

1 **The photo-physiological costs associated with acute sediment stress events in three near-shore**  
2 **turbid water corals**

3 Nicola K. Browne <sup>1,2\*</sup>, Elimar Precht<sup>1</sup>, Kim S. Last<sup>3</sup> Peter A. Todd <sup>2</sup>

4 1 DHI Water and Environment (S) Pte Ltd, 1 Cleantech Loop, #03-05 CleanTech One, Singapore  
5 637141

6 2 Experimental Marine and Ecology Laboratory, Dept. of Biological Sciences, National University of  
7 Singapore, Singapore 117543

8 3 Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll PA37 1QA

9 Corresponding author

10 Email: [Nicola.browne@my.jcu.edu.au](mailto:Nicola.browne@my.jcu.edu.au)

11 Tel: +65 8301 6079

12 **Keywords:** Turbidity, sedimentation, sediment resuspension, mesocosm experiments, coral  
13 photosynthesis, Singapore.

14 **Running page header:** Acute sediment stress and coral photo-physiology

15

16

17

18

19

20

21

## 22 **Abstract**

23 Many coral reef communities thriving in inshore coastal waters characterised by chronically high  
24 natural turbidity ( $>5 \text{ mg.l}^{-1}$ ) have adapted to low light ( $<200 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) and high  
25 sedimentation rates ( $>10 \text{ mg.cm}^2.\text{day}^{-1}$ ). Yet, short (hours) acute sediment stress events driven by  
26 wind waves, dredging operations involving suction or screening, or shipping activities with vessel  
27 wake or propeller disturbance, can result in a rise in turbidity above the natural background level.  
28 Although these may not be lethal to corals given the time frame, there could be a considerable impact  
29 on photo-trophic energy production. A novel sediment delivery system was used to quantify the  
30 effects of three acute sediment resuspension stress events (turbidity = 100, 170, 240  $\text{mg. l}^{-1}$ ,  
31 sedimentation rates = 4, 9, 13  $\text{mg.cm}^2.\text{hr}^{-1}$ ) on three inshore turbid water corals common to the Indo-  
32 Pacific (*Merulina ampliata*, *Pachyseris speciosa* and *Platygyra sinensis*). Coral photo-physiology  
33 response (respiration, net photosynthesis, maximum quantum yield) was measured immediately after  
34 two hours of exposure. The respiration rate increased (0.72-1.44 to 0.78-1.76  $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ ) as the  
35 severity of the acute sediment resuspension event increased, whereas the photosynthetic rate declined  
36 (0.25-0.41 to -0.19-0.25  $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ ). *Merulina* was the least tolerant to acute sediment  
37 resuspension with a photosynthesis and respiration ratio (P/R ratio) of  $<1.0$  when turbidity levels  
38 reached  $>170 \text{ mg.l}^{-1}$ , while *Platygyra* was most tolerant (P/R $>1.0$ ). Data on the fluorescence yield  
39 suggested that the rapid photo-acclimation abilities of *Platygyra* enable it to maintain a positive  
40 carbon budget during the experiments, illustrating species specific responses to acute sediment stress  
41 events.

42

## 43 **Introduction**

44 Acute sediment stress is caused by short, high turbidity events which can range in severity (50 to  
45  $>500 \text{ mg.l}^{-1}$  suspended sediment concentration) and duration (minutes to hours; e.g. Wolanski & Gibbs  
46 1992, Larcombe et al. 2001, Orpin et al. 2004), and represent a considerable rise over the natural  
47 background turbidity. These pulsed high turbidity events commonly occur within inshore shallow

48 (<10 m at lowest astronomical tide (LAT)) coastal waters when sediments are resuspended either due  
49 to natural drivers (e.g. river runoff, tides or wind-driven waves; Lou & Ridd 1996), or anthropogenic  
50 drivers (e.g. ship-wakes, dredging plumes, land reclamation; Thomas et al. 2003, Gelinias et al. 2013)  
51 or a combination of both. Numerous coral communities have established and continued to thrive  
52 within inshore regions characterised by both high natural background turbidity and frequent acute  
53 sediment stress events (McClanahan & Oburu 1997, DeVantier et al. 2006, Perry et al. 2009, Browne  
54 et al. 2010), suggesting that many coral species are able to survive rapid, short lived high turbidity  
55 events within a chronic sedimentary regime ( $5\text{-}10\text{ mg.l}^{-1}$ ). But coral survival within turbid waters is  
56 energetically expensive (e.g. mucus production for sediment removal; Brown & Bythell 2005), and  
57 may reduce the potential for coral growth and reproduction. The energetic costs associated with  
58 exposure to acute sediment resuspension events for turbid water corals is unknown, and yet will have  
59 a critical influence on their longer-term survival and growth, and ultimately reef health.

60 Natural turbidity regimes vary considerably over space and time (Hoitink & Hoekstra 2003, Orpin et  
61 al. 2004, Wolanski et al. 2008, Browne et al. 2013), but land based activities such as coastal  
62 development, land reclamation, deforestation and agriculture can enhance sediment loading into  
63 coastal waters thereby chronically increasing background turbidity (Erfteimeijer et al. 2012). For  
64 example, since the 1970s, coastal development has increased sedimentation rates in Singapore from  
65  $<6\text{ mg cm}^{-2}\text{ d}^{-1}$  (Chan 1980) to  $15\text{--}30\text{ mg cm}^{-2}\text{ d}^{-1}$  (Lane 1991, Low & Chou 1994, Todd et al. 2003)  
66 with average visibility reduced from 10 m (1960s) to less than 2 m (Chou 1996). The severity and  
67 duration of acute sediment stress events is also highly variable, and is dependent on the driver,  
68 sediment type and local hydrodynamic conditions (currents, natural wind waves, ship-wakes etc.). In  
69 exposed regions, wind driven waves can resuspend sediments and increase the suspended sediment  
70 concentrations (SSC) up to  $>150\text{ mg.l}^{-1}$  (Larcombe et al. 1995, Larcombe et al. 2001, Browne et al.  
71 2013), whereas in more sheltered regions ship-wakes may be the primary driving force of sediment  
72 resuspension (Gelinias et al. 2013). However, the most severe pulse events, where SSC can reach  
73  $>300\text{ mg.l}^{-1}$ , are commonly associated with dredging activities (Wolanski & Gibbs 1992). In Papua  
74 New Guinea, SSC of  $>25\text{ mg.l}^{-1}$  were recorded over coral reefs for 10-60% of the time (18 months in

75 total) during mining operations, with short lived peaks (< hour) reaching 500 mg.l<sup>-1</sup> (Thomas et al.  
76 2003). The frequency, severity and duration of acute sediment stress events combined with the  
77 chronic background turbidity regime will influence coral survival and growth.

