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AMONG-GENOTYPE VARIATION FOR SEDIMENT REJECTION IN THE REEF-BUILDING CORAL *DIPLOASTREA HELIOPORA* (LAMARCK, 1816)

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ABSTRACT. — Sediment settling on corals interferes with their feeding and photosynthesis. Near-shore construction and dredging activities can result in increased sedimentation and significantly impact coral reefs. It is well known that coral species differ in their ability to cope with sediment stress, yet within-species variation for sediment rejection is much less understood. In this study, fragments of *Diploastrea heliopora* retrieved from four different colonies (genotypes) were subjected to three levels of acute sediment (silicon carbide powder) exposure in a controlled aquarium tank environment. After five hours, significant differences in surface area cleared were found for both treatment and genotypes. Significant differences among genotypes were also found for mass of sediment removed. Previous researchers have discussed how reefs under stress may become populated by hardy genotypes and our results suggest that the necessary intraspecific variation exists for such a process in Singapore.

KEY WORDS. — selection, silicon carbide powder, silt, Singapore, stress

INTRODUCTION

Sedimentation continues to be one of the most prevalent threats to coral reefs worldwide (Erftemeijer et al., 2012). While rivers naturally deposit some sediment onto reefs, land-based human activities such as deforestation, construction, and poor land use practices greatly increase alluvial output (Bone et al., 1993; Hodgson, 1993). Benthic sediments can also be disturbed by dredging and other near-shore work such as land reclamation and drilling (Sheppard, 1980). Sediments have the capacity to be carried long distances away from the source, causing far-reaching impacts (Rogers, 1990; Erftemeijer et al., 2012). Even though suspended particulate matter may constitute an important source of food for suspension feeders, it is generally agreed that high loads of suspended and settling sediments cause stress to corals (Rogers, 1990; Riegl & Branch, 1995; Fabricius, 2005).

At the population and community levels, high sediment loads are known to affect species distribution and abundance on coral reefs (Brown et al., 1990; McClanahan & Obura, 1997; Browne et al., 2010). At the individual level, corals are affected in three principal ways. Firstly, suspended particulate matter attenuates light rapidly (Kirk, 1977) and hence reduces photosynthesis by symbiotic zooxanthellae (Rogers, 1979; Telesnicki & Goldberg, 1995). Secondly, particles settling on corals further reduce light reaching the zooxanthellae, as well as interfere with prey capture. Sediment removal mechanisms, such as polyp tissue expansion, manipulation by tentacles, and profuse mucus production incur an energetic cost (Lasker, 1980; Stafford-Smith & Ormond, 1992; Riegl & Branch, 1995; Gilmour, 2002). Furthermore, sediments that accumulate on coral surfaces can cause anoxic conditions for the underlying tissue, eventually resulting in tissue necrosis (Riegl, 1995). Thirdly, layers of accumulated sediment reduce the availability of substrate suitable for coral planulae settlement (Rogers, 1990; Babcock & Davies, 1991).

Not all sediments interact with corals in the same way. For the same mass, suspended fine sediments attenuate light more rapidly than larger sediments (Stafford-Smith, 1993). Fine grain sizes flow off a colony more easily than coarse grains (Lasker, 1980) but they can also create an oxygen diffusion barrier if they collect in hollows and crevices (Stafford-Smith & Ormond, 1992). Species that move larger grains efficiently tend to have larger corallites with higher relief and more septa (Hubbard & Pocock, 1972). A coral's behavioural response to physical contact with sediment also varies in relation to particle size (Marshall & Orr, 1931; Bak & Elgershuizen, 1976) with silts generally removed by ciliary action while larger particles cause polyp tissues to expand (Hubbard & Pocock, 1972). Coral mucus, typically secreted in large quantities in response to silts and fine sands, can be very energetically expensive and also lead to exhaustion of mucus-producing cells (Riegl & Branch, 1995; Erftemeijer et al., 2012). Taken together, the evidence suggests that fine silt has the ability to stress corals more than coarse sand, especially when water movement is low (Fabricius, 2005).

In Singapore, the effects of sedimentation must be considered in any study of coral reefs due to the long history nearshore sediment-producing infrastructural projects that have reduced live coral cover and the depth at which corals can survive (Chou, 1996; Hoeksema & Koh, 2009). Suspended materials originating from reclamation activities and dredging of shipping lanes continue to be Singapore's largest marine pollution issue (Dikou & van Woesik, 2006; Todd et al., 2010). Rogers (1990) noted that, generally, undisturbed reefs have mean sedimentation rates between 1 and 10 mg cm^{-2} day^{-1} and that levels continuously above this range could be considered 'high'. Many reefs off Singapore have sedimentation rates above this 'high' definition (Todd et al., 2004a; Dikou & van Woesik, 2006) and the associated turbidity has resulted in poor light penetration and the loss of coral cover in deeper zones, e.g., 6 m and 10 m (Chou, 1988; Chou, 1996).

