to higher survival in new environments.

Environmental factors

Numerous physical parameters affect coral reefs, making it difficult to attribute a morphological response to any one environmental variable. However, by a process of elimination, it is possible to identify the factors that could have been influencing corallite morphology in this study.

Passive sediment rejection is enhanced by tall polyps with steep surfaces as these encourage sediments to dissipate rapidly (Lasker 1980) and, in general, corals with large polyps are considered better at removing sediment than corals with small polyps (Marshall & Orr 1931, Stafford-Smith & Ormond 1992). However, no experiments have demonstrated that skeletal structure can change rapidly in response to increased sediment. In the present study, at both deep and shallow stations, sedimentation follows a pattern of decreasing rates with increasing distance from shore (Fig. 6). If this factor alone was enough to cause the observed range of morphometric variation, then CDA results for *Favia speciosa* should have depicted a separation of the 3 deep stations as well as the 3 shallow ones — but instead the deep stations remain tightly clustered (Fig. 5A).

Variation in waterflow has hydro-mechanical, feeding and mass transfer implications for most corals. The need for a coral to structurally withstand hydraulic energy is patent, and massive corals are well adapted to rapid fluctuations in water acceleration (Chamberlain & Graus 1975, Wainwright & Koehl 1976). Corals also have a range of morphological and behavioural characteristics that affect the likelihood of a polyp encountering a food particle (Lewis 1977, Johnson & Sebens 1993, Sebens et al. 1997). The rate of transfer of nutrients and gases between coral tissue and the water column is a limiting factor for both photosynthesis and respiration (Dennison & Barnes 1988), and increased hydraulic energy is believed to enhance transfer rates by reducing the thickness of the diffusion boundary layer (Montebon et al. 1992, Lesser et al. 1994, Bilger & Atkinson 1995). However, natural wave energy is low around Singapore, with the largest energy releases coming from waves generated by shipping traffic. The sea is especially calm around Pulau Hantu, as it is shielded by neighbouring islands and patch reefs. Theoretical diminution in wave energy over the depth gradient at Pulau Hantu is unlikely to cause the significant differences in corallite architecture found between the deep and shallow stations at this site.

Various researchers who have transplanted specimens and monitored their morphological change have considered light the primary control (e.g. Graus & Macintyre 1982, Willis 1985, Muko et al. 2000). There are indications that this may also be the case for *Favia speciosa* and *Diploastrea heliopora*. The observed changes in pigmentation are typical of those known to be related to light (Kawaguti 1944, Brown et al. 1999, Dove et al. 2001), and budding (associated with high light conditions) (Hidaka & Yamazato 1982, Muko et al. 2000) only occurred at the shallow stations. Goh et al. (1994) concluded that light was the primary factor controlling colony form in their study of depth-related coral morphology on reefs around Singapore, including the reefs examined in this paper.

Extreme reduction of light with depth is characteristic of all 3 reefs, with a conservative average of only 1.1% of surface PAR reaching the depths of the deep stations. TSS is an axiom component, as light rapidly attenuates in turbid waters (Kirk 1977). Decreases in TSS with increasing distance from shore (Fig. 6), with its associated effects on light penetration, may explain the differing small-scale morphologies among the 3 reefs for *Favia speciosa* (EFA Factor 3). Light reduction with depth, combined with the nearshore-to-offshore TSS gradient, conveniently matches the pattern of

variation in corallite structure identified by CDA and ANOVA. However, to test for causation, controlled experiments that partition physical variables are required.