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

95 Previous research on sediment stress effects have documented changes in coral photobiology using  
96 PAM fluorometry in the field (Winters et al. 2003, Piniak & Storlazzi 2008, Cooper et al. 2009) and  
97 in the laboratory (Philipp & Fabricius 2003, Weber et al. 2006, Piniak 2007, Flores et al. 2012).  
98 These studies have focused on either chronic, long lasting events (e.g. Flores et al. 2012) or acute sub-  
99 lethal sediment stress events (e.g. Riegl & Branch 1995, Piniak 2007) which often lead to full or  
100 partial coral mortality. In contrast, we aimed to quantify the influence of acute sediment resuspension  
101 stress events (i.e. a short, non-lethal event) on coral photo-physiology by measuring both the yield and

102 P/R ratio. Three corals (*Merulina ampliata*, *Pachyseris speciosa*, *Platygyra sinensis*) common to  
103 turbid inshore reefs in the Indo-Pacific, were used to investigate the photo-physiological costs  
104 associated with acute sediment stress. A novel sediment delivery system was fabricated and corals  
105 were exposed to one of four sediment treatments (0, 120, 180, 240 mg. l<sup>-1</sup>) over four consecutive  
106 weeks using inert silicon carbide powder as a proxy for natural sediment. Great care in the  
107 experimental design was taken to ensure that the sediment particle profile, and the severity of the  
108 event and its duration were environmentally relevant. Specifically, the objectives were: 1) to quantify  
109 the physiological effects of acute sediment resuspension events on three inshore turbid water corals,  
110 2) assess differences between species.

111

## 112 **Materials and Methods**

### 113 *Study species and sampling sites*

114 Three common Indo-Pacific corals were selected for the study: *Merulina ampliata* and *Pachyseris*  
115 *speciosa*, two plate corals, and *Platygyra sinensis*, a massive coral. These corals are commonly found  
116 within inshore turbid waters, and in Singapore are typically found in high abundance (>5%) on the  
117 upper reef slopes (<4 m LAT; Dikou & van Woesik 2006), suggesting adaptation to low-light, high  
118 sediment waters. Six colonies from each species were collected from three turbid reef slopes (3 m  
119 LAT) in Singapore to ensure genetic diversity: two colonies from each of the three species were  
120 collected from Labrador (N 1.26636, E 103.80015), Kusu Island (N 1.22838, E 103.85525) and from  
121 Palau Hantu (N 1.22640, E 103.74675). Turbidity and light levels on the reef slope (at 3 m LAT) at  
122 Labrador typically range from 10 to 150 mg.l<sup>-1</sup> and 0 to 150 PAR at 3 m LAT respectively, and at  
123 Kusu Island and Palua Hantu range from 5 to 50 mg.l<sup>-1</sup> and 50 to ~200 PAR respectively (May-June,  
124 2012; N.K Browne, unpublished).

125 Four coral fragments of approximately 5 ×5 cm were obtained from each coral colony (n = 24 for  
126 each species, total n=72 fragments) using either a chisel or cutters, and each fragment was secured  
127 onto a plastic grid using underwater epoxy resin (non-toxic) to avoid direct coral handling. Mounted

128 fragments were then transported to the aquarium facilities at the Tropical Marine Science Institute  
129 (TMSI) on St. John's Island (Singapore), where they were allowed to recover in 200 L indoor flow  
130 through tanks (water temperature  $\sim 29^{\circ}\text{C}$ , salinity 30 ppt, photoperiod 10 hr:14hr light:dark cycle at  
131  $120 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) for at least 8 wks prior to commencing the experiment. Corals were  
132 photographed with a scale, and photographs were analysed using CPCe software to determine the  
133 surface area of live tissue.

134

### 135 *Mesocosm chamber*

136 For the purpose of this study,  $12 \times 9$  L cylindrical mesocosms were fabricated to accommodate the  
137 coral fragments (Fig. 1). These were smaller versions of the 300 L Vortex Resuspension Tank (VoRT)  
138 described by Davies et al. (2009) and the rotational movement of water was provided by a motor-  
139 driven paddle ( $\sim 65$  revolutions per minute) instead of water pumps. The hollow vertical shaft of the  
140 paddle had holes near the top and doubled up as an air-lift to resuspend particulate matter that  
141 collected in the tapered well at the bottom of the chamber. The rotating paddles dissipated the  
142 sediments through the water column above the coral fragments which were positioned on a plastic  
143 grid directly above the sediment well. The amount of sediment particles forced up the central tube  
144 was controlled by the duration (seconds) of air that was pumped through the air lift. The new mini  
145 VORT (mVORT) also had a side opening covered with a 5 mm rubber membrane positioned at the  
146 same height as the corals, through which water samples were collected using a syringe and long  
147 needle.

### 148 *Sediment preparation*

149 The grain size distribution of the natural sedimentation profile at Labrador, Pulau Hantu and Kusu  
150 was analysed through laser diffraction particle size analyses (Malvern Mastersizer Particle Size  
151 Analyser, UK). The range in particulate particle size was comparable between sites (1-300  $\mu\text{m}$ ), but  
152 the median particle varied from 50 to 80  $\mu\text{m}$  at Labrador, from 80 to 100  $\mu\text{m}$  at Hantu and 60 to 100  
153  $\mu\text{m}$  at Kusu Island (n=30 from each site). The sediment profile from Labrador, the site with the

154 highest turbidity, was closely matched by combining commercially available particle sizes of silicon  
155 carbide powder (Kemet Fareast Pte Ltd) following Lui et al. (2012). The resulting silicon carbide mix  
156 contained particle sizes ranging from 1  $\mu\text{m}$  to 300  $\mu\text{m}$ , and had a median particle size of 60  $\mu\text{m}$  (Fig.  
157 2).

158 Silica carbide has been used for this purpose with success in a number studies that investigated the  
159 effects of sediment stress on corals (e.g. Stafford-Smith & Ormond 1992, Lui et al. 2012). The  
160 advantage of silicon carbide is that it provides a means whereby we can assess the physical/  
161 mechanical stress associated with an acute sediment stress event without confounding factors such as  
162 bacteria, microbes, nutrients and heavy metals which are known to exacerbate the negative effects of  
163 natural sediments on corals (Glynn et al. 1984, Bastidas et al. 1999, Fabricius 2005, Weber et al.  
164 2012). Great care was taken to replicate the natural reef sediment profile as particle size is critical not  
165 only to how corals respond to smothering (Stafford-Smith & Ormond 1992), but also the light  
166 environment. Sediments of different sizes and particle shapes will have variable influences on the  
167 light environment leading to variable wave length extinctions and shifting light fields. We  
168 acknowledge that silicon carbide may result in a different light environment than if natural reef  
169 sediments had have been used, but also consider this to be a lesser influence on coral photosynthesis  
170 given the low light levels (PAR), high turbidity and sedimentation rates replicated in this study.  
171 However, given the lack of confounding factors associated with silicon carbide, our data may  
172 underestimate the impacts of sediment on the respiratory and photosynthetic physiology of these  
173 corals.

174

### 175 ***Experimental design***

176 The mesocosm chambers were placed into 300 L water baths through which sea water flowed at a  
177 constant rate of 5 L.min<sup>-1</sup> (water temperature ~29°C). A light source (four T5 HO aquarium bulbs  
178 which provide the essential actinic blue light that corals require) was suspended 75 cm above the  
179 corals and provided ~150  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . In each mVoRT, sediment (~25 g) was placed at the

180 bottom of the well, and the tanks were slowly filled with sea water, through the side water inlet valve,  
181 from a central reservoir tank. The twelve motors were controlled by via programmable pulse width  
182 modulation (PWM) from a central microcontroller which enabled the user to set the motor speed  
183 between 1 to 65 revolutions per minute (rpm). Previous tests had verified that 20 rpm within a 20 cm  
184 diameter cylindrical tank generated a flow rate of approximately  $10 \text{ cm.s}^{-1}$ , at the midpoint between  
185 the centre and outer edge of the tank. Current speeds at reefs sites are typically  $<5 \text{ cm.s}^{-1}$ , but rise to  
186  $10\text{-}15 \text{ cm.s}^{-1}$  during resuspension events (N.K. Browne, unpublished data).

