Photo-physiological costs associated with acute sediment stress events in three near-shore turbid water corals

Nicola K. Browne[1,2,*], Elimar Precht[1], Kim S. Last[3], Peter A. Todd[2,4]

[1]DHI Water and Environment, 1 Cleantech Loop, #03-05 CleanTech One, Singapore 637141
[2]Experimental Marine and Ecology Laboratory, Department of Biological Sciences, National University of Singapore, Singapore 117543
[3]Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll PA37 1QA, UK
[4]Tropical Marine Science Institute, National University of Singapore, Singapore 117543

ABSTRACT: Many coral reef communities thriving in inshore coastal waters characterised by chronically high natural turbidity (>5 mg l^{-1}) have adapted to low light (<200 µmol photons m^{-2} s^{-1}) and high sedimentation rates (>10 mg cm^{-2} d^{-1}). Yet, short (hours) acute sediment stress events driven by wind waves, dredging operations involving suction or screening, or shipping activities with vessel wake or propeller disturbance, can result in a rise in turbidity above the natural background level. Although these may not be lethal to corals given the time frame, there could be a considerable impact on photo-trophic energy production. A novel sediment delivery system was used to quantify the effects of 3 acute sediment resuspension stress events (turbidity = 100, 170, 240 mg l^{-1}; sedimentation rates = 4, 9, 13 mg cm^{-2} h^{-1}) on 3 inshore turbid water corals common in the Indo-Pacific (*Merulina ampliata, Pachyseris speciosa* and *Platygyra sinensis*). Coral photo-physiology response (respiration, net photosynthesis, and maximum quantum yield) was measured immediately after 2 h of exposure. The respiration rate increased (from 0.72–1.44 to 0.78–1.76 µmol O_2 cm^{-2} h^{-1}) as the severity of the acute sediment resuspension event increased, whereas the photosynthetic rate declined (from 0.25–0.41 to −0.19–0.25 µmol O_2 cm^{-2} h^{-1}). *Merulina* was the least tolerant to acute sediment resuspension, with a photosynthesis and respiration ratio (P/R ratio) of <1.0 when turbidity levels reached >170 mg l^{-1}, while *Platygyra* was most tolerant (P/R > 1.0). Fluorescence yield data suggest that the rapid photo-acclimation ability of *Platygyra* enabled it to maintain a positive carbon budget during the experiments, illustrating species-specific responses to acute sediment stress events.

KEY WORDS: Turbidity · Sedimentation · Sediment resuspension · Mesocosm experiments · Coral photosynthesis · Singapore

INTRODUCTION

Acute sediment stress is caused by short, high turbidity events which can range in severity (50 to >500 mg l^{-1} suspended sediment concentration) and duration (minutes to hours; e.g. Wolanski & Gibbs 1992, Larcombe et al. 2001, Orpin et al. 2004), and represent a considerable rise over the natural background turbidity. These pulsed high turbidity events commonly occur within inshore shallow (<10 m at lowest astronomical tide [LAT]) coastal waters when sediments are resuspended either due to natural drivers (e.g. river runoff, tides or wind-driven waves; Lou & Ridd 1996), or anthropogenic drivers (e.g. ship-

wakes, dredging plumes, land reclamation; Thomas et al. 2003, Gelinas et al. 2013) or a combination of both. Numerous coral communities have established and continued to thrive within inshore regions characterised by both high natural background turbidity and frequent acute sediment stress events (McClanahan & Oburu 1997, DeVantier et al. 2006, Perry et al. 2009, Browne et al. 2010), suggesting that many coral species are able to survive rapid, short-lived high turbidity events within a chronic sedimentary regime (5 to 10 mg l^{-1}). However, coral survival within turbid waters is energetically expensive (e.g. mucus production for sediment removal; Brown & Bythell 2005), and will reduce energy available for other energetic requirements such as growth and reproduction (Tomascik & Sander 1985, Riegl & Branch 1995, Fabricius 2005). The energetic costs associated with exposure to acute sediment resuspension events for turbid water corals is unknown, and yet will have a critical influence on their longer-term survival and growth, and ultimately reef health.

Natural turbidity regimes vary considerably over space and time (Hoitink & Hoekstra 2003, Orpin et al. 2004, Wolanski et al. 2008, Browne et al. 2013), but land-based activities such as coastal development, land reclamation, deforestation and agriculture can enhance sediment loading into coastal waters — thereby chronically increasing background turbidity (Erftemeijer et al. 2012). For example, since the 1970s, coastal development has increased sedimentation rates in Singapore from <6 mg cm^{-2} d^{-1} (Chan 1980) to 15–30 mg cm^{-2} d^{-1} (Lane 1991, Low & Chou 1994, Todd et al. 2003) with average visibility reduced from ~10 m (1960s) to <2 m presently (Chou 1996). The severity and duration of acute sediment stress events is also highly variable, and is dependent on the driver, sediment type and local hydrodynamic conditions (currents, natural wind waves, ship wakes, etc.). In exposed regions, wind-driven waves can resuspend sediments and increase the suspended sediment concentrations (SSC) to >150 mg l^{-1} (Larcombe et al. 1995, Larcombe et al. 2001, Browne et al. 2013), whereas in more sheltered regions ship wakes may be the primary driving force of sediment resuspension (Gelinas et al. 2013). However, the most severe pulse events, where SSC can reach >300 mg l^{-1}, are commonly associated with dredging activities (Wolanski & Gibbs 1992). In Papua New Guinea, SSC of >25 mg l^{-1} were recorded over coral reefs for 10 to 60% of the time (18 mo in total) during mining operations, with short lived peaks (<1 h) reaching 500 mg l^{-1} (Thomas et al. 2003). The frequency, severity and duration of acute sediment

stress events combined with the chronic background turbidity regime will influence coral survival and growth.

Increased exposure to sediments stresses corals by reducing light for photosynthesis if sediments are in suspension, and/or smothering corals if deposited on the coral surface (reviewed by Fabricius 2005, Erftemeijer et al. 2012). The chronic effects of limited light availability and sedimentation have been extensively researched. High turbidity can decrease photosynthesis and increase respiration thereby reducing the ratio between photosynthesis and respiration (P/R ratio; Abdel-Salam & Porter 1988, Rogers 1990, Anthony & Fabricius 2000, Anthony & Connolly 2004). A reduction in the P/R ratio reduces energy available for growth and reproduction (Rogers 1979, Telesnicki & Goldberg 1995, Anthony & Hoegh-Guldberg 2003) and may increase coral susceptibility to infection and thermal bleaching (Anthony & Connolly 2007). To cope with declines in light availability, some corals are able to photo-acclimate by increasing the concentrations of photosynthetic pigments and/or symbiont densities (Rogers 1979, Dubinsky et al. 1984), which results in a measurable increase in the fluorescence yield and a decrease in the saturation irradiance (Anthony & Fabricius 2000, Te 2001). Coral adaptations to chronically high sedimentation include morphological changes (e.g. *Turbinaria* spp.) and/or increased mucus production which efficiently removes sediments from their surfaces (Stafford-Smith 1993). These adaptations allow turbid water corals to survive under a chronically high sedimentary regime where the background turbidity may reach 10 mg l^{-1}.

Previous research on sediment stress effects have documented changes in coral photobiology using PAM fluorometry in the field (Winters et al. 2003, Piniak & Storlazzi 2008, Cooper et al. 2009) and in the laboratory (Philipp & Fabricius 2003, Weber et al. 2006, Piniak 2007, Flores et al. 2012). These studies have focused on either chronic, long lasting events (e.g. Flores et al. 2012) or acute sub-lethal sediment stress events (e.g. Riegl & Branch 1995, Piniak 2007) which often lead to full or partial coral mortality. In contrast, we aimed to quantify the influence of acute sediment resuspension stress events (i.e. a short, non-lethal event) on coral photo-physiology by measuring both the yield and P/R ratio. Many turbid water corals that are frequently exposed to acute sediment resuspension events do not suffer tissue mortality. Nevertheless, these stress events are potentially causing declines in energy production and allocation (e.g. for growth and reproduction), which will have

longer-term repercussions on coral cover and reef health. In this study, 3 corals (*Merulina ampliata, Pachyersis speciosa*, and *Platygyra sinensis*) common in turbid inshore reefs in the Indo-Pacific were used to investigate the photo-physiological costs associated with acute sediment stress. A novel sediment delivery system was fabricated and corals were exposed to 1 of 3 sediment treatments (target values for turbidity: 120, 180, 240 mg l^{-1}) over 4 consecutive weeks using inert silicon carbide powder as a proxy for natural sediment. Great care in the experimental design was taken to ensure that the sediment particle profile and the severity of the event and its duration were environmentally relevant. Specifically, the objectives were: (1) to quantify the physiological effects of acute sediment resuspension events on 3 inshore turbid water corals and, (2) assess differences between species.