Adaptive value and functional interpretation

Attributing adaptive significance to the plastic responses of any organism is difficult (Newman 1992, Dudley & Schmitt 1996), but the life history of corals makes them particularly problematic (Bruno & Edmunds 1997). However, the morphology of both species altered comparably, suggesting that the changes were not primarily stochastic. Furthermore, disparities between stations in coral fragment growth, survival and reproduction parallelled disparities in corallite structure. From the morphometric measures corallite depth (CDTH) and rugosity (R) we can conclude that growth (skeletal extension) was greater in shallow water. Tissue loss (survival) was pronounced at the deep stations of Cyrene Reef and Pulau Hantu, whereas loss was not apparent at any of the shallow stations or the deep station at Raffles Lighthouse. Finally, with 1 exception, only shallow-station fragments produced buds. Ideally, the reproductive success of clones should be measured before and after transplantation, to help identify adaptive value. Unfortunately, in the time period necessary to record this, corallite morphology is likely to change again. Indirect and more immediate measures of fitness are needed.

If induced modifications in corallite morphology have a functional basis, and the effects of light are dominant, then what might the relationship between the two be? At the coral colony level, it is thought that tabular forms enhance light capture and are therefore ecologically advantageous in low-light conditions. Graus & Macintyre (1982) computer-simulated *Montastrea annularis* coral growth based upon changes in light intensity, photosynthesis rates, and calcification. They used transplantation techniques and detailed measurements of skeletal growth to model a continuous morphotypic gradient in which colonies became flatter with increasing depth. Willis (1985) reciprocally transplanted colonies of *Turbinaria mesenterina* across 2 depths and left them to grow for 3.5 yr. She found that *T. mesenterina* was highly plastic, with explanate forms becoming convoluted in shallow depths and convoluted forms becoming explanate in deeper water. Explanate forms existed in shallow shaded areas, but no convoluted forms at all were found in the deep sites, suggesting that light was the main factor controlling morphology in this species. Muko et al. (2000) demonstrated how explanate forms of *Porites sillimaniani* clones developed branches when exposed to high light intensities, whereas those in low light remained flat. They computer-modelled the branching morphology and demonstrated that it was advantageous for utilising the surfeit light characteristic of shallow water. An equivalent small-scale response could explain the flatter corallites at the deep stations and the more exsert corallites at the shallow stations in the present study. Flat corallites are the best form for capturing light when irradiance is low, whereas the greater rugosity of fragments at the shallow stations equates to a larger surface area, and therefore an ability to maximise light capture where irradiance is high. Alternatively, the deepening of the corallites at the shallow stations may result in self-shading and thus protect the central (oral disc) area of each polyp from the damaging UV radiation that penetrates shallow waters (Jokiel 1980, Wood 1987, Gleason 1993). To test this second hypothesis, more research into the incident light fields, UV levels, and self-shading that affect the 2 study species is needed.

Around Singapore, light appears to have the greatest influence on the corallite characters of *Favia speciosa* and *Diploastrea heliopora*, but in locations where differences in water motion, food availability, or salinity, for instance, are more in evidence they may also have an effect on morphology. For instance, Foster (1979) demonstrated plasticity in *Montastrea annularis* but, even after extensive work, was unable to pinpoint an unequivocal relationship between an environmental property and small-scale morphology, referring only to light intensity, sedimentation rate, water activity, and food availability as the probable candidates. West et al. (1993) studying *Briareum asbestinum*, and Oliver et al. (1983) studying *Acropora formosa*, considered both water movement and light important to the morphological differences they found after reciprocally transplanting colonies/fragments (respectively) across different depths. Bruno & Edmunds (1997) found plastic responses in *Madracis mirabilis*, but water activity, light levels, sedimentation rate, water temperature and salinity all varied among their study sites. Ecological factors, as well as physical variables, have been shown to induce morphological change. Potts (1976) demonstrated how growth interactions among *A. palifera* fragments affect their morphology. Similarly, neighbouring corals affected the growth rate and form of *Porites attenuate* branches in Raymundo's (2001) study.