187 For each coral species, four fragments from six colonies (24 fragments per species) were exposed to  
188 an acute sediment stress event. One fragment of each coral species was randomly selected and placed  
189 on the plastic grid platform in the mVoRT two hours before the experiment commenced. Given the  
190 large number of fragments tested ( $n=72$ ) and limited number of chambers (12), the experiment was  
191 run twice every week: each time 36 fragments were tested (3 per chamber).

192 The experiment was run over four weeks in October 2012: baseline measurements (treatment 1) on  
193 corals were conducted in week 1; sediment treatment 2 (turbidity =  $102.4 \text{ mg.l}^{-1} \pm 13.9$ ; sedimentation  
194 rate =  $4.3 \pm 0.4 \text{ mg.cm}^2.\text{hr}^{-1}$ ; light =  $62.9 \pm 3.9 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (56% light attenuation)) was  
195 conducted in week 2; sediment treatment 3 (turbidity =  $174.2 \text{ mg.l}^{-1} \pm 10.6$ ; sedimentation rate =  $9.9 \pm$   
196  $1.0 \text{ mg.cm}^2.\text{hr}^{-1}$ ; light =  $54.3 \pm 2.8 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (63% light attenuation)) was conducted in  
197 week 3; and sediment treatment 4 (turbidity =  $242.5 \text{ mg.l}^{-1} \pm 13.6$ ; sedimentation rate =  $12.9 \pm 1.2$   
198  $\text{mg.cm}^2.\text{hr}^{-1}$ ; light =  $39.5 \pm 3.3 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (72% light attenuation)) was conducted in week  
199 4. Each acute sediment stress event lasted for 2 h and light levels in the tank were recorded every 5 s  
200 using a modified mini ambient light sensor (DHI, Denmark), connected to the central control box.  
201 The light sensor measured light levels between 350-680 nm and was been calibrated with a LI-COR  
202 light sensor (Li-192) to provide the linear calibration co-efficient with which to convert internal  
203 engineering units to PAR. Water samples (20 ml) were collected after 1 h using a syringe from the  
204 side inlet, and were suction filtered through Whatman filters ( $10 \text{ } \mu\text{m}$  particle retention) to determine  
205 the suspended sediment concentrations (SSC). Sedimentation rates ( $\text{g.cm}^{-2}.\text{h}^{-1}$ ) were calculated at the  
206 end of the experiment from a 4 cm diameter plastic disc placed on the plastic grid. During week 1,

207 the corals were not subjected to a sediment event (no air burst), but remained in the chambers for 4 h  
208 prior to physiological analysis. During weeks 2 to 4, corals were subjected to four air bursts (at 0  
209 min, 30 min, 60 min, 90 min) which forced sediments up the central tube creating a sediment  
210 resuspension event and reducing light penetration (Fig. 3). Prior to the experiment, several calibration  
211 tests were performed to determine the length of air burst required to produce the required light,  
212 turbidity and sedimentation rate. During the calibration tests, light levels were recorded, water  
213 samples were taken and sedimentation rates were calculated. Corals in three of the twelve chambers  
214 were used as controls. These corals were not subjected to sediments and light levels were maintained  
215 at  $145.4 \pm 1.3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ .

216

### 217 *Physiological analyses*

218 The net photosynthetic and respiration rate, and maximum photosynthetic yield (Fv/Fm) was  
219 measured after the two hour acute sediment stress event. Photosynthesis and respiration were  
220 measured using RESP-EDU, Loligo Systems respiratory system and software (AUTO-RESP,  
221 Denmark). A circular respirometry chamber (1.5 L) was fabricated to accommodate the size of the  
222 fragments and equipped with a flush pump and a circulatory pump to maintain continuous water flow.  
223 The chamber was submerged in a 50 L water bath with running sea water, and temperature and  
224 oxygen were recorded every 5 s on a data logger (DAQ-M, Loligo Systems). Light levels outside the  
225 chamber were monitored using a cosine-corrected LI-COR probe (Li-192S) connected to a Li-1000  
226 data logger. Oxygen consumption/production rate ( $\text{mg O}_2 \text{l}^{-1}$ ) within the chamber volume (after  
227 subtracting the volume of coral) was measured continuously for 5 min using a galvanic cell oxygen  
228 probe (Loligo Systems), followed by a 2 min flush period. Photosynthetic rates were measured at  
229  $\sim 150 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and respiratory rates and the maximum photosynthetic yield were  
230 measured after 20 min incubation in the dark. The maximal photosynthetic yield (Fv/Fm) was  
231 measured using a Diving-PAM (Walz, Germany) (Beer et al. 1988). The optical-fiber probe was kept  
232 at a constant distance of 5 mm from the surface of the coral and the average of five measurements for

233 each coral fragment was calculated.  $F_o$  was measured by applying a pulsed measuring beam of  
234  $<1\mu\text{mol photon m}^{-2} \text{ s}^{-1}$  and the emission  $F_m$  was measured following the application of a saturating  
235 pulse of actinic light ( $>1000 \text{ } 1\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ). Oxygen production and respiration rates were  
236 normalised to the surface area of live tissue for each coral fragment ( $\mu\text{mol.cm}^{-2}.\text{h}^{-1}$ ), and the gross  
237 photosynthesis to respiration ratio (P/R ratio) was calculated (Cooper et al. 2011).

238

### 239 *Statistical analysis*

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

255

### 256 **Results**

257 The LME model was used to examine if treatment had a significant effect on respiration, net  
258 photosynthesis, the P/R ratio and photosynthetic yield a). within species and, b) the model was also  
259 used to determine if the controls were significantly different over the four weeks. There was no  
260 significant difference in the coral responses (respiration, net photosynthesis, yield) for the individual  
261 fragments that were used in the control chambers between weeks ( $p>0.05$ ), and no coral mortality was  
262 observed during and following the experiment (several months).

### 263 ***Respiration rate***

264 The mean O<sub>2</sub> depletion rate (hereafter referred to as respiration) for all three species increased in the  
265 high sediment treatment compared to baseline conditions measured in week 1: *Merulina* respiration  
266 rates increased from  $-1.15 \pm 0.13$  to  $-1.52 \pm 0.18$   $\mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ; *Pachyseris* respiration rates increased  
267 from  $-0.72 \pm 0.07$  to  $-0.78 \pm 0.11$   $\mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ; and *Platygyra* respiration rates increased from  $-1.44$   
268  $\pm 0.21$  to  $-1.76 \pm 0.25$   $\mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$  (Table 1). However, there was only a significant increase in the  
269 rate for *Merulina* whose respiration was significantly greater than the baseline conditions from week 2  
270 (treatment 2:  $p=0.004$ ; Table 2) when corals were subjected to a low sediment stress event (Fig. 4a).  
271 In contrast, the rise in respiration was most pronounced between the medium and high sediment stress  
272 event for *Pachyseris* and *Platygyra* (Fig. 4b and 4c), but the rise in respiration was not significantly  
273 different between weeks ( $p>0.05$ ; Table 2).