MATERIALS AND METHODS

Study species and sampling sites

Three common Indo-Pacific corals were selected for the study: the plate corals *Merulina ampliata* and *Pachyseris speciosa* (hereafter *'Merulina'* and *'Pachyseris'*) and the massive coral *Platygyra sinensis* (hereafter *'Platygyra'*). These corals are commonly found within inshore turbid waters, and in Singapore are typically found in high abundance (>5%) on the upper reef slopes (<4 m LAT; Dikou & van Woesik 2006), suggesting adaptation to low-light, high sediment waters. Six colonies from each species were collected from 3 turbid reef slopes (3 m LAT) in Singapore to ensure genetic diversity: 2 colonies from each of the 3 species were collected from Labrador Park (1.26636° N, 103.80015° E), Kusu Island (1.22838° N, 103.85525° E) and Palau Hantu (1.22640° N, 103.74675° E). Turbidity and light levels on the reef slope (at 3 m LAT) at Labrador Park typically range from 10 to 150 mg l^{-1} and 50 to 150 PAR at 3 m LAT respectively, and at Kusu Island and Palua Hantu range from 5 to 50 mg l^{-1} and 50 to ~200 PAR respectively (May to June 2012, N. K. Browne unpubl. data). Sedimentation rates throughout the year are highly variable over all 3 reefs, but typically range from 2 to 15 mg cm^{-2} d^{-1} at Kusu Island and Palau Hantu, and from 5 to 25 mg cm^{-2} d^{-1} at Labrador Park.

Four coral fragments of approx. 5 × 5 cm were obtained from each coral colony (n = 24 for each species, total n = 72 fragments) using either a chisel or

cutters, and each fragment was secured onto a plastic grid using underwater epoxy resin (non-toxic) to avoid direct coral handling. Mounted fragments were then transported to the aquarium facilities at the Tropical Marine Science Institute (TMSI) on St. John's Island (Singapore), where they were allowed to recover in 200 l indoor flow through tanks (water temperature ~29°C, salinity 30 ppt, photoperiod 10 h:14 h light:dark cycle at 120 μmol photons m^{-2} s^{-1}) for at least 8 wk prior to commencing the experiment. Water entering the holding tanks and chambers was sand filtered (20 μm); however, given the age of the filtration system (10 yr), corals may have been exposed to particles <50 μm. These particles could potentially influence rates of heterotrophy, but would have limited influence on photo-physiology relative to the sediment stress events. Corals were photographed with a scale, and photographs were analysed using CPCe software to determine the surface area of live tissue.

Mesocosm chamber

For the purpose of this study, twelve 9 l cylindrical mesocosms were fabricated to accommodate the coral fragments (Fig. 1). These were smaller versions of the 300 l Vortex Resuspension Tank (VoRT) described by Davies et al. (2009) and the rotational movement of water was provided by a motor-driven paddle (~65 revolutions min^{-1}) instead of water pumps. The hollow vertical shaft of the paddle had holes near the top and doubled as an air-lift to resuspend particulate matter that collected in the tapered well at the bottom of the chamber. The rotating paddles dissipated the sediments through the water column above the coral fragments which were positioned on a plastic grid directly above the sediment well. The amount of sediment particles forced up the central tube was controlled by the duration (seconds) of air that was pumped through the air lift. The new mini VORT (mVORT) also had a side opening covered with a 5 mm rubber membrane positioned at the same height as the corals, through which water samples were collected using a syringe and long needle.

Sediment preparation

The grain size distribution of the natural sedimentation profile at Labrador Park, Pulau Hantu and Kusu Island was analysed through laser diffraction particle size analyses (Malvern Mastersizer Particle
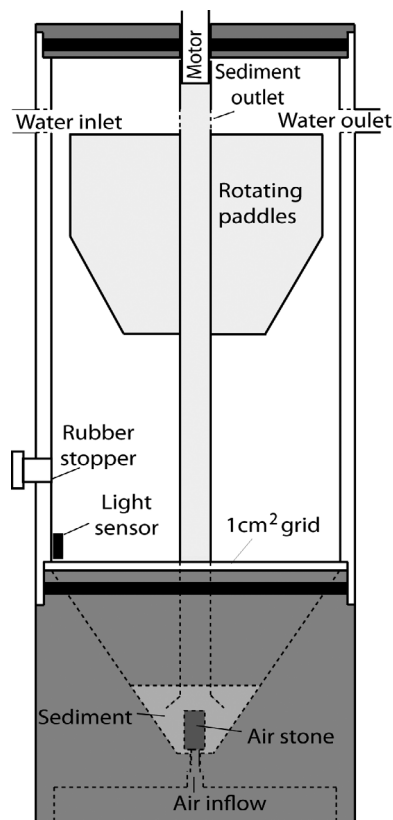
Fig. 1. Schematic diagram of the mVORT chamber illustrating position of DC motor, rotating paddles, sediment well, light sensor and the position of the grid on which corals were placed
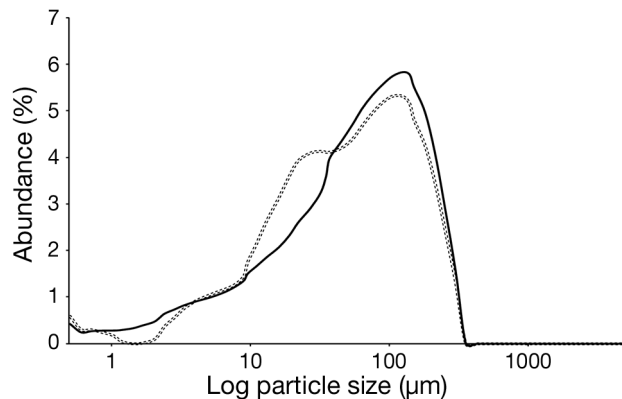

Fig. 2. Profile of sediments collected from the sediment trap at Labrador Park, Singapore (solid line), and the silicon carbide profile (broken line)

ments on corals (Glynn et al. 1984, Bastidas et al. 1999, Fabricius 2005, Weber et al. 2012). Great care was taken to replicate the natural reef sediment profile as particle size is critical not only to how corals respond to smothering (Stafford-Smith & Ormond 1992), but also the light environment. Sediments of different sizes and particle shapes will have variable influences on the light environment, leading to variable wave length extinctions and shifting light fields. We acknowledge that silicon carbide may result in a different light environment than if natural reef sediments had been used, but also consider this to be a lesser influence on coral photosynthesis given the low light levels (PAR), high turbidity and sedimentation rates replicated in this study. However, given the lack of confounding factors associated with silicon carbide, our data may underestimate the impacts of sediment on the respiratory and photosynthetic physiology of these corals.

Experimental design

The mesocosm chambers were placed into 300 l water baths through which sea water flowed at a constant rate of 5 l min^{-1} (water temperature ~29°C). A light source (4 T5 HO aquarium bulbs which provide the essential actinic blue light that corals require) was suspended 75 cm above the corals and provided ~150 µmol photons m^{-2} s^{-1}. In each mVORT, sediment (~25 g) was placed at the bottom of the well, and the tanks were slowly filled with sea water, through the side water inlet valve, from a central reservoir tank. The 12 motors were controlled by programmable pulse width modulation (PWM) from a central microcontroller which enabled the user to set

Size Analyser). The range in particle size was comparable between sites (1 to 300 µm), but the median particle size varied from 50 to 80 µm at Labrador Park, from 80 to 100 µm at Pulau Hantu and 60 to 100 µm at Kusu Island (n = 30 from each site). The sediment profile from Labrador Park, the site with the highest turbidity, was closely matched by combining commercially available particle sizes of silicon carbide powder (Kemet Fareast) following Lui et al. (2012). The resulting silicon carbide mix contained particle sizes ranging from 1 µm to 300 µm, and had a median particle size of 60 µm (Fig. 2).

Silicon carbide has been used for this purpose with success in a number studies that investigated the effects of sediment stress on corals (e.g. Stafford-Smith & Ormond 1992, Lui et al. 2012). The advantage of silicon carbide is that it provides a means whereby we can assess the physical/mechanical stress associated with an acute sediment stress event without confounding factors such as bacteria, microbes, nutrients and heavy metals which are known to exacerbate the negative effects of natural sedi-

the motor speed between 1 and 65 revolutions min^{-1} (rpm). Previous tests had verified that 20 rpm within a 20 cm diameter cylindrical tank generated a flow rate of approx. 10 cm s^{-1} at the midpoint between the centre and outer edge of the tank. Current speeds at reef sites are typically <5 cm s^{-1}, but rise to 10 to 15 cm s^{-1} during resuspension events (N. K. Browne unpubl. data).

For each coral species, 4 fragments from 6 colonies (24 fragments per species) were exposed to an acute sediment stress event. One fragment of each coral species was randomly selected and placed on the plastic grid platform in the mVORT 2 h before the experiment commenced. Given the large number of fragments tested (n = 72) and limited number of chambers (12), the experiment was run twice every week: each time 36 fragments were tested (3 per chamber).