It is well understood that coral species vary in their response to sediment deposition and reduced light penetration (Titlyanov & Latypov, 1991; Stafford-Smith & Ormond, 1992; Erftemeijer et al., 2012). Within-species variation in tolerances, however, has rarely been studied. Marshall & Orr (1931) observed intraspecific among-individual dissimilarities in mud removal and Anthony (1999) showed variation in among-colony responses to particle load and shading. Todd et al. (2001) related within-species differences in polyp size in *Favia speciosa* (Dana) to a near- to off-shore sediment gradient and, in a subsequent manipulative experiment, Todd et al. (2004b) found slight differences in surface rugosity among genotypes of *F. speciosa* and *Diploastrea heliopora* (Lamarck) grown in an artificial sediment regime. As Hughes et al. (2003) state, stress resistant genotypes are likely to persist, resulting in re-configured but still viable coral reefs (however, others doubt this possibility, see Hoegh-Guldberg, 2009). To investigate whether such resistant genotypes exist, we used coral fragments as replicates to examine among-genotype variation in sediment rejection abilities in the reef-building massive species *D. heliopora*. We tested the following two hypotheses: (1) The rate of sediment clearance by *D. heliopora* is dependent on the quantity of sediment deposition it is exposed to, and (2) its genotypes vary in their ability to reject sediment.

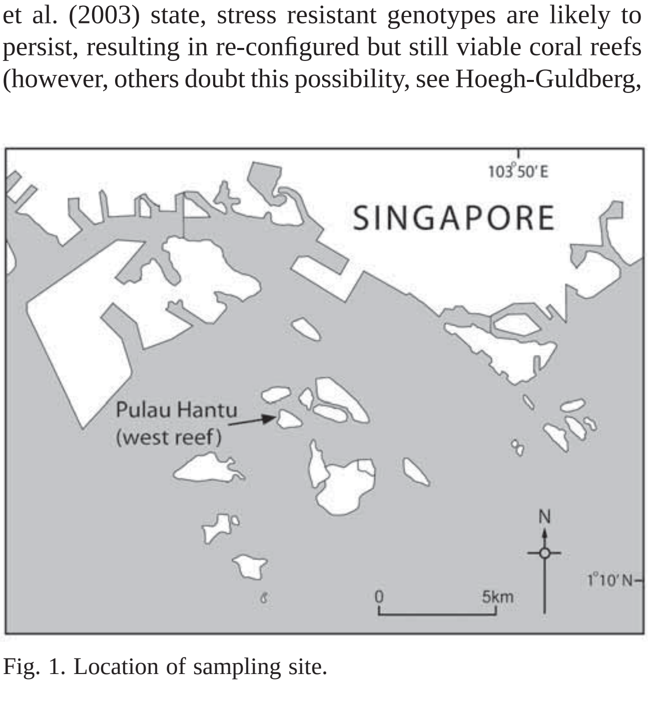

Fig. 1. Location of sampling site.

MATERIAL AND METHODS

Study species and sampling technique. — *Diploastrea heliopora* is the only species in its genus and, due to its relatively invariable form, is easy to identify (Veron, 1986). However, its colour and small-scale morphology can be induced to change when transplanted to new habitats (Todd et al., 2002a, 2002b). It is widespread in the Indo-Pacific and commonly known as the moon or honeycomb coral. Colonies tend to be dense and can grow to >2 m high and >7 m in diameter (Veron et al., 1977; Veron, 2000), the largest in the family Faviidae. *D. heliopora* is hardy, aggressive and able to survive in a wide range of light and hydraulic energy regimes (Sprung, 1999). Polyps are relatively large; around 8 to 10 mm diameter in Singapore (Todd et al., 2004a), and Stafford-Smith (1992) noted that it is a highly active sediment shedder, using cilia action and/or tissue expansion.