### 274 ***Net photosynthesis***

275 The net photosynthesis declined for all coral species in the medium and high sediment treatments,  
276 with lowest rates recorded following the high sediment treatment: *Merulina* declined from  $0.31 \pm 0.07$   
277 to  $-0.19 \pm 0.13$   $\mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ; *Pachyseris* declined from  $0.25 \pm 0.04$  to  $0.08 \pm 0.08$   $\mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ;  
278 and *Platygyra* declined from  $0.41 \pm 0.07$  to  $0.25 \pm 0.14$   $\mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$  in (Table 1, Fig. 4). However,  
279 the decline from baseline conditions during both the medium and high turbidity treatments was only  
280 significant for *Merulina* and *Pachyseris* ( $p<0.05$ ; Table 2).

### 281 ***P/R ratio***

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

### 288 ***Maximum photosynthetic yield***

289 The maximum photosynthetic yield did not vary significantly for *Merulina* over the course of the  
290 experiment, however, there was a significant increase in the yield for *Pachyseris* and *Platygyra*. The  
291 yield for *Pachyseris* increased from  $0.52 \pm 0.01$  to  $0.56 \pm 0.01$  ( $p = 0.00$ ) between the low and medium  
292 sediment stress events, and from  $0.56 \pm 0.01$  to  $0.61 \pm 0.02$  ( $p = 0.01$ ) between the medium and high  
293 sediment stress events, and the yield for *Platygyra* increased from  $0.58 \pm 0.01$  to  $0.65 \pm 0.01$  ( $p = 0.00$ )  
294 between the medium and high sediment stress events (Table 2; Fig. 6).

### 295 **Among species responses**

296 Over the course of the experiment the respiration rate for *Pachyseris* ( $0.78 \pm 0.23 \mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ) was  
297 significantly lower than *Platygyra* ( $1.76 \pm 0.16 \mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ) and *Merulina* ( $1.58 \pm 0.23 \mu\text{mol}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$ ;  
298 Table 3). In contrast there was no consistent and significant difference in the net photosynthetic  
299 rate among species ( $p > 0.05$ ). However, the P/R ratio of *Merulina* ( $0.93 \pm 0.16$ ) was significantly  
300 lower than both *Pachyseris* ( $1.18 \pm 0.16$ ) and *Platygyra* ( $1.24 \pm 0.11$ ), and the maximum  
301 photosynthetic yield of *Platygyra* ( $0.65 \pm 0.14$ ) was significantly higher than for *Merulina* ( $0.57 \pm$   
302  $0.02$ ).

303

### 304 **Discussion**

305 Acute sediment stress events are energetically expensive for corals as they limit light and reduce  
306 energy production from photo-trophy. This paper quantifies the reduction in energy production

307 following a two hour acute sediment event. Short-lived peaks in turbidity typically occur in locations  
308 characterised by naturally high background turbidity, where sediment supply is not limited, and  
309 sediments are frequently resuspended. Corals in chronically turbid waters have photo-acclimated to  
310 low light (Dubinsky et al. 1984) and may also have increased rates of heterotrophic feeding to offset  
311 energy deficits from photosynthesis (Anthony 2000, Anthony & Fabricius 2000). However, the  
312 increase in the frequency and severity of acute sediment stress events in coastal waters, due to  
313 changing land use, coastal construction and port activities (Smith & Buddemeier 1992, Chou 1996,  
314 Todd et al. 2010, Gelinas et al. 2013), provides an additional stress for corals potentially surviving at  
315 the edge of their environmental and physiological tolerances. How corals respond to these pulse  
316 events and the associated physiological costs involved will determine rates of survival and growth  
317 within these marginal reef environments. Environmental extremes rather than background constants  
318 will structure populations (Done 1999), and, as such, frequent acute sediment stress events may play  
319 an important role in coral community composition on inshore turbid reefs.

320 Variability in physiological response of the coral between species indicate species specific thresholds  
321 to acute sediment stress levels. During low light conditions ( $\sim 120 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ ) all three  
322 coral species were producing more energy from photo-trophy than respiring and had a positive energy  
323 budget. Net photosynthesis and respiration rates were comparable to rates measured for *Turbinaria*  
324 and *Stylphora* under low light conditions ( $\sim 120 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ ; fed and at  $26^{\circ}\text{C}$ ) where corals  
325 photosynthesised at  $1.20$  and  $2.0 \mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ , and respired at  $-0.5$  and  $-0.75 \mu\text{mol.cm}^{-2}.\text{hr}^{-1}$   
326 (Hoogenboom et al. 2012). There was limited change in photosynthesis during the low sediment  
327 stress event for the three coral species ( $\sim 100 \text{mg.l}^{-1}$ ), but rates did decline significantly for *Merulina*  
328 and *Pachyseris* when corals were exposed to  $>170 \text{mg.l}^{-1}$ . The data suggests that *Merulina* is the least  
329 tolerate to sediment stress events given that the net photosynthetic rate was negative ( $<-0.12 \mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ ) and the P/R ratio was  $<1.0$  i.e. the coral was using more energy than it was producing. In  
330 contrast, *Platygyra* was the most tolerant to sediments as its net photosynthetic rate declined the least  
331 during the high sediment treatment, and remained high ( $0.25 \mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ ) compared to both  
332 *Pachyseris* ( $0.08 \mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ ) and *Merulina* ( $-0.19 \mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ ).

334

335 The decline in net energy production for the three coral species was largely due to the reduction in  
336 photosynthesis, driven by high turbidity and limited light, and not by increasing respiration rates. It is  
337 well known that sediments can severely affect the coral energy budget by both reducing  
338 photosynthesis and increasing respiration rates, the latter due to increased energy expenditure as  
339 corals remove sediments from their surfaces (Riegl & Branch 1995, Brown & Bythell 2005, Fabricius  
340 2005, Negri et al. 2009, Flores et al. 2012). Some consider that the effects of sedimentation on coral  
341 physiology to be the main physiological process that drive coral sediment tolerances (Anthony &  
342 Connolly 2004) and reductions in light and photosynthesis are less important. In the present study,  
343 sedimentation rates were high (4 to 13 mg.cm<sup>-2</sup>.hr<sup>-1</sup>) and respiration rates did increase for all three  
344 coral species, most likely due to settling sediments. But the increase in respiration was not  
345 consistently significant between treatments. Significant increases in respiration are typically observed  
346 during chronic sediment exposure regimes (Pastorok & Bilyard 1985, Rogers 1990, Telesnicki &  
347 Goldberg 1995), where corals have to constantly remove sediments, presumably to aid  
348 photosynthesis, therefore expending more energy over longer time periods. In contrast, declines in  
349 photosynthesis during acute sediment stress events may dictate coral tolerances to these extreme  
350 conditions. Furthermore, reductions in photosynthesis equate to a reduced energy budget which may  
351 influence energy expensive processes such as sediment clearing in chronically turbid waters.

