Effect of suspended sediment on fertilization success in the scleractinian coral *Pectinia lactuca*

PAUL L.A. ERFTEMEIJER^{1,6}, MARY HAGEDORN^{2,7}, MICHAEL LATERVEER³, JAMIE CRAGGS⁴ AND JAMES R. GUEST⁵

¹Deltares (formerly Delft Hydraulics), PO Box 177, 2600 MH Delft, The Netherlands, ²Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744, ³Rotterdam Zoo, PO Box 532, 3000 AM Rotterdam, The Netherlands, ⁴Horniman Museum & Gardens, 100 London Road, Forest Hill, London, SE23 3PQ United Kingdom, ⁵Marine Biology Laboratory, Department of Biological Sciences, National University of Singapore, Singapore 117543, ⁶Present addresses: Sinclair Knight Merz (SKM), PO Box H615, Perth WA 6001, Australia, ⁷Smithsonian Conservation Biology Institute, Department of Reproductive Sciences, Smithsonian National Zoological Park, Washington, DC 20008

The effect of increased levels of suspended sediment on fertilization success in the scleractinian coral Pectinia lactuca was investigated in a laboratory experiment following a mass coral spawning event on reefs off Singapore. Egg-sperm bundles were collected from tank-spawned coral colonies collected from the field several days prior to the anticipated mass spawning. Eggs and sperm from each colony were separated and distributed systematically across replicated treatments (N = 9) with three concentrations of fine suspended sediment. Spawning and embryo development in Pectinia lactuca followed a pattern similar to other scleractinian coral species. There was a significant effect of increased suspended sediment concentration on fertilization success (P < 0.05). Both high- (169 mg Γ^{-1}) and medium- (43 mg Γ^{-1}) suspended sediment treatments decreased fertilization success compared to controls. These results imply that increased turbidity levels (whether chronic, such as in the waters around Singapore, or short-term, caused by a dredging operation)—when coinciding with the coral spawning season—may affect the reproductive success of corals and compromise coral recruitment and recovery of degraded reefs.

Keywords: Pectinia lactuca, coral spawning, fertilization success, turbidity, suspended sediment, dredging

Submitted 7 January 2011; accepted 24 May 2011; first published online 6 February 2012

INTRODUCTION

Coral reefs around the world are under increasing threat from anthropogenic activities. Increased turbidity and sedimentation caused by dredging, land reclamation, maritime construction and poor watershed management, are among some of the main threats to reef corals, particularly when exceeding the magnitude, frequency and duration of natural sediment disturbances as caused by storms and river plumes (PIANC, 2010; Erftemeijer et al., unpublished results). Potential impacts of increased levels of turbidity and sedimentation on a reef include reduced light availability, smothering and burial of coral polyps, reduced feeding efficiency, tissue necrosis and population explosions of bacteria in coral mucus (e.g. Rogers, 1990; Rice & Hunter, 1992; Riegl, 1995; Fabricius, 2005). As sediment stress increases, the response of corals shifts from photo-physiological effects, changes in polyp activity and mucus production at the level of individual coral polyps, to colour changes, bleaching and partial tissue necrosis at the colony level. Ultimately, severe and longlasting stress from sustained sediment disturbances may result in wide-spread coral mortality, changes in community

Corresponding author: J.R. Guest Email: James.Guest@nus.edu.sg structure and major decreases in density, diversity and coral cover of entire reef systems (Gilmour *et al.*, 2006). High levels of sedimentation may also hamper the successful settlement of coral larvae (Babcock & Davies, 1991; Babcock & Smith, 2000; Goh & Lee, 2008).