Four colonies, at least 20 m apart (and therefore assumed to be different genotypes), were identified at 4 to 7 m depth (Todd et al., 2004a) on the sheltered western reef of Pulau Hantu (1°13'30"N, 103°44'56"E), an island to the south of mainland Singapore (Fig. 1). In late Feb.2010, a pneumatic drill fitted with a 55 mm inner-diameter diamond coring bit and powered by compressed air from a SCUBA tank was used to drill twelve circular cores from flat seaward-facing surfaces of each of the *D. heliopora* colonies. The fragments were maintained in tanks of seawater while transported to the marine aquarium at the Department of Biological Sciences, National University of Singapore. The number of complete polyps per fragment was counted from close-up underwater images taken while the fragments were acclimatising in the aquarium. These data were used to calculate the mean density of polyps (as a surrogate of polyp size) per genotype.

Recreating the profile of sediments found in the waters around Pulau Hantu. — The mechanical effects of sediment deposition on *D. heliopora* were tested. To avoid confounding factors such as organic matter and microbes that are usually associated with natural sediments (Weber et al., 2006), silicon carbide powder was used to mimic the particle size profile of the sediments found around P. Hantu. Silicon carbide was chosen because it is chemically inert, up to 99 % pure, and had earlier been used by Stafford-Smith & Ormond (1992) to substitute silt.

Natural sediments from P. Hantu were collected in 15 sediment traps deployed over a period of two weeks in Aug.2009 at a depth (3 to 4 m) close to where the *D. heliopora* colonies used in this study were found. Cylindrical

PVC traps (5 cm diameter × 11.5 cm deep) were arranged in sets of 3 and fixed to aluminum stakes ~50 cm above the substrate (English et al., 1997). A composition profile of the pooled sediment samples was obtained by laser diffraction (Malvern Mastersizer Particle Size Analyzer). Ultrasound was used to deflocculate any clumps during measurement. The natural sediment profile of Pulau Hantu was mimicked by mixing various proportions of silicon carbide powder of grit sizes 1200, 1000, 800, 600, 400, 280, 220, and 150 (Kemet Fareast Pte Ltd). The mixture was suspended in seawater and profiled with the same laser diffraction method. This process was repeated until the two profiles (natural and artificial) matched closely (Fig. 2).

Testing the response of D. heliopora to sediment exposure. — Three tanks were used, each consisting of a 25 × 25 × 30 cm^3 (W × L × H) chamber where a single coral core was placed on a plastic mesh affixed horizontally 10 cm from the bottom. A sliding tray at the base of the chamber allowed for cleared sediments to be moved into a second compartment through a trapdoor for collection and analysis. The experiment was initiated with the introduction of silicon carbide powder via a 55 mm inner diameter PVC pipe placed over the core (so that the inner surface of the pipe fitted closely to the outer circumference of the core) and protruding from the tank. Pilot trails showed that dry powder poured into the top of the pipe resulted in an even spread of sediment on the coral after five minutes of settlement time. The pipe was then removed carefully and the tank left undisturbed for the duration of the experiment.

Four replicate coral cores from each of the four genotypes were subjected to one of three sediment load treatments (high: 250 mg cm^{-2}, medium: 150 mg cm^{-2}, and low: 50 mg cm^{-2}), resulting in a total of 48 independent experiment runs. All three tanks were used simultaneously and the first run started four days after extraction of the cores from P. Hantu. For each trial, the core and the sediment level it was exposed to were assigned randomly using a random number generator. Digital photographs were taken immediately after the introduction of the silicon carbide powder, and then hourly until the end of the run, five hours later. These images were analysed using ImageJ version 1.41 (National Institute of Health, USA) to calculate the area of the coral fragment that had been cleared of the silicon carbide powder. At the end of five hours, the cleared sediments were collected from the tray at the bottom of the tank and filtered using a Gast vacuum filtration system before being oven dried following Guy (1969). Water temperature during the experiments ranged from ~29 to ~31 °C. To ensure the sediments were not disturbed by factors other than the action of the corals, no aeration or water flow was provided during the five hour treatments. The facility where the experiments took place used a combination of both natural and artificial lighting (the latter timed to coincide with the local 12:12 h photo-period).