352 The maximum quantum yield increased with a decline in light levels associated with sediment  
353 resuspension. The maximum quantum yield is a 'direct' measure of how efficient a coral is at  
354 utilising what light is available for photosynthesis (Krause & Weis 1991). Hence, as the yield  
355 increases, less light is required to maintain photosynthesis at the same level. The increase in the  
356 quantum yield was most notable between the medium and high turbidity treatments for *Pachyseris*  
357 and *Platygyra*, but there was no significant change between treatments for *Merulina*. It may be  
358 argued that the increase in the maximum quantum yield from week to week (and treatment to  
359 treatment) is due to a potential carry over effect from the previous week. However, given the short  
360 exposure duration and comparatively large recovery period, this is very unlikely as evidenced from

361 previous sediment stress studies. For example, Piniak (2007) demonstrated that *Porites* colonies  
362 whose maximum quantum yield declined with increasing sediment amount (1.0 to ~30 g.hr<sup>-1</sup>.cm<sup>-2</sup>)  
363 and exposure (6 h to 90 h), recovered to pre-treatment fluorescence levels within 48 h following  
364 exposure. Given that the sediment conditions to which the corals were exposed to in this study were  
365 considerably less stressful, a carry-over effect from week to week is unlikely.

366 The rise in the maximum quantum yield of *Platygyra* and *Pachyseris* occurred over a considerably  
367 short timescale (hours), suggesting that some corals are responding and rapidly acclimating to  
368 reductions in light. Seasonal and daily changes in the quantum yield have been observed with higher  
369 maximum quantum yields recorded during the winter months, when surface irradiance levels were  
370 reduced (Warner et al. 2002, Winters et al. 2006), and higher effective quantum yields during the day  
371 when turbidity levels have increased (Piniak & Storlazzi 2008). Yet, there is limited evidence that the  
372 maximum quantum yield can increase/decrease over a matter of hours, as this study suggests is  
373 possible. A comparable rapid change in both the maximum and effective quantum yield of corals was  
374 observed in the field in a study by Brown et al. (1999). In this study, maximum quantum yield  
375 declined rapidly from dawn to midday as light levels increased, recovering to dawn levels by early  
376 evening, illustrating diurnal patterns of dynamic photo-inhibition as a means of protecting  
377 Photosystem II. During photo-inhibition,  $F_o$  (defined as the minimum fluorescence yield when all  
378 reaction centres are open in the dark adapted state) declines which, it is believed, dissipates excess  
379 energy within the light harvesting antennae. The rate and scale with which a coral can photo-  
380 acclimate to low light levels, will determine the energy output from photosynthesis and, as such, their  
381 tolerance to sediments.

382 The rapid photo-acclimatory abilities of *Pachyseris* and *Platygyra* have enabled these two coral  
383 species to maintain a positive carbon budget, whereas *Merulina*, whose yield did not change, entered  
384 into a negative carbon budget state. Linking rates of oxygen production and carbon assimilation to  
385 fluorescence yield should be carried out with caution as previous studies indicate that the fluorescence  
386 yield and oxygen production can become decoupled in corals (Hoogenboom et al. 2006, Ulstrup et al.  
387 2006). Hence a change in yield may not always influence energy production. However, the

388 decoupling between yield and oxygen production typically occurs at high light intensities (> 200  
389 PAR), whereas a positive linear relationship has been observed at lower light intensities (Ulstrup et al.  
390 2006). In this study, we were well within the lower light levels where oxygen production and yields  
391 are typically coupled. As such we can assume that higher yields measured in *Pachyseris*, and  
392 particularly in *Platygyra*, will provide these corals with more energy from photosynthesis, and enable  
393 them to survive acute sediment stress events.

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

412

413 The use of silicon carbide in the assessment of sediment stress on corals eliminates the potential for  
414 corals to offset reductions in photosynthesis through heterotrophy (Anthony & Fabricius 2000). It is

415 well known that many corals survive low light conditions on inshore turbid reefs due to heterotrophic  
416 feeding, with some corals being more effective heterotrophic feeders than others (e.g. Goniastrea;  
417 Anthony & Fabricius 2000) and are, hence, often found in greater abundance on turbid reefs. The  
418 relative importance of heterotrophic feeding to phototrophic feeding on turbid reefs can be high given  
419 that many corals are not only surviving but thriving within highly variable sedimentary regimes as  
420 evidenced from rapid coral (Browne 2012) and reef growth rates (Perry et al. 2009, Perry et al. 2012).  
421 The benefits of heterotrophy are likely to function over longer timescales (>2 hours) thereby having  
422 limited influence on the immediate oxygen production rates following an acute sediment stress event.  
423 However, the combined influence of an immediate reduction in photosynthesis and carbon  
424 assimilation during an acute sediment stress event with an assessment of heterotrophic feeding in the  
425 proceeding hours will provide a detailed assessment of the carbon source and its production over time.  
426

427 The continual rise in human utilisation of the coastal zone will lead to an increase in the frequency  
428 and severity of acute sediment stress events in coastal regions (Nicholls et al. 2007). As such, an  
429 improved knowledge on how corals respond immediately after an acute sediment stress event, will be  
430 critical in assessing their longer-term survival within a variable sedimentary regime. Those corals that  
431 can rapidly photo-acclimate and maintain a high level of photo efficiency, critical for maintaining a  
432 positive carbon energy balance during low light conditions, will be better equipped to handle the  
433 increased energy costs associated with sediment removal, and may also still be able to grow and  
434 reproduce. In this study, of the three species tested, *Platygyra* was least influenced by the sediment  
435 resuspension events and maintained a positive carbon energy budget. In contrast, based on the  
436 negative carbon energy budget observed during the medium and high sediment stress events,  
437 *Merulina* was the most influenced. Data on the fluorescence yield suggested that it may be the rapid  
438 photo-acclimation abilities of *Platygyra* that enabled it to maintain a positive carbon budget during  
439 the acute sediment stress events. In summary, our results illustrate that turbid water corals show  
440 species specific variability in their photo-physiology and energy production in response to acute

441 sediment stress events of a short duration, and hence highlight the potential importance of such events  
442 in structuring future coral populations in areas most heavily impacted by anthropogenic disturbances.

443

#### 444 **Acknowledgements**

445 This study was co-funded by the National Parks Board of Singapore (NParks), the Economic  
446 Development Board of Singapore (EDB) through the DHI-NTU Research Centre and Education Hub,  
447 and DHI Water & Environment (S), Singapore, under the project entitled ‘Impacts of ship-wake  
448 induced resuspension on corals and sea grass in Singapore’. The project was supported by the  
449 Experimental Marine and Ecology Laboratory at the National University of Singapore, and all field  
450 work was conducted under the research permit NP/RP 12-007 and with permission from the  
451 Singaporean Marine Port Authorities (MPA). We specially thank Rosa Poquita, Jason Tay, Dominic  
452 Soon Kiat Tan and Nova Olivia Pandi with their assistance with the field work and the experimental  
453 setup, and Karin Cooper for her invaluable comments.