The experiment was run over 4 wk in October 2012: baseline measurements (Treatment 1) on corals were conducted in Week 1, sediment Treatment 2 (turbidity = 102.4 mg l^{-1} ± 13.9; sedimentation rate = 4.3 ± 0.4 mg cm^{-2} h^{-1}; light = 62.9 ± 3.9 µmol photons m^{-2} s^{-1} [56% light attenuation]) was conducted in Week 2, sediment Treatment 3 (turbidity = 174.2 mg l^{-1} ± 10.6; sedimentation rate = 9.9 ± 1.0 mg cm^{-2} h^{-1}; light = 54.3 ± 2.8 µmol photons m^{-2} s^{-1} [63% light attenuation]) was conducted in Week 3, and sediment Treatment 4 (turbidity = 242.5 mg l^{-1} ± 13.6; sedimentation rate = 12.9 ± 1.2 mg cm^{-2} h^{-1} ; light = 39.5 ± 3.3 µmol photons m^{-2} s^{-1} [72% light attenuation]) was conducted in Week 4. Each acute sediment stress event lasted for 2 h and light levels in the tank where recorded every 5 s using a modified mini ambient light sensor (DHI), connected to the central control box. The light sensor measured light levels between 350 and 680 nm and had been calibrated with a LI-COR light sensor (Li-192) to provide the linear calibration co-efficient with which to convert internal engineering units to PAR. Water samples (20 ml) were collected after 1 h using a syringe from the side inlet, and were suction filtered through Whatman filters (10 µm particle retention) to determine the suspended sediment concentrations (SSC). Sedimentation rates (g cm^{-2} h^{-1}) were calculated at the end of the experiment from a 4 cm diameter plastic disc placed on the plastic grid. During Week 1, the corals were not subjected to a sediment event (no air burst), but remained in the chambers for 4 h prior to physiological analysis. During Weeks 2 to 4, corals were subjected to 4 air bursts (at 0 min, 30 min, 60 min, 90 min) which forced sediments up the central tube, creating a sediment resuspension event

and reducing light penetration (Fig. 3). Prior to the experiment, several calibration tests were performed to determine the length of air burst required to produce the required light, turbidity and sedimentation rate. During the calibration tests, light levels were recorded, water samples were taken and sedimentation rates were calculated. To ensure that all other conditions that may influence coral physiology (e.g. temperature, salinity) were comparable between Weeks 1 to 4, 3 of the 12 chambers were used as controls in Weeks 2, 3 and 4. Conditions in the controls were the same as the baseline conditions during Week 1. These corals were not subjected to sediments (air burst only) and light levels were maintained at 145.4 ± 1.3 µmol photons m^{-2} s^{-1}. Water flow through and temperature within the control chambers were the same as for the sediment chambers.

Physiological analyses

The net photosynthetic and respiration rate, and maximum photosynthetic yield (F_v/F_m) was measured after the 2 h acute sediment stress event. Photosynthesis and respiration were measured using a RESP-EDU (Loligo Systems) respiratory system and associated software (AUTO-RESP). A circular respirometry chamber (1.5 l) was fabricated to accommodate the size of the fragments and equipped with a flush pump and a circulatory pump to maintain continuous water flow. The chamber was submerged in a 50 l water bath with running sea water, and temperature and oxygen were recorded every 5 s on a data logger
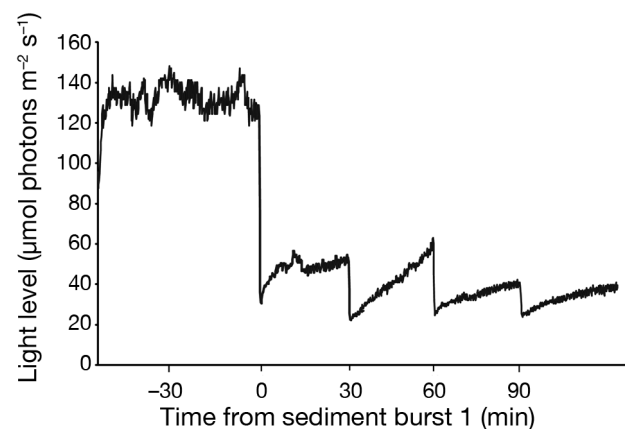

Fig. 3. Light level (PAR) inside a chamber during a high turbidity event. Light level declines at 0 min when the first air burst is triggered pushing sediments up the central column and into the water. As sediments settle, light levels slowly increase until the second air burst at 30 min. The average light level from 0 min to 120 min was 39 PAR

(DAQ-M, Loligo Systems). Light levels outside the chamber were monitored using a cosine-corrected LI-COR probe (Li-192S) connected to a Li-1000 data logger. Oxygen consumption/production rate (mg O_2 l^{-1}) within the chamber volume (after subtracting the volume of coral) was measured continuously for 5 min using a galvanic cell oxygen probe (Loligo Systems), followed by a 2 min flush period. Net photosynthetic (NP) rates were measured at ~150 μmol photons m^{-2} s^{-1} and respiratory rates (R) and the maximum photosynthetic yield were measured after 20 min incubation in the dark. The maximal photosynthetic yield (F_v/F_m) was measured with a pulse-amplitude modulated fluorometer (Diving-PAM, Walz) (Beer et al. 1998). The optical-fiber probe was kept at a constant distance of 5 mm from the surface of the coral and the average of 5 measurements for each coral fragment was calculated with the following settings: measuring intensity = 8, saturating intensity = 8, saturating pulse width = 0.8 s, gain = 1, dampening = 1. The minimum fluorescence (F_o) was measured by applying a pulsed measuring beam of <1 μmol photon m^{-2} s^{-1} and the maximum fluorescence (F_m) was measured following the application of a saturating pulse of actinic light (>1000 μmol photon m^{-2} s^{-1}). The change in fluorescence ($F_v = F_m - F_o$) was used to calculate the maximum quantum yield (F_v/F_m). Net oxygen production and respiration rates were normalised to the surface area of live tissue for each coral fragment (μmol cm^{-2} h^{-1}), and the gross photosynthesis (Gp = NP + R) to respiration ratio (P/R ratio) was calculated (Cooper et al. 2011).

Statistical analysis

A 4 wk cross-over repeated measures analysis was conducted using a Linear Mixed Effects (LME) model to test if treatment resulted in a statistically significant effect on the measured variable (SPSS v. 20). LME models accommodate data collection at different time points and enable the user to model covariance structures (Lindstrom & Bates 1988). The model included fixed effects (treatment, species) and random effects (individuals); repeated measures (weeks) were conducted using the unstructured covariance matrix which allowed measures to be correlated and have equal variance in the model. Carry-over effects are a potential risk in cross-over trials, but we considered the risk of carry-over effects to be small given the long recovery period (1 wk) in between treatments. The model used a restricted maximum likelihood (REML) iteration to estimate the parameters of a linear expectation function containing both fixed and random effects. The output provides a statistical test of the hypothesis that a given fixed parameter is significantly different from zero. In this case, the model chose the high sediment treatment (Treatment 4) and *Platygyra* as the reference categories, with a parameter estimate of zero, against which Treatments 1, 2 and 3, and *Merulina* and *Pachyseris* respectively, were statistically examined to determine if treatment and species had a statistically significant effect on coral response.

RESULTS

The LME model examined if treatment had a significant effect on coral respiration, net photosynthesis, the P/R ratio and photosynthetic yield. The model also determined if the 3 additional control chambers run during Weeks 2 to 4 were significantly different from baseline conditions in Week 1. There was no significant difference in the coral responses (respiration, net photosynthesis, yield) for the individual fragments that were used in the control chambers between weeks (p > 0.05), and no coral mortality was observed during or following the experiment (several months).

Respiration rate

The mean O_2 depletion rate (hereafter referred to as respiration) for all 3 species increased in the high sediment treatment compared to baseline conditions measured in Week 1: *Merulina* respiration rates increased from −1.15 ± 0.13 to −1.52 ± 0.18 μmol O_2 cm^{-2} h^{-1}, *Pachyseris* respiration rates increased from −0.72 ± 0.07 to −0.78 ± 0.11 μmol O_2 cm^{-1} h^{-1}, and *Platygyra* respiration rates increased from −1.44 ± 0.21 to −1.76 ± 0.25 μmol O_2 cm^{-2} h^{-1} (Table 1). However, the rise was only significant for *Merulina*, whose respiration was significantly greater than the baseline conditions by Week 4 (Treatment 2: p = 0.004; Table 2) when corals where subjected to a low sediment stress event (Fig. 4a). In contrast, the rise in respiration for *Pachyseris* and *Platygyra* (Fig. 4) was not significantly different between weeks. (p > 0.05; Table 2).