While the effects of sediment stress on mature corals and larval settlement are relatively well studied, surprisingly little is known about the effects of high suspended sediment loads on the success of sexual reproduction of corals including gametogenesis, fertilization, embryo development and larval survival (Erftemeijer et al., unpublished results). In some coral species ('brooders'), fertilization takes place within the mature polyp where the effects of increased loads of suspended sediment on fertilization success are probably small. The majority of corals, however, are hermaphroditic broadcast spawners with fertilization occurring in the water column (Baird et al., 2009). Thus for most coral species abiotic factors such as environmental variability and disturbance (including high turbidity) are likely to exert a major influence on fertilization and recruitment success (Richmond & Hunter, 1990). Synchronized mass spawning of populations of corals is likely to be adaptive if it increases fertilization success and subsequent recruitment rates (Babcock et al., 1986). The timing of mass spawning events within species is usually highly predictable at least at a local scale (Guest et al., 2008). In Singapore waters, multi-specific, synchronous spawning by broadcasting corals was first documented in 2002 and the peak of spawning activity occurs in late March/early April, typically 3 to 6 nights after the full moon (Guest *et al.*, 2005). Sediment disturbances (e.g. from dredging) during such events could potentially compromise fertilization success, but this has been poorly studied to date.

Singapore is a small, industrialized and heavily populated island, located approximately 1° north of the equator. Chronic levels of sedimentation resulting from dredge and fill operations and runoff over the last 30-40 years have resulted in underwater visibility being reduced from 10 m recorded in the early 1960s to a contemporary average of 2 m (Chou, 1996) and sedimentation rates ranging from $5-45 \text{ mg cm}^{-2}$ day⁻¹ at reef sites south of mainland Singapore (Low & Chou, 1994). Despite there being high levels of sedimentation and turbidity in the coastal waters, reasonably diverse coral communities can be found around many of the islands to the south of the mainland (Huang et al., 2009). Here we describe the results of a laboratory experiment on the effect of increased suspended sediment concentrations on the fertilization success in the common lettuce coral Pectinia lactuca (Pallas, 1766) from Singapore's sedimented waters.

MATERIALS AND METHODS

This research was carried out as part of the SECORE (Sexual Coral Reproduction) Project, a network of public aquaria and research institutions aimed at applying sexual reproduction techniques to enhance sustainability among *in situ* and *ex situ* coral populations (Petersen *et al.*, 2006; www.secore. org). From 30 March – 8 April 2010, the 5th SECORE training workshop was organized at St John's Island in Singapore to disseminate and exchange sexual reproduction techniques and experiences among public aquaria and coral scientists.

Pectinia lactuca, a hermaphroditic broadcast spawner, is relatively common on lower reef slopes in Singapore, where it is well-adapted to low light conditions (Veron, 2000). The species is reported as particularly susceptible to bleaching and disease and has been listed as 'vulnerable' in the *IUCN Red List of Threatened Species* (Sheppard *et al.*, 2008).

Thirteen gravid colonies or colony fragments of Pectinia lactuca were collected from the southern-most reef off Singapore (Raffles Lighthouse: 1°10'N 103°45'E), during the week preceding the full moon of 30 March 2010. Colonies selected for collection were located at least 5 m apart to minimize chances of genetically identical colonies, which would compromise the chances of successful fertilization. The collected colonies were carefully transported in containers with seawater to the laboratory of the Tropical Marine Science Institute (TMSI) at St John's Island, where they were kept outdoors in flow through sand filtered seawater (SFSW) in a shaded 1800 l volume tank. Each night at sunset (approximately 19:00 h) each colony or fragment was isolated in plastic containers that were kept floating within the larger tank. These tanks had small holes at the base to allow moderate water exchange, but did not allow gametes to flow out of the tank during spawning. Colonies were monitored for bundle release at 30 m intervals until approximately 2230 or until spawning occurred.

Nine of the colonies spawned in the tanks on the 5th night after the full moon (4 April) at approximately 21:00 h. Eggsperm bundles were carefully collected from the water surface in the tanks using a pipette, according to the methods of Negri & Heyward (2000). Following their collection, eggs and sperm from the different colonies were separated and rinsed repeatedly with 0.2 μ m SFSW to remove sperm and subsequently maintained in separate stock solutions for use in the experiment. Eggs and sperm were not mixed together at all before being added to the sediment suspension.