454

#### 455 **References**

- 456 Abdel-Salam H, Porter JW (1988) Physiological effects of sediment rejection on photosynthesis and  
457 respiration in three Caribbean reef corals. Proc Proceedings Sixth International Coral Reef  
458 Symposium Australia  
459 Anthony KRN (2000) Enhanced particle feeding capacity of corals on turbid reefs (Great Barrier  
460 Reef). *Coral Reefs* 19:50-67  
461 Anthony KRN, Connolly SR (2004) Environmental limits to growth: Physiological niche boundaries of  
462 corals along turbidity:light gradients. *Oecologia* 141:373-384  
463 Anthony KRN, Connolly SR (2007) Bleaching, energetics, and coral mortality risk: Effects of  
464 temperature, light, and sediment regime. *Limnol. Oceanogr.* 52:716-726  
465 Anthony KRN, Fabricius K (2000) Shifting roles of heterotrophy and autotrophy in coral energetics  
466 under varying turbidity *Journal of Experimental Marine Biology and Ecology* 252:221-253  
467 Anthony KRN, Hoegh-Guldberg O (2003) Kinetics of photoacclimatization in corals. *Oecologia*  
468 134:23-31  
469 Bastidas C, Bone D, Garcia EM (1999) Sedimentation rates and metal content of sediments in a  
470 Venezuelan coral reef. *Marine Pollution Bulletin* 38:16-24  
471 Beer S, Vilenkin B, Weil A, Veste M, Susel, Eshel A (1988) Measuring photosynthetic rates in  
472 seagrasses by pulse amplitude modulated (PAM) fluorometry. *Marine Ecology Progress*  
473 *Series* 174:293-300

474 Brown BE, Ambarsari I, Warner ME, Fitt WK, Dunne RP, Gibb SW, Cummings DG (1999) Diurnal  
475 changes in photochemical efficiency and xanthophyll concentrations in shallow water reef  
476 corals : evidence for photoinhibition and photoprotection. *Coral Reefs* 18:99-105  
477 Brown BE, Bythell JC (2005) Perspectives on mucus secretion in reef corals. *Marine Ecology*  
478 *Progress Series* 296:291-309  
479 Browne NK (2012) Spatial and temporal variations in coral growth on an inshore turbid reef  
480 subjected to multiple disturbance events. *Marine Environmental Research* 77:71-83  
481 Browne NK, Smithers SG, Perry CT (2010) Geomorphology and community structure of Middle  
482 Reef, central Great Barrier Reef, Australia: an inner-shelf turbid zone reef subjected to  
483 episodic mortality events. *Coral Reefs* 29:683-689  
484 Browne NK, Smithers SG, Perry CT (2013) Spatial and temporal variations in turbidity on two  
485 inshore turbid reefs on the Great Barrier Reef, Australia. *Coral Reefs* 32:195-210  
486 Chan LT (1980) A preliminary study of the effects of land reclamation on the marine fauna of  
487 Singapore, with particular reference to the hard corals (Scleractinians). Honours Thesis,  
488 National University of Singapore, Singapore  
489 Chou LM (1996) Response of Singapore reefs to land reclamation. *Galaxea* 13:85-92  
490 Cooper TF, Gilmour JP, Fabricius KE (2009) Bioindicators of changes in water quality on coral reefs:  
491 review and recommendations for monitoring programmes. *Coral Reefs* 28:589-606  
492 Cooper TF, Ulstrup KE, Dandan SS, Heyward AJ, Kuhl M, Muirhead A, O'Leary RA, ziersen BEF,  
493 Van Oppen MJ (2011) Niche specilisation of reef-building corals in the mesophotic zone:  
494 metabolic trade-offs between divergent Symbiodinium types. *Proceedings of the Royal*  
495 *Society B* 278: 1840-1850  
496 Cortes, N. J, Risk MJ (1985) A reef under siltation stress: Cahuita, Costa Rica. *Bulletin of Marine*  
497 *Science* 36:339-356  
498 Crabbe JC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from  
499 fringing reefs of Sulawesi, Indonesia. *Coral Reefs* 24:437-441  
500 DeVantier LM, De'ath G, Turak E, Done T, Fabricius KE (2006) Species richness and community  
501 structure of reef building corals on the near shore reefs of the Great Barrier Reef. *Coral Reefs*  
502 25:329-340  
503 Dikou A, van Woesik R (2006) Survival under chronic stress from sediment load: Spatial patterns of  
504 hard coral communities in the southern islands of Singapore. *Marine Pollution Bulletin*  
505 52:1340-1354  
506 Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, Reefs  
507 and reef zones. *American Zoologist* 39:66-79  
508 Done TJ, Turak E, Wakeford M, DeVantier L, McDonald A, Fisk D (2007) Decadal changes in  
509 turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? *Coral*  
510 *Reefs* 26:789-805  
511 Dubinsky Z, Falkowski PG, Porter JW, Muscatine L (1984) Absorption and utilization of radiant  
512 energy by light- and shade-adapted colonies of the hermatypic coral *Stylophora pistillata*.  
513 *Proc R Soc Lond B* 222:203-214  
514 Erfteimeijer PLA, Riegl B, Hoeksema BW, Todd P (2012) Environmental impacts of dredging and  
515 other sediment disturbances on corals: A review. *Marine Pollution Bulletin* 64:1737-1765  
516 Fabricius KE (2005) Effects of terrestrial run of on the ecology of corals and coral reefs: review and  
517 synthesis. *Marine Pollution Bulletin* 50:125-146  
518 Flores F, Hoogenboom MO, Smith LD, Cooper TF, Abrego D (2012) Chronic exposure of corals to  
519 fine sediments: lethal and sub-lethal impacts. *PLoS ONE* 7 (5): 37795  
520 Gelin M, Bokuniewicz H, Rapaglia J, Lwiza KMM (2013) Sediment resuspension by ship wakes in  
521 the Venice Lagoon. *Journal of Coastal Research* 29:8-17  
522 Glynn PW, Howard LS, Corcoran E, Freay AD (1984) The occurrence and toxicity of herbicides in  
523 reef-building corals. *Marine Pollution Bulletin* 15:370-374  
524 Hoitink AJF, Hoekstra P (2003) Hydrodynamic control of the supply of reworked terrigenous  
525 sediment to coral reefs in the Bay of Banten (NW Java, Indonesia). *Estuarine, Coastal and*  
526 *Shelf Science* 58:743-755  
527 Hoogenboom MO, Anthony KRN, Connolly SR (2006) Energetic cost of photoinhibition in corals.  
528 *Marine Ecology Progress Series* 313:1-12

529 Hoogenboom MO, Campbell DA, Beraud E, DeZeeuw K, Ferrier-Page` s C (2012) Effects of light,  
530 food availability and temperature stress on the function of photosystem II and photosystem I  
531 of coral symbionts. PLoS ONE 7:1-14

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

534 Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: The basics. Annual review  
535 of plant physiology and plant molecular biology 42:313-317

536 Lane DJW (1991) Growth of scleractinian corals on sediment-stressed reefs at Singapore. In: Alcala  
537 AC (ed). Proc Regional Symposium on Living Resources in Coastal Areas

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

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

543 Lindstrom MJ, Bates DM (1988) Newton-Raphson and EM algorithms for linear mixed-effects models  
544 for repeated-measures data. Journal of the American Statistical Association 83:1014-1022

545 Lou J, Ridd PV (1996) Wave-current bottom shear stresses and sediment resuspension in Cleveland  
546 Bay, Australia. Coastal Engineering 29:169-186

547 Lough JM, Barnes DJ (1997) Several centuries of variation in skeletal extension, density and  
548 calcification in massive *Porites* colonies from the Great Barrier Reef: A proxy for seawater  
549 temperature and a background of variability against which to identify unnatural change.  
550 Journal of Experimental Marine Biology and Ecology 211:29-67