Net photosynthesis

The net photosynthesis declined for all coral species in the medium and high sediment treatments, with lowest rates recorded following the high sedi-

Table 1. Mean values and standard errors (SE) for respiration and net photosynthesis (μmol O_2 cm^{-2} h^{-1}); P/R values and the maximum quantum yield for each coral species following 2 h of each treatment

	Merulina	Pachyseris	Platygyra
Treatment 1 Baseline			
Respiration	−1.15 (0.13)	−0.72 (0.07)	−1.44 (0.21)
Net photosynthesis	0.31 (0.07)	0.25 (0.04)	0.41 (0.07)
P/R ratio	1.25 (0.02)	1.25 (0.11)	1.52 (0.14)
Yield	0.57 (0.01)	0.53 (0.01)	0.59 (0.02)
Treatment 2 Low sediment			
Respiration	−1.46 (0.16)	−0.63 (0.12)	−1.49 (0.19)
Net photosynthesis	0.43 (0.09)	0.36	0.47 (0.15)
P/R ratio	1.3 (0.02)	1.2 (0.05)	1.4 (0.13)
Yield	0.56 (0.02)	0.52 (0.01)	0.6 (0.01)
Treatment 3 Medium sediment			
Respiration	−1.52 (0.12)	−0.74 (0.07)	−1.97 (0.23)
Net photosynthesis	−0.12 (0.08)	0.05 (0.08)	0.27 (0.26)
P/R ratio	0.95 (0.01)	1.2 (0.1)	1.28 (0.12)
Yield	0.55 (0.01)	0.56 (0.01)	0.58 (0.01)
Treatment 4 High sediment			
Respiration	−1.52 (0.18)	−0.78 (0.11)	−1.76 (0.25)
Net photosynthesis	−0.19 (0.13)	0.08 (0.08)	0.25 (0.14)
P/R ratio	0.93 (0.02)	1.18 (0.10)	1.24 (0.11)
Yield	0.57 (0.01)	0.61 (0.02)	0.65 (0.01)

ment treatment: *Merulina* declined from 0.31 ± 0.07 to −0.19 ± 0.13 μmol O_2 cm^{-2} h^{-1}, *Pachyseris* declined from 0.25 ± 0.04 to 0.08 ± 0.08 μmol O_2 cm^{-2} h^{-1}, and *Platygyra* declined from 0.41 ± 0.07 to 0.25 ± 0.14 μmol O_2 cm^{-2} h^{-1} in (Table 1, Fig. 4). However, the decline from baseline conditions during both the medium and high turbidity treatments was only significant for *Merulina* and *Pachyseris* (p < 0.05; Table 2).

P/R ratio

The P/R ratio for *Pachyseris* and *Platygyra* decreased as sediment load increased: the P/R ratio declined from 1.25 ± 0.11 to 1.18 ± 0.1 (*Pachyseris*) and from 1.52 ± 0.14 to 1.24 ± 0.11 (*Platygyra*); however, this was not significant (Table 1, Fig. 5). In contrast, the P/R ratio was significantly lower for *Merulina* between Weeks 2 and 3 (p < 0.008; Table 2) when the P/R ratio fell from 1.3 ± 0.02 during the low sediment stress event to 0.95 ± 0.01 during the medium sediment stress event. The P/R ratio fell further during the high sediment stress event (0.93 ± 0.02).

Maximum photosynthetic yield

The maximum photosynthetic yield did not vary significantly for *Merulina* over the course of the ex-

periment; however, there was a significant increase in the yield for *Pachyseris* and *Platygyra.* The yield for *Pachyseris* increased from 0.52 ± 0.01 to 0.56 ± 0.01 (p < 0.001) between the low and medium sediment stress events, and from 0.56 ± 0.01 to 0.61 ± 0.02 (p = 0.01) between the medium and high sediment stress events, and the yield for *Platygyra* increased from 0.58 ± 0.01 to 0.65 ± 0.01 (p = 0.00) between the medium and high sediment stress events (Table 2, Fig. 6).

Among-species responses

Over the course of the experiment the respiration rate for *Pachyseris* (−0.78 ± 0.23 μmol O_2 cm^{-2} h^{-1}) was significantly lower than *Platygyra* (−1.76 ± 0.16 μmol O_2 cm^{-2} h^{-1}) and *Merulina* (−1.58 ± 0.23 μmol O_2 cm^{-2} h^{-1}; Table 3). In contrast, there was no consistent and significant difference in the net photosynthetic rate among species (p > 0.05). However, the P/R ratio of *Merulina* (0.93 ± 0.16) was significantly lower than both *Pachyseris* (1.18 ± 0.16) and *Platygyra* (1.24 ± 0.11), and the maximum photosynthetic yield of *Platygyra* (0.65 ± 0.14) was significantly higher than for *Merulina* (0.57 ± 0.02).

DISCUSSION

Acute sediment stress events are energetically expensive for corals as they limit light and reduce energy production from phototrophy. This study quantified the reduction in energy production following a 2 h acute sediment event. Short-lived peaks in turbidity typically occur in locations characterised by naturally high background turbidity, where sediment supply is not limited and sediments are frequently resuspended. Corals in chronically turbid waters have photo-acclimated to low light (Dubinsky et al. 1984) and may also have increased rates of heterotrophic feeding to offset energy deficits from photosynthesis (Anthony 2000, Anthony & Fabricius 2000). However, the increase in the frequency and severity of acute sediment stress events in coastal waters, due to changing land use, coastal construction and port activities (Smith & Buddemeier 1992, Chou 1996, Todd et al. 2010, Gelinas et al. 2013) provides an additional stress for corals potentially surviving at the edge of their environmental and physiological tolerances. How corals respond to these pulse events and the associated physiological costs involved will determine rates of survival and growth within these marginal reef environments. Environmental extremes

Table 2. Results from the Mixed Model with treatment (α = 0.05). The Type III fixed effects demonstrate if there was a significant effect of treatment on each photo-physiological variable (respiration, photosynthesis, P/R ratio, yield) for each species. The estimate of fixed effects demonstrates between which treatments (weeks) the effects were significant, using Treatment 4 as the reference category for the analysis; see 'Statistical analysis' in the text. E.g. *Merulina* respiration rate following Treatment 1 was significantly different (p = 0.004) from Treatment 4 (baseline conditions) but Treatments 2 and 3 were not. BIC: Bayesian information criterion; Num. df: numerator df; Den. df: denominator df

| Variable | BIC | — Type III fixed effects — | | | | | — Estimates of fixed effects — | | | | | |
		Source	Num. df	Den. df	*F*	p	Parameter	Estimate	SE	df	*t*	p
Merulina ampliata												
Respiration	137.76	Intercept	1	17	129.015	0.000	Intercept	1.576	0.176	17	−8.893	0.00
		Treatment	3	17	4.821	*0.013*	Treatment 1	−0.328	0.10	17	3.297	*0.004*
							Treatment 2	−0.057	0.14	17	0.4	0.694
							Treatment 3	0.031	0.111	17	−0.281	0.782
							Treatment 4	0.00	0.00			
Net photo-synthesis	113.44	Intercept	1	17	1.453	0.245	Intercept	−0.194	0.132	17	−1.47	0.16
		Treatment	3	17	7.561	*0.002*	Treatment 1	0.45	0.151	17	2.98	*0.008*
							Treatment 2	0.61	0.158	17	3.871	*0.001*
							Treatment 3	0.012	0.115	17	0.1	0.921
							Treatment 4	0.00	0.00			
P/R	77.39	Intercept	1	17	485.214	0.000	Intercept	0.927	0.083	17	11.1	0.00
		Treatment	3	17	11.92	*0.000*	Treatment 1	0.323	0.083	17	3.902	*0.001*
							Treatment 2	0.372	0.124	17	2.995	*0.008*
							Treatment 3	0.0097	0.066	17	0.148	0.884
							Treatment 4	0.00	0.00			
Yield	−155.79	Intercept	1	17	4791.05	0.000	Intercept	0.5668	0.0094	9	60.55	0.00
		Treatment	3	17	0.355	0.787	Treatment 1	0.0013	0.0158	15	0.082	0.936
							Treatment 2	−0.006	0.164	11	−0.371	0.718
							Treatment 3	−0.0124	0.0144	10	−0.858	0.411
							Treatment 4	0.00	0.00			
Pachyseris speciosa												
Respiration	99.068	Intercept	1	17	113.12	0.000	Intercept	0.777	0.113	17	−6.87	0.00
		Treatment	3	17	1.321	0.300	Treatment 1	0.0611	0.086	17	−0.712	0.49
							Treatment 2	0.204	0.139	17	−1.464	0.16
							Treatment 3	−0.041	0.822	17	0.497	0.63
							Treatment 4	0.00	0.00			
Net photo-synthesis	61.46	Intercept	1	17	5.814	0.028	Intercept	0.107	0.083	17	1.282	0.22
		Treatment	3	17	10.82	*0.000*	Treatment 1	0.16	0.074	17	−0.237	*0.04*
							Treatment 2	0.298	0.057	17	5.247	*0.00*
							Treatment 3	−0.059	0.059	17	−0.992	0.36
							Treatment 4	0.00	0.00			
P/R	119.5	Intercept	1	17	326.53	0.000	Intercept	1.195	0.097	17	12.2	0.00
		Treatment	3	17	0.052	0.984	Treatment 1	0.049	0.126	17	0.394	0.70
							Treatment 2	0.007	0.194	17	0.039	0.97
							Treatment 3	0.006	0.064	17	0.096	0.92
							Treatment 4	0.00	0.00			
Yield	−137	Intercept	1	17	2114.25	0.000	Intercept	0.611	0.0152	9	40.17	0.00
		Treatment	3	17	10.58	*0.000*	Treatment 1	−0.074	0.0164	15	−4.53	*0.00*
							Treatment 2	−0.089	0.0179	11	−4.953	*0.00*
							Treatment 3	−0.047	0.0174	10	−2.73	*0.01*
							Treatment 4	0.00	0.00			
Platygyra sinensis												
Respiration	223.13	Intercept	1	17	141.93	0.00	Intercept	1.76	0.25	17.00	−7.08	0.00
		Treatment	3	17	0.48	0.70	Treatment 1	−0.23	0.25	17.00	0.84	0.41
							Treatment 2	−0.27	0.32	17.00	0.84	0.41
							Treatment 3	0.03	0.24	17.00	−0.13	0.90
							Treatment 4	0.00	0.00			