The findings of this research cannot provide any insights into the genes involved in plasticity other than demonstrating, via reaction norms, that both *Favia speciosa* and *Diploastrea heliopora* exhibit among-genotype variation in the level of plasticity expressed. This variation means that, if the plasticity had some functional advantage, selection should favour the more

plastic genotypes. Determining the costs and limits of phenotypic plasticity (sensu DeWitt et al. 1998) can only be attempted after establishing its adaptive value. From the present research it is impossible to calculate the production, maintenance, information acquisition, or genetic costs for phenotypic plasticity in *F. speciosa* and *D. heliopora*. Similarly, information reliability and developmental range limits cannot be determined. However, because they grow so slowly, plastic corals are probably affected by lag-time limits, i.e. they are likely to experience a period of maladaption after first encountering a new environment.

Implications of plasticity in corals

Scleractinian corals that exhibit high degrees of variation are often presumed to be plastic. The fact that Miller (1993) could find no genetic differences, or environmental influences, to explain the growth forms of *Platygyra daedalea* illustrates how difficult it can be to correctly decipher intraspecific morphological variation. However, it is clear that the role of genotype × environment interactions vary according to species (Willis 1985, Ayre & Willis 1988, Weil 1993).

Best et al. (1984) suggested that the high variation in skeletal morphology has led to overestimates in the number of both fossil and recent coral species. Conversely, Knowlton & Jackson (1994) proposed that, as traditional coral taxonomy assumes a high level of phenotypic variation, it consequently underestimates the true number of taxa. Both these possibilities are valid, and each taxon needs to be considered separately (Wijsman-Best 1974). New approaches, including molecular techniques, and a growing knowledge of the ecology, behaviour, and life-history of corals has meant that populations previously considered a single species are now being subdivided into new species, subspecies, sibling species, ecomorphs, and morphotypes (e.g. Knowlton et al. 1992, 1997, Weil 1993, Van Veghel & Bak 1993, Knowlton & Jackson 1994, Lasker et al. 1996), whereas other 'morphological species' are being found to have only small genetic or reproductive differences (e.g. Miller 1994, Szmant et al. 1997).

The conditions favouring phenotypic plasticity are certainly found on coral reefs, that is, sessile corals experience disruptive selection both in space and time (Bradshaw 1965, Potts 1984). The dispersal of larvae, with little motility and limited capacity for substrate selection, into the heterogeneous reef environment almost eliminates any chance of predicating what habitat offspring will settle in. Coral that can reproduce through fragmentation fare no better. During short timescales (weeks to months) a coral may encounter considerable environmental variation, for example, fluctuations in water quality, changes in reef topography (e.g. due to storm damage), and the growth or death of neighbouring organisms. Previously, excluding freak events, most environmental variation in longer timescales would not have encouraged plastic responses, i.e. seasons (predictable), or geological change, as both of these could be adapted to through genetic change. However, as global climate change is now evidenced in periods of less than a century (Pittock 1999), and corals, or at least coral genets, can live for hundreds of years (Potts et al. 1985, Lasker & Coffroth 1999), those species capable of adaptive plastic responses may have a survival advantage over their phenotypically stable cousins.

CONCLUSION

Although *Favia speciosa* displays greater environment-induced variation than *Diploastrea heliopora*, the tested genotypes of both species are phenotypically plastic and respond in analogous ways. The corallites of the fragments transplanted to shallow water tend to be larger and more exsert than those transplanted to deep water. The highly significant G × E interactions described for *F. speciosa* EFA Factor 1 indicate that genotypes of this species vary in the level of plasticity expressed. Depth has the greatest effect, but significant differences among reefs are also apparent for *F. speciosa*. Light and TSS emerge as the physical parameters that most probably influence morphology, although other factors possibly act additively, synergystically or antagonistically with them. Increased corallite exsertion may maximise use of available light or, alternatively, protect central areas of tissue from UV radiation. Morphological variability, combined with changes in pigmentation, is likely to impede accurate identification of these taxa, especially of *F. speciosa*. In contemporary, rapidly changing environments, phenotypic plasticity could be advantageous to corals that, due to their long generation time and infrequent reproduction, might not be able to survive through adaptation alone.

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