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

553 Lui GCY, Setiawan W, Todd P, Erftemeijer PLA (2012) Among genotype variation for sediment  
554 rejection in the reef building coral *Diploastrea Heliopora* (Lamarck, 1816). The Raffles  
555 Bulletin of zoology 60:525-531

556 McClanahan TR, Oburu D (1997) Sedimentation effects on shallow coral communities in Kenya.  
557 Journal of Experimental Marine Biology and Ecology 209:103-122

558 Meesters EH, Hilterman M, Kardinall E, Keetman M, deVries M, Bak RPM (2001) Colony size-  
559 frequency distributions of scleractinian coral populations: spatial and interspecific variations.  
560 Marine Ecology Progress Series 209:43-54

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

564 Nicholls RJ, Wong PP, Burkett VR, Codignotto JO, Hay JE, McLean RF, Ragoonaden S, Woodroffe  
565 CD (2007) Coastal systems and low-lying areas. Climate Change 2007: Impacts, adaptation  
566 and vulnerability. In: M.L. Parry OFC, J.P. Palutikof, P.J. van der Linden and C.E. Hanson,  
567 Eds. (ed) Contribution of Working Group II to the Fourth Assessment Report of the  
568 Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK

569 Orpin AR, Ridd PV, Thomas S, Anthony KRN, Marshall P, Oliver J (2004) Natural turbidity  
570 variability and weather forecasts in risk management of anthropogenic sediment discharge  
571 near sensitive environments. Marine Pollution Bulletin 49:602-612

572 Pastorok RA, Bilyard GR (1985) Effects of sewage pollution on coral-reef communities. Marine  
573 Ecology Progress Series 21:175-189

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

576 Perry CT, Smithers SG, Johnson KG (2009) Long-term coral community records from Luggier Shoal  
577 on the terrigenous inner shelf of the central Great Barrier Reef, Australia. Coral Reefs 28:941-  
578 948

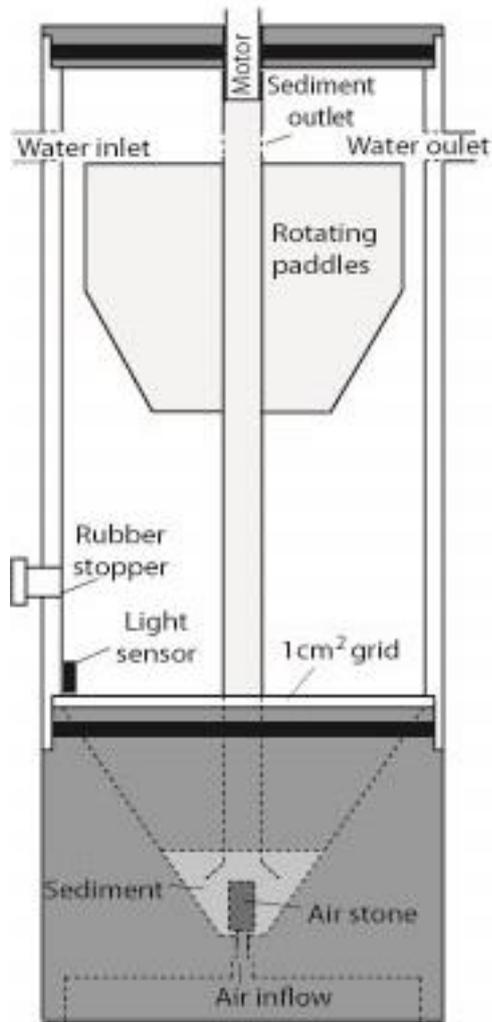
579 Philipp E, Fabricius K (2003) Photophysiological stress in scleractinian corals in response to short-  
580 term sedimentation. Journal of Experimental Marine Biology and Ecology 287:57-78

581 Piniak GA (2007) Effects of two sediment types on the fluorescence yield of two Hawaiian  
582 scleractinian corals. Marine Environmental Research 64:456-468

583 Piniak GA, Storlazzi CD (2008) Diurnal variability in turbidity and coral fluorescence on a fringing  
584 reef flat: Southern Molokai, Hawaii. *Estuarine, Coastal and Shelf Science* 77:56-64  
585 Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne  
586 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine*  
587 *Biology and Ecology* 186:259-275  
588 Rogers CS (1979) The effect of shading on coral reef structure and function. *Journal of Experimental*  
589 *Marine Biology and Ecology* 41:269-288  
590 Rogers CS (1983) Sublethal and lethal effects of Sediments applied to common Caribbean reef corals  
591 in the field. *Marine Pollution Bulletin* 14:378-382  
592 Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation *Marine Ecology*  
593 *Progress Series* 62:185-202  
594 Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. *Annual Review of*  
595 *Ecology and Systematics* 23:89-118  
596 Stafford-Smith MG (1993) Sediment-rejection efficiency of 22 species of Australian scleractinian  
597 corals. *Marine Biology* 115:229-243  
598 Stafford-Smith MG, Ormond RFG (1992) Sediment rejection mechanisms of 42 scleractinian corals.  
599 *Australian Journal of Marine and Freshwater Sciences* 43:638-705  
600 Te FT (2001) Responses of Hawaiian scleractinian corals to different levels of terrestrial and  
601 carbonate sediment. Ph.D. thesis, University of Hawaii,  
602 Telesnicki GJ, Goldberg WM (1995) Effects of turbidity of photosynthesis and respiration of two  
603 South Florida reef coral species. *Bulletin of Marine Science* 57:527-539  
604 Thomas S, Ridd PV, G D (2003) Turbidity regimes over fringing coral reefs near a mining site at  
605 Lihir Island, Papua New Guinea. *Marine Pollution Bulletin* 46:1006-1014  
606 Todd P, Ong X, Chou L (2010) Impacts of pollution on marine life in Southeast Asia. *Biodiversity*  
607 *and Conservation* 19:1063-1082  
608 Todd P, Sanderson P, Chou L (2001) Morphological variation in the polyps of the scleractinian coral  
609 *Favia speciosa* (Dana) around Sinapore. *Hydrobiologia* 444:227-235  
610 Todd PA (2008) Morphological plasticity in scleractinian corals. *Biological Reviews* 83:315-337  
611 Todd PA, Sidle RC, Lewin-Koh NJI (2003) An aquarium experiment for identifying the physical  
612 factors inducing morphological change in two massive scleractinian corals. *Journal of*  
613 *Experimental Marine Biology and Ecology* 299:97-113  
614 Ulstrup K, Ralph P, Larkum A, Kühl M (2006) Intra-colonial variability in light acclimation of  
615 zooxanthellae in coral tissues of *Pocillopora damicornis*. *Marine Biology* 149:1325-1335  
616 Warner ME, Chilcoat GC, McFarland FK, Fitt WK (2002) Seasonal fluctuations in photosynthetic  
617 capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef-building coral  
618 *Montastraea*. *Mar Biol* 141:31-38  
619 Weber M, de Beer D, Lott C, Polerecky L, Kohls K, Abed R, Ferdelman T, Fabricius KE (2012)  
620 Mechanisms of damage to corals exposed to sedimentation. *PNAS* 109:E1558-E1567  
621 Weber M, Lott C, Fabricius KE (2006) Sedimentation stress in a scleractinian coral exposed to  
622 terrestrial and marine sediments with contrasting physical, organic and geochemical  
623 properties. *Journal of Experimental Marine Biology and Ecology* 336:18-32  
624 Winters G, Loya Y, Beer S (2006) In situ measured seasonal variations in Fv/Fm of two common Red  
625 Sea corals. *Coral Reefs* 25:593-598  
626 Winters G, Loya Y, Rottgers R, Beer S (2003) Photoinhibition in shallow-water colonies of the coral  
627 *Stylophora pistillata* as measured in situ. *Limnol Oceanogr*, 48:1388-1393  
628 Wolanski E, Fabricius KE, Cooper TF, Humphrey C (2008) Wet season fine sediment dynamics on  
629 the inner shelf of the Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 77:755-762  
630 Wolanski E, Gibbs R (1992) Resuspension and clearing of dredge spoils after dredging, Cleveland  
631 Bay, Australia. *Water Environment Research* 64:910-914