Table 2 (continued)

Variable	Type III fixed effects						Estimates of fixed effects					
	BIC	Source	Num. df	Den. df	F	p	Parameter	Estimate	SE	df	t	p
Net photo-synthesis	155.25	Intercept	1	17	5.52	0.03	Intercept	0.24	0.14	17.00	1.71	0.11
		Treatment	3	17	0.62	0.61	Treatment 1	0.00	0.15	17.00	−0.24	0.98
							Treatment 2	0.17	0.14	17.00	1.21	0.24
							Treatment 3	0.02	0.16	17.00	0.15	0.88
							Treatment 4	0.00	0.00			
P/R	150.5	Intercept	1	17	299.50	0.00	Intercept	1.24	0.12	17.00	10.70	0.00
		Treatment	3	17	1.03	0.41	Treatment 1	0.28	0.17	17.00	1.63	0.12
							Treatment 2	0.17	0.13	17.00	1.26	0.22
							Treatment 3	0.05	0.14	17.00	0.33	0.75
							Treatment 4	0.00	0.00			
Yield	−178.4	Intercept	1	17	20929.80	0.00	Intercept	0.65	0.01	9.00	62.84	0.00
		Treatment	3	17	6.97	**0.00**	Treatment 1	-0.05	0.02	15.00	−0.39	**0.01**
							Treatment 2	−0.05	0.02	11.00	−2.75	**0.01**
							Treatment 3	−0.07	0.02	10.00	−3.83	**0.00**
							Treatment 4	0.00	0.00			

rather than background constants will structure populations (Done 1999), and, as such, frequent acute sediment stress events may play an important role in coral community composition on inshore turbid reefs.

Variability in physiological response of the coral between species indicates species-specific thresholds to acute sediment stress levels. During low light conditions (~120 µmol photons m^{-2} s^{-1}), all 3 coral species were producing more energy from phototrophy than respiring and had a positive energy budget. Net photosynthesis and respiration rates were comparable to rates measured for *Turbinaria reniformis* and *Stylphora pistillata* under low light conditions (~120 µmol photon m^{-2} s^{-1}; fed and at 26°C) where corals photosynthesised at 1.20 and 2.0 µmol O$_2$ cm^{-2} h^{-1}, and respired at −0.5 and −0.75 µmol O$_2$ cm^{-2} h^{-1} (Hoogenboom et al. 2012). There was limited change in photosynthesis during the low sediment stress event for the 3 coral species (~100 mg l^{-1}), but rates did decline significantly for *Merulina ampliata* and *Pachyseris speciosa* when corals were exposed to >170 mg l^{-1}. The data suggests that *M. ampliata* is the least tolerant to sediment stress events given that the net photosynthetic rate was negative (<−0.12 µmol O$_2$ cm^{-2} h^{-1}) and the P/R ratio was <1.0, i.e. the coral was using more energy than it was producing. In contrast, *Platygyra sinensis* was the most tolerant to sediments as its net photosynthetic rate declined the least during the high sediment treatment, and remained high (0.25 µmol O$_2$ cm^{-2} h^{-1}) compared to both *P. speciosa* (0.08 µmol O$_2$ cm^{-2} h^{-1}) and *Merulina* (−0.19 µmol O$_2$ cm^{-2} h^{-1}).

The decline in net energy production for the 3 coral species was largely due to the reduction in photosynthesis, driven by high turbidity and limited light, and not by increasing respiration rates. It is well known that sediments can severely affect the coral energy budget by reducing photosynthesis and increasing respiration rates, the latter due to increased energy expenditure as corals remove sediments from their surfaces (Riegl & Branch 1995, Brown & Bythell 2005, Fabricius 2005, Negri et al. 2009, Flores et al. 2012). Some consider that the effects of sedimentation on coral physiology are the main physiological process that drive coral sediment tolerances (Anthony & Connolly 2004) and reductions in light and photosynthesis are less important. In the present study, sedimentation rates were high (4 to 13 mg cm^{-2} h^{-1}) and respiration rates did increase for all 3 coral species, most likely due to settling sediments. But the increase in respiration was not consistently significant between treatments. Significant increases in respiration are typically observed during chronic sediment exposure regimes (Pastorok & Bilyard 1985, Rogers 1990, Telesnicki & Goldberg 1995), where corals have to constantly remove sediments, presumably to aid photosynthesis, therefore expending more energy over longer time periods. In contrast, declines in photosynthesis during acute sediment stress events may dictate coral tolerances to these extreme conditions. Furthermore, reductions in photosynthesis equate to a reduced energy budget which may influence energy expensive processes such as sediment clearing in chronically turbid waters.
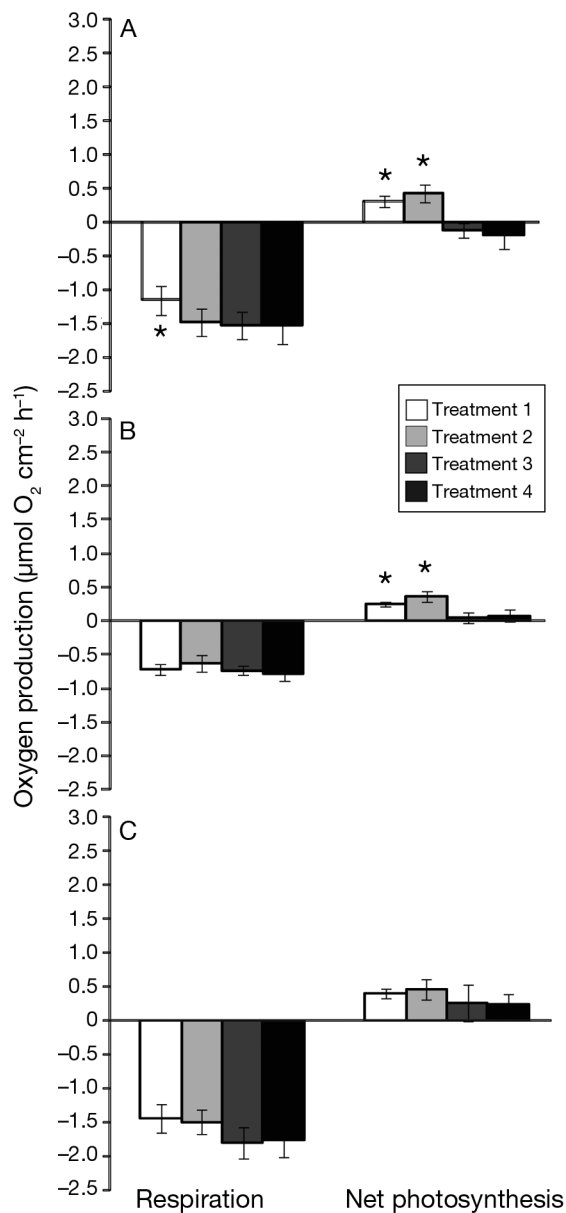
Fig. 4. Respiration rate and net photosynthetic rate during all treatments (1 = baseline, 2 = low sediment level, 3 = medium sediment level, 4 = high sediment level) for (A) *Merulina ampliata*, (B) *Pachyseris speciosa*, and (C) *Platygyra sinensis*. Standard errors are represented by error bars (n = 24) and * indicates a significant difference compared to Treatment 4
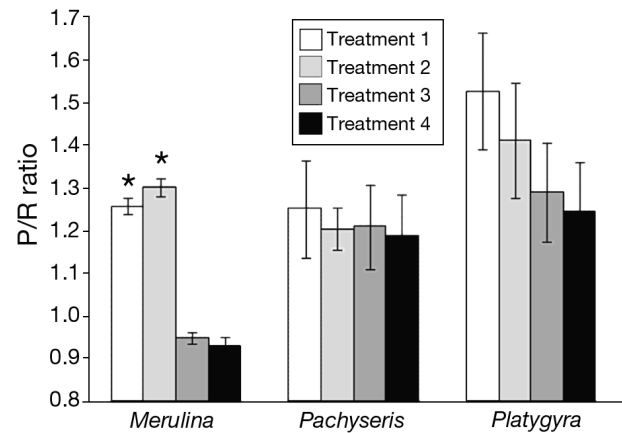