Gamete-free seawater treatments with three concentrations of suspended sediment were prepared several hours prior to the experiment. Sediment treatment solutions were 6 mg/l (controls), 43 mg/l (medium) and 169 mg/l (high), corresponding to measured turbidity levels of 4 nephelometric turbidity units (NTU) (control), 39 NTU (medium) and 154 NTU (high). Such high turbidity levels correspond to (peak) levels measured during natural disturbance events (medium) and dredging operations (high) (Orpin et al., 2004; Wolanski et al., 2005). The sediment treatment solutions were prepared using ambient seawater and sediment samples collected locally from a sheltered but well-flushed, non-polluted bay on St John's Island. Coarser sediment fractions from these samples were removed prior to the experiment (through a repeated process of agitation, settlement and siphoning off the supernatant), until nearly all sediment would remain in suspension for at least 10-20 minutes following agitation. As such, the suspended sediments used for the experiment consisted primarily of fine sand and silt fractions. The relatively high ratio (1.1-1.5) of suspended sediment concentration (mg/l) to NTU as used in our experiment indicates that it was somewhat coarse (i.e. poor in clay fractions).

Eggs derived from 3 of the spawned colonies were crossed with sperm from at least 4 of the other colonies. Approximately, 50 eggs were placed into replicate 15 ml glass test vials (diameter 2.5 cm, height 5 cm) with seawater solutions of known suspended sediment concentrations. To each of 7 replicate 15 ml glass test vials (diameter 2.5 cm, height 5 cm) per sediment treatment, 50 eggs and 0.25 ml of sperm solution were added to create a working fertilization solution of 10⁶ cells/ml. Vials were loosely capped and placed (floating) in a temperature-controlled ($\sim 29^{\circ}$ C) seawater tank system. During the first hour, all vials were gently agitated by hand at 10-minute intervals to keep the sediment in suspension. After 12 hours, the percentage of eggs that were fertilized and successfully developed into surviving embryos was assessed using a stereo microscope.

To describe the normal embryogenic cycle, samples were taken from a stock of developing embryos approximately hourly following fertilization and were photographed and examined under a dissecting microscope to monitor embryogenesis. A few developmental abnormalities (*sensu* Humphrey *et al.*, 2008) were observed in some of the embryos, these were noted, but were not systematically quantified to allow testing for significance.

Comparisons of fertilization success between the different treatments were statistically tested by a one-way analysis of variance (ANOVA) followed by a Tukey (honestly significant difference) multiple comparison test (P < 0.05). Data are presented as means \pm standard error (SE).

RESULTS

Spawning and embryo development followed a pattern similar to that of other scleractinian coral species (Okubo &



Fig. 1. Spawning and development of *Pectinia lactuca* embryo from first cleavage at 1 hour post-fertilization until 18 hours post-fertilization. Scale bars: (a) approximately 5 mm; (b-j) approximately 150 μ m (photographs: Jamie Craggs).

Motokawa, 2007) (Figure 1). Pectinia lactuca colonies released large (up to 1 cm diameter), unevenly sized, buoyant eggsperm bundles with spherical evenly sized oocytes (approximately 350 µm diameter) (Figure 1a). Fertilized eggs began first cleavage to become two blastomeres at around 1 hour after fertilization (Figure 1b). Second and third cleavage continued to produce 4 and 8 cell embryos after 2 hours and embryos with at least 32 cells were present 3 hours after fertilization (Figure 1c-e). At 4.5 hours post-fertilization, most embryos had become balls consisting of many cells (known as a morula) (Figure 1f). At 5.5 hours post-fertilization embryos had taken on the distinctive convex-concave 'prawn chip' shape (Figure 1g) and this was followed by a 'bowl shape' at around 9.5 hours post-fertilization, marking the beginning of gastrulation (Figure 1h). Between 12 and 18 hours embryos completed gastrulation, became ball shaped and began to exhibit rotary motion (Figure 1i). By 18 hours most larvae had become elongated 'planulae' and were rapidly motile (Figure 1j).

Increasing sediment concentrations had a marked effect on fertilization success (Figure 2). The controls were characterized by high levels of fertilization and subsequent 12



Fig. 2. Percentage of fertilization in gametes of the coral *Pectinia lactuca* in response to exposure to three levels of suspended sediment. Values are means \pm SE, N = 7. The relationship between suspended sediment concentration and % fertilization was significant (analysis of variation; *P*=0.039; F value = 3.194; mean square = 1082.476).