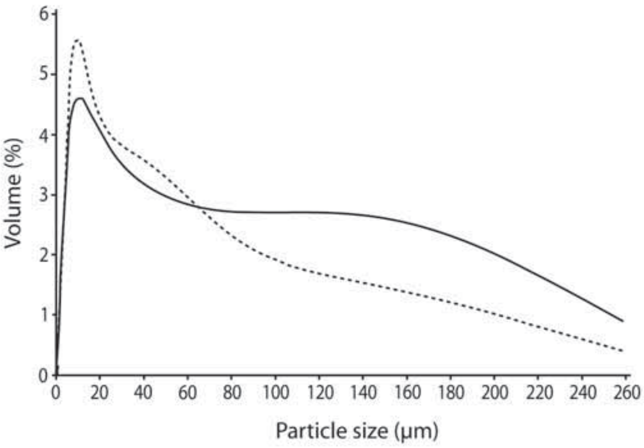

Fig. 2. Profiles of natural sediments retrieved from sediment traps positioned at Pulau Hantu (solid line) and the artificial silicon carbide mixture (dotted line).

Table 1. One-way ANOVA results for polyp density.

	df	SS	F	P
Genotype	3	162.23	4.9769	<0.005
Error	44	478.08		

Statistical analyses. — The mean density of polyps among genotypes was tested with a single factor ANOVA (normality assumptions fulfilled). Percentage area clearance data were normal but percentage mass clearance data needed to be square-root transformed to fulfill this assumption. The variance of all data sets was homogenous (Levene's test). The percentage area cleared over time was tested with a two factor (genotype × sediment load) repeated measures ANOVA whereas percentage mass cleared after five hours (the length of each experimental run) was tested with a regular two-factor ANOVA. All pairwise comparisons were performed with post-hoc Tukey's Honest Significant Difference (HSD) tests. Analyses were conducted using R and the associated R Commander package.

RESULTS

Polyp density differed among the four genotypes (Fig. 3, Table 1) and post-hoc HSD tests indicated that polyp density for

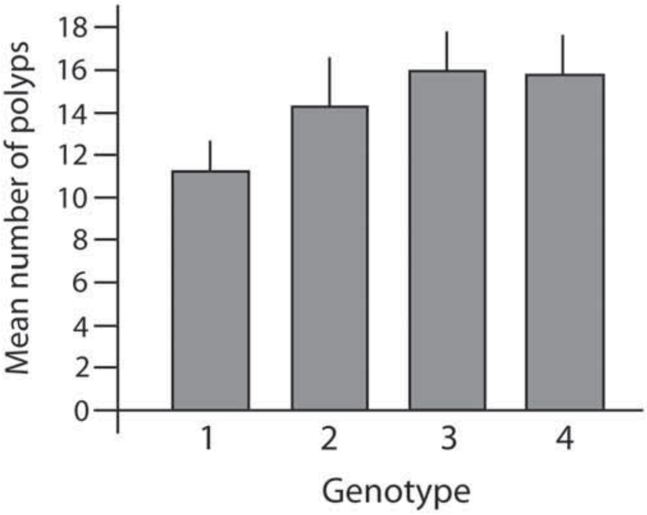

Fig. 3. Mean number of polyps (23.75 cm^2 surface area) calculated from 12 fragments per genotype (bars represent S.E.).

Table 2. Repeated measures ANOVA results for percentage area cleared.

	df	SS	F	P
Genotype	3	3829	4.4950	<0.005
Time	4	156355	137.6743	<0.001
Treatment	2	12306	21.6712	<0.001
Genotype × Time	12	3628	1.0648	0.390
Genotype × Treatment	6	4477	2.6283	0.018
Time × Treatment	8	1353	0.5959	0.781
Genotype × Time × Treatment	24	3328	0.4884	0.980
Error	180	51106		

genotype 1 was significantly lower than genotypes 3 and 4, which were not significantly different from each other. The polyp density for genotype 2 was not significantly different from the other three genotypes. All coral fragments were able to remove at least 50% area of the deposited sediment within five hours, even when exposed to the highest loads (Fig. 4). Significant differences were observed among genotypes and across the three treatment groups for percentage area cleared; interactions between genotype and treatment were non-significant (Fig. 4, Table 2). Post-hoc HSD tests showed that significantly more area was cleared under the low sediment load, compared to the medium and high loads, which were not significantly different from each other. Post-hoc HSD tests on genotype showed that genotypes 2 and 4 were significantly different from each other. For the percentage sediment mass cleared, significant differences were only found for genotype, again only between genotypes 2 and 4 (Fig. 5, Table 3).

DISCUSSION

Unnaturally high levels of sedimentation have posed longstanding environmental challenges to the coral reefs of Singapore, however, surprisingly few studies have examined its effects on local corals experimentally. Stressful environments are thought to select for more resilient coral genotypes (Hughes et al., 2003) and in Singapore it has been suggested that corals could be adapting to its sedimented waters (Chou, 1988). In her sediment-rejection efficiency study, Stafford-Smith (1993: 232) noted that "although there was considerable intraspecific variation, *D. heliopora…*also cleared their tissues relatively fast". By using multiple fragments from individual colonies we were able to expand on this observation and test fully for among-genotype variation in sediment clearing abilities. This research represents the first attempt to demonstrate experimentally that some genotypes are more capable of removing sediments than others.