Fig. 5. P/R ratio for all coral species during baseline conditions and all sediment resuspension treatments (1 = baseline, 2 = low sediment level, 3 = medium sediment level, 4 = high sediment level). Standard errors are represented by error bars (n = 24) and * indicates a significant difference compared to Treatment 4
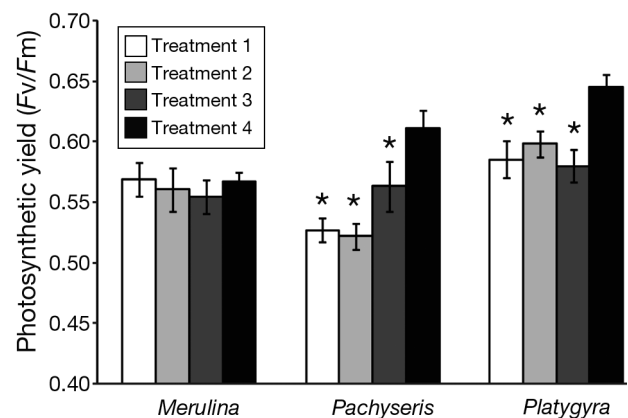

Fig. 6. Maximum photosynthetic yield (F_v/F_m) for all coral species during baseline conditions and all sediment resuspension treatments (1 = baseline, 2 = low sediment level, 3 = medium sediment level, 4 = high sediment level). Standard errors are represented by error bars (n = 24) and * indicates a significant difference compared to Treatment 4

The maximum quantum yield increased with a decline in light levels associated with sediment resuspension. The maximum quantum yield is a 'direct' measure of how efficient a coral is at utilising what light is available for photosynthesis (Krause & Weis 1991). Hence, as the yield increases, less light is required to maintain photosynthesis at the same level. The increase in the quantum yield was most notable between the medium and high turbidity treatments for *Pachyseris speciosa* and *Platygyra sinensis*, but there was no significant change between treatments for *Merulina ampliata*. It may be argued that the increase in the maximum quantum yield from week to week (and treatment to treatment) is due to a potential carry over effect from the previous week. However, given the short exposure duration and comparatively large recovery period, evidence from previous sediment stress studie suggests this is not the case. For example, Piniak (2007) demonstrated that *Porites* colonies whose maximum quantum yield declined with increasing sediment

Table 3. Results from Mixed Model analysis with species. The Type III fixed effects demonstrate if there was a significant difference between coral species responses for each of the photo-physiological variables, and the estimates of fixed effects demonstrate between which species effects of the treatments were significant, e.g. *Pachyseris* respiration rate was significantly different from *Platygyra* (p < 0.001) but *Merulina* was not

| Variable | BIC | Type III fixed effects | | | | | Estimates of fixed effects | | | | | |
		Source	Num. df	Den. df	F	p	Parameter	Estimate	SE	df	t	p
Respiration	438	Intercept	1	51	370.41	0.00	Intercept	1.76	0.16	143.18	−10.80	0.00
		Species	2	51	13.06	**0.00**	*Merulina*	0.18	0.23	143.18	0.79	0.43
							Pachyseris	0.98	0.23	143.18	4.26	**0.00**
							Platygyra	0.00	0.00			
Net photosynthesis	322.89	Intercept	1	51	11.09	0.00	Intercept	0.24	0.13	151.43	1.93	0.06
		Species	2	51	1.58	0.22	*Merulina*	−0.44	0.18	148.80	−2.47	**0.02**
							Pachyseris	−1.15	0.18	151.22	−0.85	0.40
							Platygyra	0.00	0.00			
P/R ratio	290.98	Intercept	1	51	1012.40	0.00	Intercept	1.24	0.11	185.41	11.06	0.00
		Species	2	51	3.87	0.27	*Merulina*	−0.31	0.16	184.45	−1.98	**0.05**
							Pachyseris	−0.05	0.16	185.71	−0.32	0.75
							Platygyra	0.00	0.00			
Yield	−544.77	Intercept	1	51	11955.85	0.00	Intercept	0.65	0.14	172.95	46.34	0.00
		Species	2	51	12.21	**0.00**	*Merulina*	−0.08	0.02	172.95	−3.99	**0.00**
							Pachyseris	−0.03	0.02	172.95	−1.76	**0.08**
							Platygyra	0.00	0.00			

amount (1.0 to ~30 g h^{-1} cm^{-2}) and exposure (6 to 90 h), recovered to pre-treatment fluorescence levels within 48 h following exposure. Given that the sediment conditions to which the corals were exposed to in this study were considerably less stressful, a carry-over effect from week to week is very unlikely.

The rise in the maximum quantum yield of *Platygyra sinensis* and *Pachyseris speciosa* occurred over a considerably short timescale (hours), suggesting that some corals are responding and rapidly acclimating to reductions in light. Seasonal and daily changes in the quantum yield have been observed with higher maximum quantum yields recorded during the winter months, when surface irradiance levels were reduced (Warner et al. 2002, Winters et al. 2006), and higher effective quantum yields during the day when turbidity levels have increased (Piniak & Storlazzi 2008). Yet there is limited evidence that the maximum quantum yield can increase/decrease over a matter of hours, as this study suggests is possible. A comparable rapid change in both the maximum and effective quantum yield of corals was observed in the field in a study by Brown et al. (1999), who found that the maximum quantum yield declined rapidly from dawn to midday as light levels increased, recovering to dawn levels by early evening, illustrating diurnal patterns of dynamic photo-inhibition as a means of protecting Photosystem II. The reverse process of photoacclimation to declines in light intensities occurs at different time

scales (minutes to weeks) and involves a number of processes in both the symbiont and coral. Cellular mechanisms that occur during low light intensities in the symbiont are well understood and include: increases in the size and number of symbionts, increases in photosynthetic pigment concentrations (Rogers 1979, Dubinsky et al. 1984, Warner et al. 2002, Ulstrup et al. 2008), a decline in antioxidant concentrations and a decline in levels of ultraviolet radiation absorbing amino acids (Shick et al. 1995). Corals can also respond to light variation with behavioural and morphological changes, but cellular mechanisms within the coral are less well understood. A recent study by Roth et al. (2010) found that corals can regulate their Green Fluorescent Protein (GFP) to alter their internal light environment. In the present study, the cellular mechanisms that lead to such a rapid photo-acclimatory response will potentially include some of these processes, and requires further investigation. It is clear that the rate and scale with which a coral can photo-acclimate to low light levels will determine the energy output from photosynthesis and, as such, their tolerance to sediments.

The rapid photo-acclimatory abilities of *Pachyseris speciosa* and *Platygyra sinensis* have enabled these 2 coral species to maintain a positive carbon budget, whereas *Merulina ampliata*, whose yield did not change, entered into a negative carbon budget state. Linking rates of oxygen production and carbon assimilation to fluorescence yield should be carried

out with caution as previous studies indicate that the fluorescence yield and oxygen production can become decoupled in corals (Hoogenboom et al. 2006, Ulstrup et al. 2006). Hence a change in yield may not always influence energy production. However, the decoupling between yield and oxygen production typically occurs at high light intensities (>200 PAR), whereas a positive linear relationship has been observed at lower light intensities (Ulstrup et al. 2006). In this study, we were well within the lower light levels where oxygen production and yields are typically coupled. As such we can assume that higher yields measured in *P. speciosa*, and particularly in *P. sinensis*, will provide these corals with more energy from photosynthesis, and enable them to survive acute sediment stress events.

Carbon assimilation from photosynthesis (and heterotrophy) in corals is used for a number of important functions including growth, immunity and reproduction, as well as providing energy for sediment removal in turbid waters. Sediment removal from the coral surfaces is achieved by both active mechanisms that require energy, as well as passive mechanisms that depend on coral morphology and corallite structure (Todd et al. 2001, Todd 2008, Erftemeijer et al. 2012, Flores et al. 2012). Poor sediment removal rates may result in prolonged periods (days) of sediment burial which causes coral tissue mortality by (1) suffocation of tissue under anoxic conditions (Rogers 1983) which can be exacerbated by nutrient composition and microbial activity (Weber et al. 2006, 2012) and (2) starvation following a decline in photosynthesis or heterotrophic feeding (Rogers 1990). Corals that typically rely on active sediment removal mechanisms (e.g. *Goniopora*), such as the use of their cilia and tentacles, distension of coral polyps (Philipp & Fabricius 2003) and mucus production to capture and remove particles (Hubbard & Pocock 1972, Brown & Bythell 2005), will require energy. If more energy is channelled to sediment clearing, less energy is available for other essential coral functions, thereby having longer-term consequences on coral and reef health. These 'knock-on' effects are more difficult to test given the complexity of interactions, but may be reflected in lower carbonate production and reef growth rates (Cortes & Risk 1985, Lough & Barnes 1997, Crabbe & Smith 2005), higher occurrence of disease (Fabricius 2005) and negatively skewed age populations due to limited reproduction (Meesters et al. 2001, Done et al. 2007).