Table 1. Results of one-way analysis of variance for differences in fertil	i1-
zation success among two sediment treatments and control $(N = 9)$ are	ıd
results of Tukey's <i>post-hoc</i> test. *, denotes significance at $P < 0.05$.	

Source of variation	SS	df	MS	F	Р
Treatment	2164.95	2	1082.48	3.194	*
Tukey's test High sediment = medium sediment = low sediment					

hour-old embryo survival (95.7 \pm 2.8%). Sediment treatments significantly (F = 3.194, P < 0.05) affected fertilization success, reducing it to 84.0 \pm 9.8% at 43 mg l⁻¹ suspended sediments, and 70.9 \pm 4.8% at 169 mg l⁻¹ (Figure 2). *Post-hoc* testing (Tukey) revealed significant differences between 'high' sediment treatments and controls, but 'medium' sediment treatments were not statistically significant from both control and 'high' treatments due to high variance in the data for the 'medium' treatment level (Table 1). Sediment treatments had no apparent effect on embryogenesis (based on qualitative observations only) with developmental abnormalities generally rare in all test vials.

DISCUSSION

Previous studies have shown that corals experience reductions in fecundity and reproductive effort when subjected to reductions in water quality (e.g. elevated turbidity, sedimentation and nutrients) (Kojis & Quinn, 1984; Tomascik & Sander, 1987; Ward & Harrison, 2000). For example, in Papua New Guinea, fecundity in the brooding coral *Acropora palifera* was negatively correlated with depth, turbidity and sedimentation (Kojis & Quinn, 1984). Similarly, in Barbados, Tomascik & Sander (1987) found in the gonochoric brooder *Porites porites*, that colonies exposed to elevated turbidity and eutrophication, contained lower numbers of larvae compared to colonies on a less disturbed reef. However, little is still known about the effects of reduced water quality on fertilization success and embryo development.

Our results for *Pectinia lactuca* indicate that turbidity indeed significantly affected fertilization success in this coral species, with significantly lower fertilization (and subsequent embryo survival) under the highest turbidity treatment. The 'medium' and 'high' sediment treatments used here correspond to (peak) turbidity levels that corals may experience during natural disturbance events (e.g. storms or river plumes), or dredging operations (PIANC, 2010). Significant declines in fertilization success were reported for *Acropora millepora* at suspended sediment levels $\geq 100 \text{ mg l}^{-1}$ compared to lower levels ranging from $0-50 \text{ mg l}^{-1}$ with approximately 36% fertilization at the highest tested suspended sediment levels of 200 mg l⁻¹ (Humphrey *et al.*, 2008). Similarly, a significant drop in fertilization success was found for *A. digitifera* with only 30-40% success found in suspended sediment treatments of $50-100 \text{ mg l}^{-1}$ compared to 80-90% fertilization in controls 6 hours after mixing gametes (Gilmour, 1999).

The exact mechanism of the interference of suspended sediment particles with the fertilization of coral eggs (beyond the scope of the present study) is not understood. For the effects of turbidity on fertilization of fish eggs it has been suggested that sediment particles may directly affect sperm mobility and sperm-micropyle encounter rates or that micropyle may be blocked by a coating of sediment particles (Galbraith et al., 2006), although the recent discovery of a non-adhesive region around the micropyle in eggs of Pacific herring (Clupea pallasi) suggests that sediment particles are unlikely to interfere with sperm access to the micropyle and micropylar channel, at least in this species (Griffin et al., 2009). Microbes and contaminants associated with sediment particles (e.g. when resuspended during dredging) may further contribute to reduced fertilization and larval survival in corals (Negri & Heyward, 2000, 2001). The sediment type (size fraction etc.) may also influence the effect on fertilization, although this factor was not tested during the present study.

Mortality of embryos within our 'small volume' sampling vials may have introduced some additional mortality (as methodological artefact) not due to the sediment treatment, although this was probably acceptably low due to the relatively short duration (12 hours) of the experiment. This risk might be further reduced in future experiments by carrying out the treatments in a flow-through set-up. 'Kreisel' systems that allow for gentle stirring, as used successfully by SECORE for the rearing of coral larvae, may be ideal for this purpose (see: www.secore.org).