Previous studies examining the effects of sediments on corals have used a variety of materials from a range of sources. For example, Wesseling et al. (1999) used near-shore littoral sediments (silt, fine, and coarse sand; 28% $CaCo_3$), Riegl (1995) collected 'biogenic carbonate sand' (very fine, fine, and coarse sand), and Todd et al. (2004b) mixed reef-collected carbonate material with commercial quartz sand to create coarse, medium, fine, and very fine sand fractions. Stafford-Smith & Ormond (1992) used 70/30% carbonate/quartz sand of four grain sizes but they also used carborundum powder to mimic silt. Apart from the carborundum powder, all these materials had the opportunity to retain some of their 'organo-detrital' (Hubbard & Pocock, 1972) properties such as nutrients and/or microbes. By using inert silicon carbide

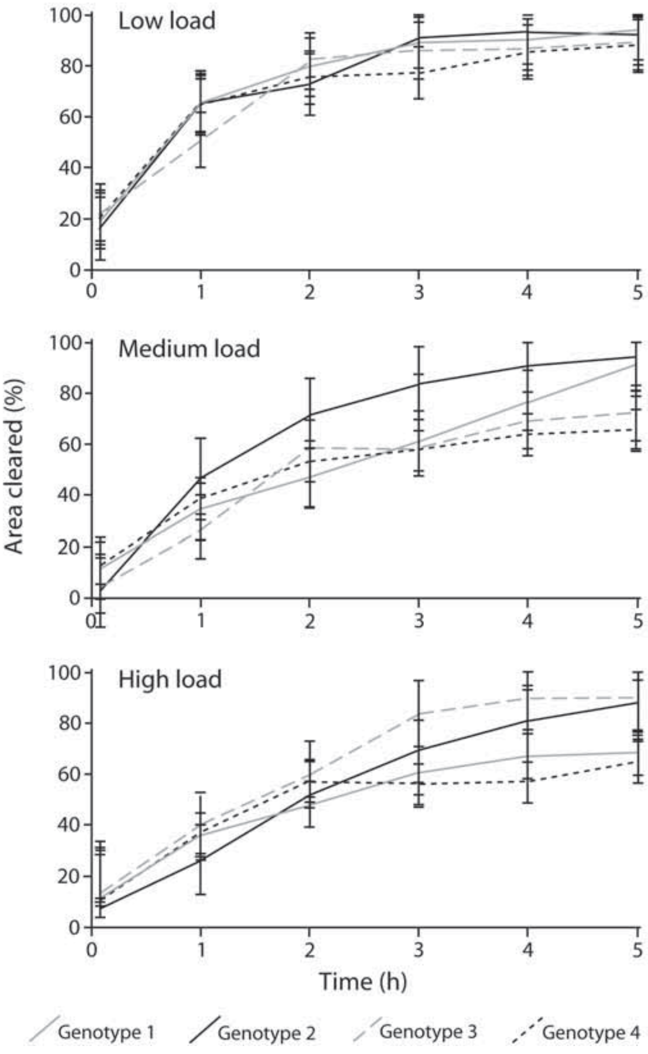

Fig. 4. Percentage area cleared of sediment over the five-hour duration of the experiment calculated from 12 fragments (four replicates × three treatment) per genotype. Significantly more sediment was cleared under the 'low' sediment load compared to the 'medium' and 'high' loads (Table 2).

Table 3. Two-way ANOVA results for percentage mass cleared.

	df	SS	F	P
Genotype	3	2494.7	3.9812	0.015
Treatment	2	251.6	0.6023	0.553
Genotype × Treatment	6	2256.7	1.8007	0.127
Error	36	7519.4		

powder these potential confounding factors were removed. Furthermore, as particle size is critical to how corals respond to smothering (Stafford-Smith & Ormond, 1992) it was important to replicate the particle size profile of sediments ‘naturally’ falling on corals in Singapore in the field. As silicon carbide powder is available in a wide range of grit sizes, it was possible to achieve a high degree of control over the recreated profile.