Coral morphology is an important determinant of coral depth distribution on a reef (Done 1986, Browne et al. 2012). Light and water flow as well as sediment dynamics vary with depth (Wolanski et al. 2005), and certain coral morphologies are better suited to certain light, water flow and sedimentary conditions. Foliose corals with a large surface area and small polyps, such as *Merulina* spp. and *Pachyseris* spp., are typically limited to shallow depths (<5 m) in turbid waters where sediments are frequently resuspended and there is limited sedimentation. In contrast, massive corals, such as *Platygyra* spp., have large polyps and a rugose skeleton capable of withstanding higher rates of sedimentation as they are able to slough off sediments trapped within their mucus. As such, these corals are found on reef flats where levels of sedimentation may be elevated. The longer-term consequences of elevated sedimentation rates on foliose and massive corals will differ: massive corals will expend more energy for mucus production to aid the rapid removal of sediments, whereas foliose corals may be smothered by sediments for extended periods of time leading to tissue mortality. In our study, we did not observe either of these impacts, as we concentrated on the immediate effects of sediment resuspension on coral photophysiology. However, sediment settling on corals on turbid reefs is critical for coral condition, and may have more immediate impacts on coral health than declines in the coral energy budget — particularly in low energy environments.

The use of silicon carbide in the assessment of sediment stress on corals eliminates the potential for corals to offset reductions in photosynthesis through heterotrophy (Anthony & Fabricius 2000). It is well known that many corals survive low light conditions on inshore turbid reefs due to heterotrophic feeding, with some corals being more effective heterotrophic feeders than others (e.g. *Goniastrea*; Anthony & Fabricius 2000) and are, hence, often found in greater abundance on turbid reefs. The relative importance of heterotrophic feeding to phototrophic feeding on turbid reefs can be high given that many corals are not only surviving but thriving within highly variable sedimentary regimes as evidenced from rapid coral (Browne 2012) and reef (Perry et al. 2009, 2012) growth rates. The benefits of heterotrophy are likely to function over longer timescales (>2 h) thereby having limited influence on the immediate oxygen production rates following an acute sediment stress event. However, the combined influence of an immediate reduction in photosynthesis and carbon assimilation during an acute sediment stress event with an assessment of heterotrophic feeding in the preceding hours will provide a detailed assessment of the carbon source and its production over time.

The continual rise in human utilisation of the coastal zone will lead to an increase in the frequency and severity of acute sediment stress events in coastal regions (Nicholls et al. 2007). As such, improving our knowledge on how corals respond immediately after an acute sediment stress event will be critical in assessing their longer-term survival within a variable sedimentary regime. Coral sediment thresholds need to take into account processes that require energy production but function over longer time scales, rather than just rely on tissue mortality rates. Those corals that can rapidly photo-acclimate and maintain a high level of photo efficiency, critical for maintaining a positive carbon energy balance during low light conditions, will be better equipped to handle the increased energy costs associated with sediment removal, and may also still be able to grow and reproduce. In the present study, of the 3 species tested, *Platygyra* was least influenced by the sediment resuspension events and maintained a positive carbon energy budget. In contrast, based on the negative carbon energy budget observed during the medium and high sediment stress events, *Merulina* was the most influenced. Data on the fluorescence yield suggested that it may be the rapid photo-acclimation abilities of *Platygyra* that enabled it to maintain a positive carbon budget during the acute sediment stress events. In summary, our results illustrate that turbid water corals show species specific variability in their photo-physiology and energy production in response to acute sediment stress events of a short duration, and hence highlight the potential importance of such events in structuring future coral populations in areas most heavily impacted by anthropogenic disturbances.

LITERATURE CITED

Abdel-Salam H, Porter JW (1988) Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. Proc 6th Int Coral Reef Symp, Australia

Anthony KRN (2000) Enhanced particle feeding capacity of corals on turbid reefs (Great Barrier Reef). Coral Reefs 19:59–67

Anthony KRN, Connolly SR (2004) Environmental limits to growth: physiological niche boundries of corals along turbidity:light gradients. Oecologia 141:373–384

Anthony KRN, Connolly SR (2007) Bleaching, energetics, and coral mortality risk: effects of temperature, light, and sediment regime. Limnol Oceanogr 52:716–726

Anthony KRN, Fabricius K (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Biol Ecol 252:221–253

Anthony KRN, Hoegh-Guldberg O (2003) Kinetics of photo-acclimatization in corals. Oecologia 134:23–31

Bastidas C, Bone D, Garcia EM (1999) Sedimentation rates and metal content of sediments in a Venezuelan coral reef. Mar Pollut Bull 38:16–24

Beer S, Vilenkin B, Weil A, Veste M, Susel L, Eshel A (1998) Measuring photosynthetic rates in seagrasses by pulse amplitude modulated (PAM) fluorometry. Mar Ecol Prog Ser 174:293–300

Brown BE, Bythell JC (2005) Perspectives on mucus secretion in reef corals. Mar Ecol Prog Ser 296:291–309

Brown BE, Ambarsari I, Warner ME, Fitt WK, Dunne RP, Gibb SW, Cummings DG (1999) Diurnal changes in photochemical efficiency and xanthophyll concentrations in shallow water reef corals: evidence for photoinhibition and photoprotection. Coral Reefs 18:99–105

Browne NK (2012) Spatial and temporal variations in coral growth on an inshore turbid reef subjected to multiple disturbance events. Mar Environ Res 77:71–83

Browne NK, Smithers SG, Perry CT (2010) Geomorphology and community structure of Middle Reef, central Great Barrier Reef, Australia: an inner-shelf turbid zone reef subjected to episodic mortality events. Coral Reefs 29: 683–689

Browne NK, Smithers SG, Perry CT (2012) Coral reefs of the turbid inner Great Barrier Reef: an environmental and geological perspective on occurrence, composition and growth. Earth Sci Rev 115:1–20

Browne NK, Smithers SG, Perry CT (2013) Spatial and temporal variations in turbidity on two inshore turbid reefs on the Great Barrier Reef, Australia. Coral Reefs 32:195–210

Chan LT (1980) A preliminary study of the effects of land reclamation on the marine fauna of Singapore, with particular reference to the hard corals (Scleractinians). Honours thesis, National University of Singapore

Chou LM (1996) Response of Singapore reefs to land reclamation. Galaxea 13:85–92

Cooper TF, Gilmour JP, Fabricius KE (2009) Bioindicators of changes in water quality on coral reefs: review and recommendations for monitoring programmes. Coral Reefs 28:589–606

Cooper TF, Ulstrup KE, Dandan SS, Heyward AJ, Kuhl M and others (2011) Niche specialization of reef-building corals in the mesophotic zone: metabolic trade-offs between divergent *Symbiodinium* types. Proc Biol Sci 278: 1840–1850

Cortes NJ, Risk MJ (1985) A reef under siltation stress: Cahuita, Costa Rica. Bull Mar Sci 36:339–356

Crabbe JC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs 24:437–441

Davies AJ, Last KS, Hendrick VJ (2009) Maintaining turbid and high flow conditions in laboratory studies, a case study using *Sabellaria spinulosa.* J Exp Mar Biol Ecol 370:35–40

DeVantier LM, De'ath G, Turak E, Done T, Fabricius KE (2006) Species richness and community structure of reef building corals on the near shore reefs of the Great Barrier Reef. Coral Reefs 25:329–340

Dikou A, van Woesik R (2006) Survival under chronic stress from sediment load: spatial patterns of hard coral communities in the southern islands of Singapore. Mar Pollut Bull 52:1340–1354

Done T (1986) Zonation and disturbances in coral communities on fringing reefs. In: Fringing reef workshop: science, industry and management. Book workshop series 9. GBRMPA, Townsville, p 34–38

Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. Am Zool 39:66–79

Done TJ, Turak E, Wakeford M, DeVantier L, McDonald A, Fisk D (2007) Decadal changes in turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? Coral Reefs 26:789–805

Dubinsky Z, Falkowski PG, Porter JW, Muscatine L (1984) Absorption and utilization of radiant energy by light- and shade-adapted colonies of the hermatypic coral *Stylophora pistillata.* Proc R Soc Lond B Biol Sci 222:203–214