Successful fertilization, high larval survival and recruitment are essential to the persistence of healthy coral reefs. The finding that high levels of turbidity negatively affect fertilization success in Singapore's waters implies that dredging activities during the major spawning period may be detrimental to the persistence of local reefs. Dredging activities are essential to the maintenance of Singapore as one of the world's busiest ports and to the continuation of other maritime activities such as the offshore oil refining industry. However, as the major spawning period in Singapore is relatively short (approximately 1 week following the March or April full moon), dredging activities could conceivably be reduced or halted during this short period to minimize impacts of (even short-term) increases in turbidity on coral reproduction and recruitment.

ACKNOWLEDGEMENTS

We acknowledge Ecoshape-Building with Nature for their financial support for the SECORE coral breeding workshop (30 March-8 April 2010) in Singapore. The Tropical Marine Science Institute of the National University of Singapore and Underwater World Singapore are thanked for help with preparations, facilities and logistics during the workshop. Astrid Kramer (Hydronamic) participated in the laboratory experiments and data analysis. We appreciate the help of all other participants of the 5th SECORE workshop with the field and laboratory work. The authors acknowledge the support & contributions of the Singapore-Delft Water Alliance (SDWA) and Singapore Ministry of Education Academic Research Fund Tier 1 FRC Grant (Grant number: R-154-000-432-112). The research presented here was carried out as part of the SDWA Marine & Coastal Research Programme (Theme 2): 'Dredging and infrastructure development near critical marine ecosystems' (R-264-001-001-272) and presented at the Euro ISRS Symposium 2010: 'Reefs in a Changing Environment', 13-17 December 2010, Wageningen, The Netherlands. We thank Bert Hoeksema and Pippa Mansell for allowing us to submit our paper for publication in this special issue of JMBA.

REFERENCES

- Babcock R. and Davies P. (1991) Effects of sedimentation on settlement of Acropora millepora. Coral Reefs 9, 205-208.
- Babcock R. and Smith L. (2000) Effects of sedimentation on coral settlement and survivorship. In Moosa M.K., Soemodihardjo S., Soegiarto A., Romimohtarto K., Nontji A., Soekarno and Suharsono (eds) *Proceedings 9th International Coral Reef Symposium, Bali, Indonesia* 23–27 October 2000, 1, pp. 245–248.
- Babcock R.C., Bull G.D., Harrison P.L., Heyward A.J., Oliver J.K., Wallace C.C. and Willis B.L. (1986) Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Marine Biology* 90, 379–394.
- Baird A.H., Guest J.R. and Willis B.L. (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* 40, 551–571.
- Chou L.M. (1996) Response of Singapore reefs to land reclamation. *Galaxea* 13, 85-92.
- **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.
- Galbraith R.V., MacIsaac E.A., Macdonald J.S. and Farrell A.P. (2006) The effect of suspended sediment on fertilization success in sockeye (*Oncorhynchus nerka*) and coho (*Oncorhynchus kisutch*) salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 2487–2494.
- **Gilmour J.** (1999) Experimental investigation into the effects of suspended sediment on fertilization, larval survival and settlement in a scleractinian coral. *Marine Biology* 135, 451–462.
- Gilmour J., Cooper T.F., Fabricius K.E. and Smith L.D. (2006) Early warning indicators of change in the condition of corals and coral communities in response to key anthropogenic stressors in the Pilbara, Western Australia. Australian Institute of Marine Science, Technical Report, 94 pp.
- Goh B.P.L. and Lee C.S. (2008) A study of the effect of sediment accumulation on the settlement of coral larvae using conditioned tiles. In *Proceedings 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7–11 July 2008, 2, pp. 1240–1244.*
- Griffin F.J., Smith E.H., Vines C.A. and Cherr G.N. (2008) Impacts of suspended sediments on fertilization, embryonic development, and early larval life stages of the Pacific Herring, *Clupea pallasi*. *Biological Bulletin*. Marine Biological Laboratory, Woods Hole 216, 175–187.