Stafford-Smith (1993) identified *D. heliopora* as an efficient sediment rejecter and just the fact that it is present in Singapore’s turbid waters suggests this species is resistant to sediment stress. During our experiments, substantial mucus production was observed. The silicon carbide powder stuck to the mucus and, because there was no flow in the tanks, we assume this was moved off the surface of the coral via ciliary action. Stafford-Smith & Ormond (1992) and Stafford-Smith (1993) made similar observations. Sediment load, however, negatively affected the efficiency of this process in *D. heliopora*. The percentage area cleared was significantly different among the sediment treatments, with greater loads taking longer to clear. This response has been shown previously, and is known to vary across species (see Stafford-Smith, 1993), but our results also demonstrate variation within species. For example, significant differences between genotypes 2 and 4 were found for both area and sediment mass cleared.

The specimens of *D. helipora* in this study were able to clear themselves of substantial amounts of sediment, but it took them several hours—even at the lowest sediment levels. Hence, the frequency of such sediment deposition becomes a critical question. The waters around Singapore are relatively calm, being surrounded by Malaysia to the north and Indonesia to the south, although there are strong currents as well as sporadic wave events caused by the wakes of large passing ships (Swan, 1971). This low energy environment, coupled with extensive dredging and land reclamation operations, has led to high levels of sediments deposited on the reefs. The ship wakes are not frequent and strong enough to keep the reefs clear of sediments, but they can still play an important role in sporadically re-suspending material that has accumulated on the substratum. Exactly how often this happens remains unknown, but work is underway to measure these occurrences. Acute stress, as defined by Connell (1997), is usually thought to have little or no long term impacts on corals. Instead, several previous studies (e.g. Connell, 1997; Fabricius, 2005) contend that chronic sediment stresses pose a greater problem to coral species and require a longer recovery time. However, there is little or no research on the ‘middle way’ of repeated acute deposition events.

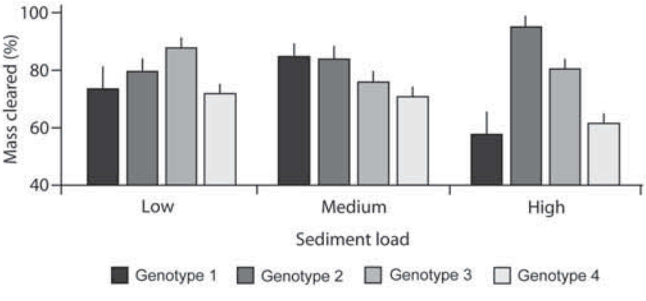

Fig. 5. Percentage of sediment mass cleared after five hours (the duration of the experiment) calculated from 12 fragments (four replicates × three treatment) per genotype.

Significant intra-specific differences between genotypes 2 and 4 for both percentage area and mass clearance were found. However, differences in polyp density were only identified for genotype 1, which had significantly fewer polyps per fragment than genotypes 3 and 4. This suggests that polyp size had minimal effect on sediment rejection efficiency in *D. helipora*. But, as this species is not known to use tentacular manipulation of particles, this is perhaps not surprising. Among all the host colonies on P. Hantu, genotypes 2 and 4 were the furthest (~250 m) apart from each other. Hence, it is possible that they have acclimatized to different micro-environments and one has had greater historical exposure to sediment. However, nothing is known of the spatial environmental variation at P. Hantu other than the typical depth-associated changes in light penetration (but all the host colonies were sampled from similar depths). From personal observations, there was little disparity among the environments from where the colonies were sampled. Alternatively, the two genotypes had fundamental genetic differences in their ability to remove sediment. Hoegh-Guldberg (1999) proposes that corals on reefs subjected to environmental changes such as rising global temperatures will likely be able to adapt, with some species surviving and reproducing better than others. Much less attention has been given to within-species, i.e., among-genotype, variability for stress resistance. In one of the few papers to mention this, Hughes et al. (2003) discuss how reefs may become populated by hardy genotypes and our results suggest that the necessary intraspecific variation exists for such a process in Singapore.

Scleractinian corals have been exposed to settling sediments for millennia and have evolved mechanisms to cope with them, for instance Marshall & Orr (1931: 17) note that “the common types of corals, when they are helped by water movements as well as by their own ciliary action, are well able to deal with any ordinary amount of sand falling on them”. But the levels of sediment that Singapore’s corals are exposed to are no longer “ordinary”, with high levels of background sedimentation plus material sporadically stirred up by ship wakes. Our study showed that, even though *D. helipora* is an efficient sediment rejecter (Stafford-Smith, 1992), significantly more material was remaining at five hours post exposure for the high sediment treatment compared to the low treatment. The four genotypes tested varied in their ability to remove sediments, but this was not due to differences in polyp density (i.e., polyp size). It has been discussed at length how diversity of life-history strategies and physiological tolerance are important to ensuring resilience of coral reefs to environmental disturbances (see Done et al., 1996) and, although generally discussed in terms of among-species differences, the same argument holds true for intraspecific variation for these traits. Other studies have suggested that certain coral genotypes should be selected for under regimes of increasing temperature (Hoegh-Guldberg, 1999) and similar selection may be expected when corals are exposed to increasing sedimentation stress.