Erftemeijer PLA, Riegl B, Hoeksema BW, Todd P (2012) Environmental impacts of dredging and other sediment disturbances on corals: a review. Mar Pollut Bull 64:1737–1765

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar Pollut Bull 50:125–146

Flores F, Hoogenboom MO, Smith LD, Cooper TF, Abrego D (2012) Chronic exposure of corals to fine sediments: lethal and sub-lethal impacts. PLoS ONE 7:e37795

Gelinas M, Bokuniewicz H, Rapaglia J, Lwiza KMM (2013) Sediment resuspension by ship wakes in the Venice Lagoon. J Coast Res 29:8–17

Glynn PW, Howard LS, Corcoran E, Freay AD (1984) The occurrence and toxicity of herbicides in reef-building corals. Mar Pollut Bull 15:370–374

Hoitink AJF, Hoekstra P (2003) Hydrodynamic control of the supply of reworked terrigenous sediment to coral reefs in the Bay of Banten (NW Java, Indonesia). Estuar Coast Shelf Sci 58:743–755

Hoogenboom MO, Anthony KRN, Connolly SR (2006) Energetic cost of photoinhibition in corals. Mar Ecol Prog Ser 313:1–12

Hoogenboom MO, Campbell DA, Beraud E, DeZeeuw K, Ferrier-Pagès C (2012) Effects of light, food availability and temperature stress on the function of photosystem II and photosystem I of coral symbionts. PLoS ONE 7: e30167

Hubbard JAEB, Pocock YP (1972) Sediment rejection by recent scleractinian corals: a key to paleo-environmental reconstruction. Geol Rundsch 61:598–626

Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: the basics. Annu Rev Plant Physiol Plant Mol Biol 42:313–317

Lane DJW (1991) Growth of scleractinian corals on sediment-stressed reefs at Singapore. In: Alcala AC (ed) Proc Reg Symp Living Resource Coastal Areas, Manila. Marine Science Institute, University of the Philippines, Manila, p 97–106

Larcombe P, Ridd PV, Wilson B, Prytz A (1995) Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. Coral Reefs 14:163–171

Larcombe P, Costen A, Woolfe KJ (2001) The hydrodynamic and sedimentary setting of near shore coral reefs, central Great Barrier Reef shelf, Australia: Paluma Shoals, a case study. Sedimentology 48:811–835

Lindstrom MJ, Bates DM (1988) Newton-Raphson and EM algorithms for linear mixed-effects models for repeated-measures data. J Am Stat Assoc 83:1014–1022

Lou J, Ridd PV (1996) Wave-current bottom shear stresses and sediment resuspension in Cleveland Bay, Australia. Coast Eng 29:169–186

Lough JM, Barnes DJ (1997) Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: a proxy for seawater temperature and a background of variability against which to identify unnatural change. J Exp Mar Biol Ecol 211:29–67

Low JKY, Chou LM (1994) Sedimentation rates in Singapore waters. Proc 3rd ASEAN-Aust Symp Living Coral Resour 2:697–701

Lui GCY, Setiawan W, Todd P, Erftemeijer PLA (2012) Among genotype variation for sediment rejection in the reef building coral *Diploastrea heliopora* (Lamark, 1816). Raffles Bull Zool 60:525–531

McClanahan TR, Oburu D (1997) Sedimentation effects on shallow coral communities in Kenya. J Exp Mar Biol Ecol 209:103–122

Meesters EH, Hilterman M, Kardinall E, Keetman M, deVries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variations. Mar Ecol Prog Ser 209:43–54

Negri AP, Flores F, Hoogenboom MO, Abrego D, Freckelton M, Cooper TF (2009) Effects of dredging on shallow corals: experimental sediment exposure. Interim report to Woodside Energy: Browse Joint Venture Partners. Australian Institute of Marine Science, Townsville

Nicholls RJ, Wong PP, Burkett VR, Codignotto JO and others (2007) Coastal systems and low-lying areas. Climate change 2007: impacts, adaptation and vulnerability. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, p 315–356

Orpin AR, Ridd PV, Thomas S, Anthony KRN, Marshall P, Oliver J (2004) Natural turbidity variability and weather forecasts in risk management of anthropogenic sediment discharge near sensitive environments. Mar Pollut Bull 49:602–612

Pastorok RA, Bilyard GR (1985) Effects of sewage pollution on coral-reef communities. Mar Ecol Prog Ser 21: 175–189

Perry CT, Smithers SG, Johnson KG (2009) Long-term coral community records from Lugger Shoal on the terrigenous inner shelf of the central Great Barrier Reef, Australia. Coral Reefs 28:941–948

Perry CT, Smithers SG, Gulliver P, Browne NK (2012) Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation. Geology 40:719–722

Philipp E, Fabricius K (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. J Exp Mar Biol Ecol 287:57–78

Piniak GA (2007) Effects of two sediment types on the fluorescence yield of two Hawaiian scleractinian corals. Mar Environ Res 64:456–468

Piniak GA, Storlazzi CD (2008) Diurnal variability in turbidity and coral fluorescence on a fringing reef flat: southern Molokai, Hawaii. Estuar Coast Shelf Sci 77:56–64

Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J Exp Mar Biol Ecol 186:259–275

Rogers CS (1979) The effect of shading on coral reef structure and function. J Exp Mar Biol Ecol 41:269–288

Rogers CS (1983) Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Mar Pollut Bull 14:378–382

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202

Roth MS, Latz MI, Goericke R, Deheyn DD (2010) Green fluorescent protein regulation in the coral *Acropora yongei* during photoacclimation. J Exp Biol 213:3644–3655

Shick JM, Lesser MP, Dunlap WC, Stochaj WR, Chalker BE, Won JW (1995) Depth-dependent responses to solar ultraviolet-radiation and oxidative stress in the zooxanthellate coral *Acropora microphthalma.* Mar Biol 122:41–51

Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. Annu Rev Ecol Syst 23:89–118

Stafford-Smith MG (1993) Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar Biol 115:229–243

Stafford-Smith MG, Ormond RFG (1992) Sediment rejection mechanisms of 42 scleractinian corals. Aust J Mar Freshw Res 43:638–705

Te FT (2001) Responses of Hawaiian scleractinian corals to different levels of terrestrial and carbonate sediment. PhD thesis, University of Hawaii at Manoa, Honolulu

Telesnicki GJ, Goldberg WM (1995) Effects of turbidity of photosynthesis and respiration of two South Florida reef coral species. Bull Mar Sci 57:527–539

Thomas S, Ridd PV, Day G (2003) Turbidity regimes over fringing coral reefs near a mining site at Lihir Island, Papua New Guinea. Mar Pollut Bull 46:1006–1014

Todd PA (2008) Morphological plasticity in scleractinian corals. Biol Rev Camb Philos Soc 83:315–337

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

Todd PA, Sidle RC, Lewin-Koh NJI (2003) An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals. J Exp Mar Biol Ecol 299:97–113

Todd P, Ong X, Chou L (2010) Impacts of pollution on marine life in Southeast Asia. Biodivers Conserv 19:1063–1082

Tomascik T, Sander F (1985) Effects of eutrophication on reef-building corals. Mar Biol 87:143–155

Ulstrup K, Ralph P, Larkum A, Kühl M (2006) Intra-colonial variability in light acclimation of zooxanthellae in coral tissues of *Pocillopora damicornis.* Mar Biol 149:1325–1335

Ulstrup KE, Hill R, van Oppen MJH, Larkum AWD, Ralph PJ (2008) Seasonal variation in the photo-physiology of homogeneous and heterogeneous *Symbiodinium* consortia in two scleractinian corals. Mar Ecol Prog Ser 361:139–150

Warner ME, Chilcoat GC, McFarland FK, Fitt WK (2002) Seasonal fluctuations in photosynthetic capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef-building coral *Montastraea.* Mar Biol 141:31–38

Weber M, Lott C, Fabricius KE (2006) Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. J Exp Mar Biol Ecol 336:18–32

Weber M, de Beer D, Lott C, Polerecky L and others (2012) Mechanisms of damage to corals exposed to sedimentation. Proc Natl Acad Sci USA 109:E1558–E1567

Winters G, Loya Y, Rottgers R, Beer S (2003) Photoinhibition in shallow-water colonies of the coral *Stylophora pistillata* as measured in situ. Limnol Oceanogr 48:1388–1393

Winters G, Loya Y, Beer S (2006) In situ measured seasonal variations in Fv/Fm of two common Red Sea corals. Coral Reefs 25:593–598

Wolanski E, Gibbs R (1992) Resuspension and clearing of dredge spoils after dredging, Cleveland Bay, Australia. Water Environ Res 64:910–914

Wolanski E, Fabricius K, Spagnol S, Brinkman R (2005) Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. Estuar Coast Shelf Sci 65:153–158

Wolanski E, Fabricius KE, Cooper TF, Humphrey C (2008) Wet season fine sediment dynamics on the inner shelf of the Great Barrier Reef. Estuar Coast Shelf Sci 77:755–762