- Guest J.R., Baird A.H., Goh B.P.L. and Chou L.M. (2005) Seasonal reproduction in equatorial reef corals. *Invertebrate Reproduction and Development* 48, 207–218.
- **Guest J.R., Baird A.H., Clifton K.E. and Heyward A.J.** (2008) From molecules to moonbeams: spawning synchrony in coral reef organisms. *Invertebrate Reproduction and Development* 51, 145–149.
- Huang D., Tun K.P.P., Chou L.M. and Todd P.A. (2009) An inventory of zooxanthellate scleractinian corals in Singapore, including 33 new records. *Raffles Bulletin of Zoology* Supplement 22, 69–80.
- Humphrey C., Weber M., Lott C., Cooper T. and Fabricius K. (2008) Effects of suspended sediments, dissolved inorganic nutrients and salinity on fertilisation and embryo development in the coral Acropora millepora (Ehrenberg, 1834). Coral Reefs 27, 837–850.
- Kojis B.L. and Quinn N.J. (1984) Seasonal and depth variation in fecundity of Acropora palifera at two reefs in Papua New Guinea. Coral Reefs 3, 165–172.
- Low J.K.Y. and Chou L.M. (1994) Sedimenation rates in Singapore waters. In Sudara S., Wilkinson C.R. and Chou L.M. (eds) 3rd ASEAN-Australian Symposium on Living Coastal Resources. Chulalongkorn University, Bangkok, Thailand 2, 697–701.
- Negri A.P. and Heyward A.J. (2000) Inhibition of fertilisation and larval metamorphosis of the coral *Acropora millepora* (Ehrenberg, 1834) by petroleum products. *Marine Pollution Bulletin* 41, 420–427.
- **Negri A.P. and Heyward A.J.** (2001) Inhibition of coral fertilisation and larval metamorphosis by tributyltin and copper. *Marine Environmental Research* 51, 17–27.
- Okubo N. and Motokawa T. (2007) Embryogenesis in the reef-building coral *Acropora* spp. *Zoological Science* 24, 1169–1177
- Orpin A.R., Ridd P.V., Thomas S., Anthony K.R.N., Marshall P. and Oliver J. (2004) Natural turbidity variability and weather forecasts in risk management of anthropogenic sediment discharge near sensitive environments. *Marine Pollution Bulletin* 49, 602–612.
- Petersen D., Laterveer M., Van Bergen D., Hatta H., Hebbinghaus R., Janse M., Jones R., Richter U., Ziegler T., Visser G. and Schuhmacher H. (2006) The application of sexual coral recruits for sustainable management of ex situ populations in public aquariums—SECORE Project. Aquatic Conservation: Marine and Freshwater Ecosystems 16, 167–179.

- **PIANC** (2010) Dredging and port construction around coral reefs. The World Association of Waterborne Transport Infrastructure (PIANC), PIANC EnviCom Report No. 108, 75 pp.
- Rice S.A. and Hunter C.L. (1992) Effects of suspended sediment and burial on scleractinian corals from west central Florida patch reefs. *Bulletin of Marine Science* 51, 429–442.
- Richmond R.H. and Hunter C.L. (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series* 60, 185–203.
- **Riegl B.** (1995) Effects of sand deposition on scleractinian and alcyonacean corals. *Marine Biology* 121, 517–526.
- Rogers C.S. (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62, 185–202.
- Sheppard A., Fenner D., Edwards A., Abrar M. and Ochavillo D. (2008) Pectinia lactuca. In IUCN (2010) IUCN Red List of Threatened Species. Version 2010.4. <www.iucnredlist.com> (accessed 9 December 2010).
- **Tomascik T. and Sander F.** (1987) Effects of eutrophication on reef building corals. III. Reproduction of the reef-building coral *Porites porites*. *Marine Biology* 94, 77–94.
- Veron J.E.N. (2000) *Corals of the world.* Townsville, QL: Australian Institute of Marine Science.
- Ward S. and Harrison P. (2000) Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. *Journal of Experimental Marine Biology and Ecology* 246, 179–221.

and

- Wolanski E., Fabricius K., Spagnol S. and Brinkman R. (2005) Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. *Estuarine, Coastal and Shelf Science* 65, 153–158.
- Correspondence should be addressed to:
 - J.R. Guest
 - Marine Biology Laboratory
 - Department of Biological Sciences
 - National University of Singapore, Singapore 117543
 - email: James.Guest@nus.edu.sg