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LITERATURE CITED

Anthony, K. R. N., 1999. A tank system for studying benthic aquatic organisms at predictable levels of turbidity and sedimentation: Case study examining coral growth. *Limnology and Oceanography*, **44**: 1415–1422.

Babcock, R. & P. Davies, 1991. Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs*, **9**: 205–208.

Bak, R. P. M. & J. H. B. W. Elgershuizen, 1976. Patterns of oil sediment rejection in corals. *Marine Biology*, **37**: 715–730.

Bone, D., F. Losada & E. Weil, 1993. Origin of sedimentation and its effect on the coral communities of a Venezuelan national park. *Ecotropicos*, **6**: 10–21.

Brown, B. E., M. D. A. Le Tissier, T. P. Scoffin & A. W. Tudhope, 1990. Evaluation of the environmental impact of dredging on intertidal coral reefs at Ko Phuket, Thailand, using ecological and physiological parameters. *Marine Ecology Progress Series*, **65**: 273–281.

Browne, N. K., S. G. Smithers & C. T. Perry, 2010. Geomorphology and community structure of Middle Reef, central Great Barrier Reef, Australia: An inner-shelf turbid zone reef subject to episodic mortality events. *Coral Reefs*, **29**: 683–689.

Chou, L. M., 1988. Community structure of sediment-stressed reefs in Singapore. *Galaxea*, **7**: 101–111.

Chou, L. M., 1996. Response of Singapore reefs to land reclamations. *Galaxea*, **13**: 85–92.

Connell, J. H., 1997. Disturbance and recovery of coral assemblages. *Coral Reefs, Supplement*, **16**: S101–113.

Dikou, A. & R. van Woesik, 2006. Survival under chronic stress from sediment load: Spatial patterns of hard coral communities in the southern islands of Singapore. *Marine Pollution Bulletin*, **52**: 1340–1354.

Done, T. J., J. C. Ogden, W. J. Wiebe & B. R. Rosen, 1996. Biodiversity and ecosystem function of coral reefs. In: Mooney, H. A., J. H. Cushman, E. Medina, O. E. Sala, & E. D. Schulze (eds.), *Functional Roles of Biodiversity: A Global Perspective.* John Wiley & Sons Ltd., U.K. 493 pp.

English, S., C. Wilkinson & V. Baker, 1997. *Survey Manual for Tropical Marine Resources*. Australian Institute of Marine Science, Townsville. 390 pp.

Erftemeijer, P. L. A., B. Riegl, B. W. Hoeksema & P. A. Todd, 2012. Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin*, (in press).

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, **50**: 125–146.

Gilmour, J. P., 2002. Acute sedimentation causes size-specific mortality and asexual budding in the mushroom coral, *Fungia fungites*. *Marine & Freshwater Research*, **53**: 805–812.

Guy, H. P., 1969. C1: Laboratory theory and methods of sediment analysis. In: *Techniques of Water Resources Investigations*. Pp. 1–56.

Hodgson, G., 1993. Sedimentation damage to reef corals. *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History*. Atlantic Reef Committee. Pp. 298–303.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine & Freshwater Research*, **50**: 839–866.

Hoegh-Guldberg, O., 2009. Climate change and coral reefs:Trojan horse or false prophecy? A response to Maynard et al. (2008). *Coral Reefs*, **28**: 569–575.

Hoeksema, B. W. & E. G. L. Koh, 2009. Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. *Raffles Bulletin of Zoology, Supplement*, **22**: 91–101.

Hubbard, J. A. E. B. & Y. P. Pocock, 1972. Sediment rejection by recent scleractinian corals: A key to paleoenvironmental reconstruction. *Geologische Rundschau*, **61**: 598–626.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen & J. Roughgarden, 2003. Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**: 929–933.

Kirk, J. T. O., 1977. Attenuation of light in natural waters. *Australian Journal of Marine and Freshwater Research*, **28**: 497–508.

Lasker, H. R., 1980. Sediment rejection by reef corals: The roles of behavior and morphology in *Montastrea cavernosa* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, **47**: 77–87.

Marshall, S. M. & A. P. Orr, 1931. Sedimentation in Low Isles reefs and its relation to coral growth. In: *Scientific Reports of the Great Barrier Reef Expedition 1928–1929*. British Museum of Natural History, London. Pp. 93–133.

McClanahan, T. & D. Obura, 1997. Sediment effects on shallow coral reef communities in Kenya. *Journal of Experimental Marine Biology and Ecology*, **209**: 103–122.

Riegl, B., 1995. Effects of sand deposition on scleractinian and alcyonacean corals. *Marine Biology*, **121**: 517–526.

Riegl, B. & G. M. Branch, 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology*, **186**: 259–275.

Rogers, C. S., 1979. The effect of shading on coral reef structure and function. *Journal of Experimental Marine Biology and Ecology*, **41**: 269–288.

Rogers, C. S., 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, **62**: 185–202.

Sheppard, C., 1980. Coral fauna on Diego Garcia lagoon following harbour construction. *Marine Pollution Bulletin*, **11**: 227–230.

Sprung, J., 1999. *Corals: A Quick Reference Guide*. Ricordea Publishing, Miami, USA. 240 pp.

Stafford-Smith, M. G., 1992. Mortality of the hard coral *Leptoria phrygia* under persistent sediment influx. *Proceedings 7th International Coral Reef Symposium*, **1**: 289–299.

Stafford-Smith, M. G. & R. F. G. Ormond, 1992. Sediment rejection mechanisms of 42 species of Australian scleractinian corals. *Australian Journal of Marine and Freshwater Research*, **43**: 683–705.

Stafford-Smith, M. G., 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Marine Biology*, **115**: 229–243.

Swan, S. B. St. C., 1971. Coastal geomorphology in a humid tropical low energy environment: The islands of Singapore. *Journal of Tropical Geography*, **33**: 43–61.

Telesnicki, G. J. & W. M. Goldberg, 1995. Effects of turbidity on the photosynthesis and respiration of two South Florida reef coral species. *Bulletin Marine Science*, **57**: 527–539.

Titlyanov, E. A. & Y. Y. Latypov, 1991. Light dependence in scleractinian distribution in the sublittoral zone of South China Sea Islands. *Coral Reefs*, **10**: 133–138.

Todd, P. A., P. G. Sanderson & L. M. Chou, 2001. Morphological variation in the polyps of the scleractinian coral *Favia speciosa* (Dana) around Singapore. *Hydrobiologia*, **444**: 227–235.

Todd, P. A., R. C. Sidle & L. M. Chou, 2002a. Plastic corals from Singapore:1. *Coral Reefs*, **21**: 391–392

Todd, P. A., R. C. Sidle & L. M. Chou, 2002b. Plastic corals from Singapore: 2. *Coral Reefs*, **21**: 407–408

Todd, P. A., R. J. Ladle, N. J. I. Lewin-Koh & L. M. Chou, 2004a. Genotype × environment interactions in transplanted clones of the massive corals *Favia speciosa* and *Diploastrea heliopora*. *Marine Ecology Progress Series*, **271**: 167–182.

Todd, P. A., R. C. Sidle & N. J. I. Lewin-Koh, 2004b. An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals. *Journal of Experimental Marine Biology and Ecology*, **299**: 97–113.

Todd, P. A., X. Ong & L. M. Chou, 2010. Impacts of pollution on marine life in Southeast Asia. *Biodiversity and Conservation*, **19**: 1063–1082.

Veron, J. E. N., M. Pichon & M. Wijsman-Best, 1977. *Scleractinia of Eastern Australia. Part II. Families Faviidae, Trachyphylliidae.* Monograph Series of the Australian Institute of Marine Science, Townsville, Australia.

Veron, J. E. N., 1986. Distribution of reef-building corals. *Oceanus*, **29**: 27–31.

Veron, J. E. N., 2000. *Corals of the World, Volume 3.* Australian Institute of Marine Science, Australia. 489 pp.

Weber, M., C. Lott & K. E. Fabricius, 2006. Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. *Journal of Experimental Marine Biology and Ecology*, **336**: 18–32.

Wesseling, I., A. J. Uychiaoco, P. M. Aliño, T. Aurin & J. E. Vermaat, 1999. Damage and recovery of four Philippine corals from short-term burial. *Marine Ecology Progress Series*, **176**: 11–15.