632

633



635

636 Figure 1: Schematic diagram of the mVORT chamber illustrating position of DC motor, rotating  
637 paddles, sediment well, light sensor and the position of the grid on which corals were placed.

638

639

640

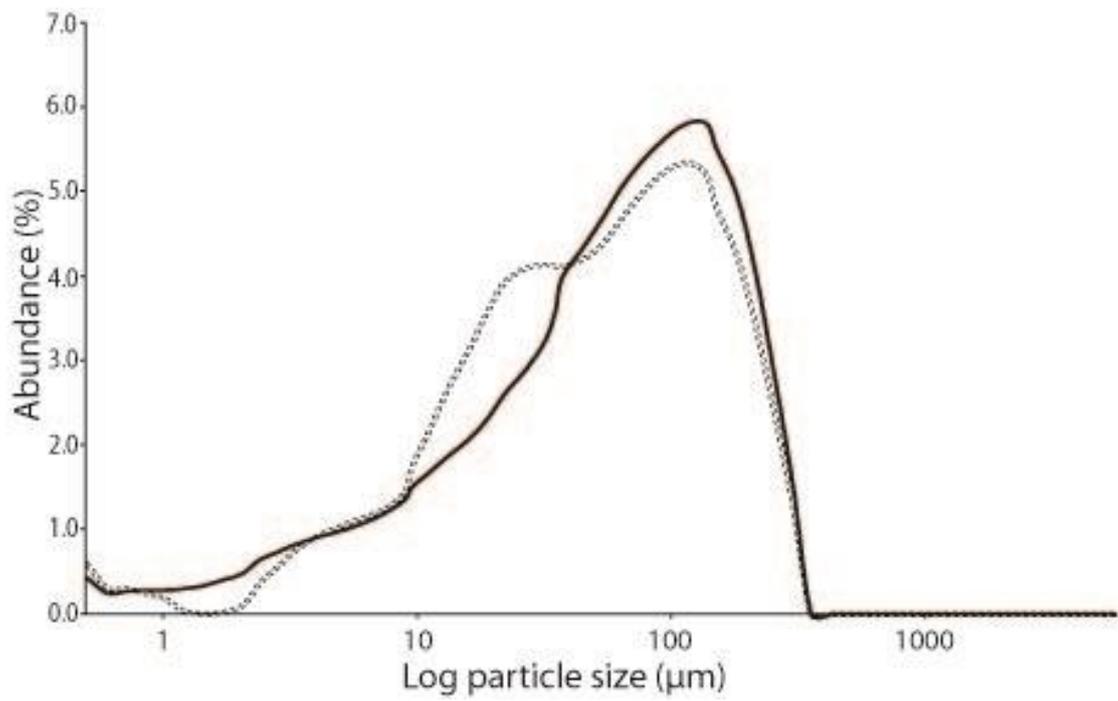
641

642

643

644

645



646

647 Figure 2: The sediment profile of sediments collected from the sediment trap at Labrador (black line)

648 and the silica carbide profile (dashed line).

649

650

651

652

653

654

655

656

657

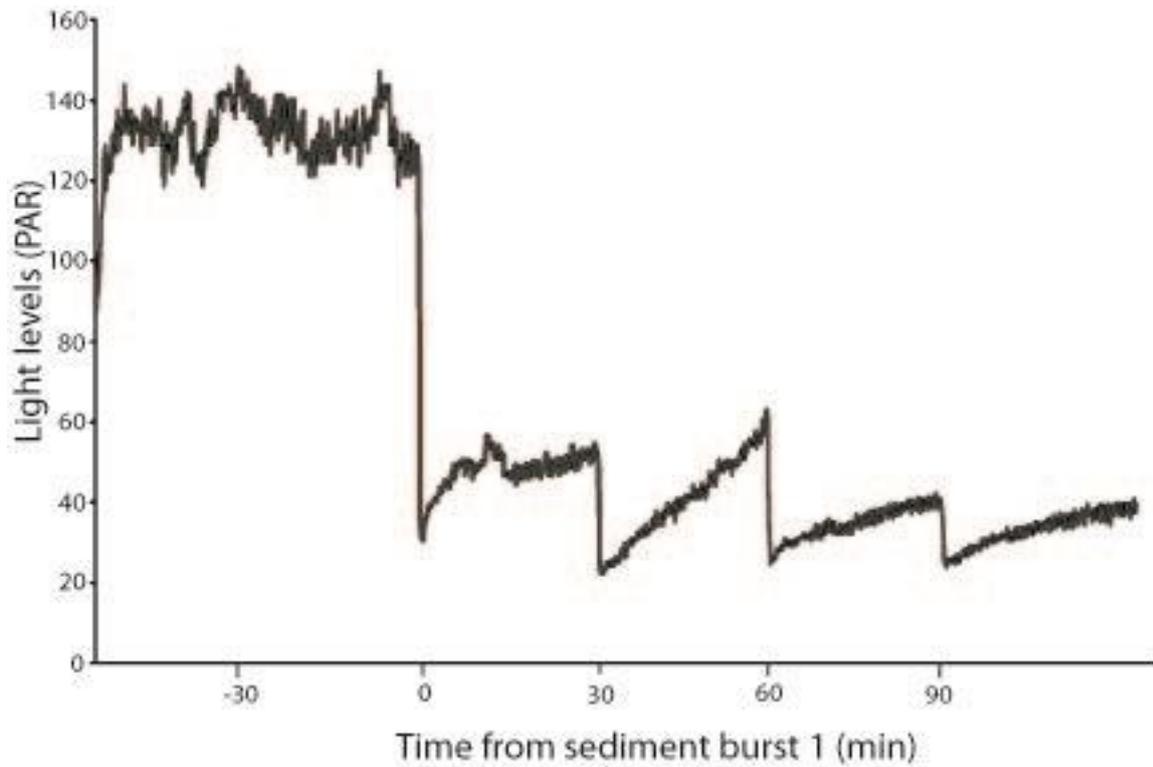
658

659

660

661

662



663

664 Figure 3: Graphic illustration of the light levels (PAR) inside a chamber during a high turbidity event.

665 Light levels decline at 0 min when the first air burst is triggered pushing sediments up the central

666 column and into the water. As sediments settle, light levels slowly increase until the second air burst

667 at 30 min. The average light levels from 0 min to 120 min was 39 PAR.

668

669

670

671

672

673

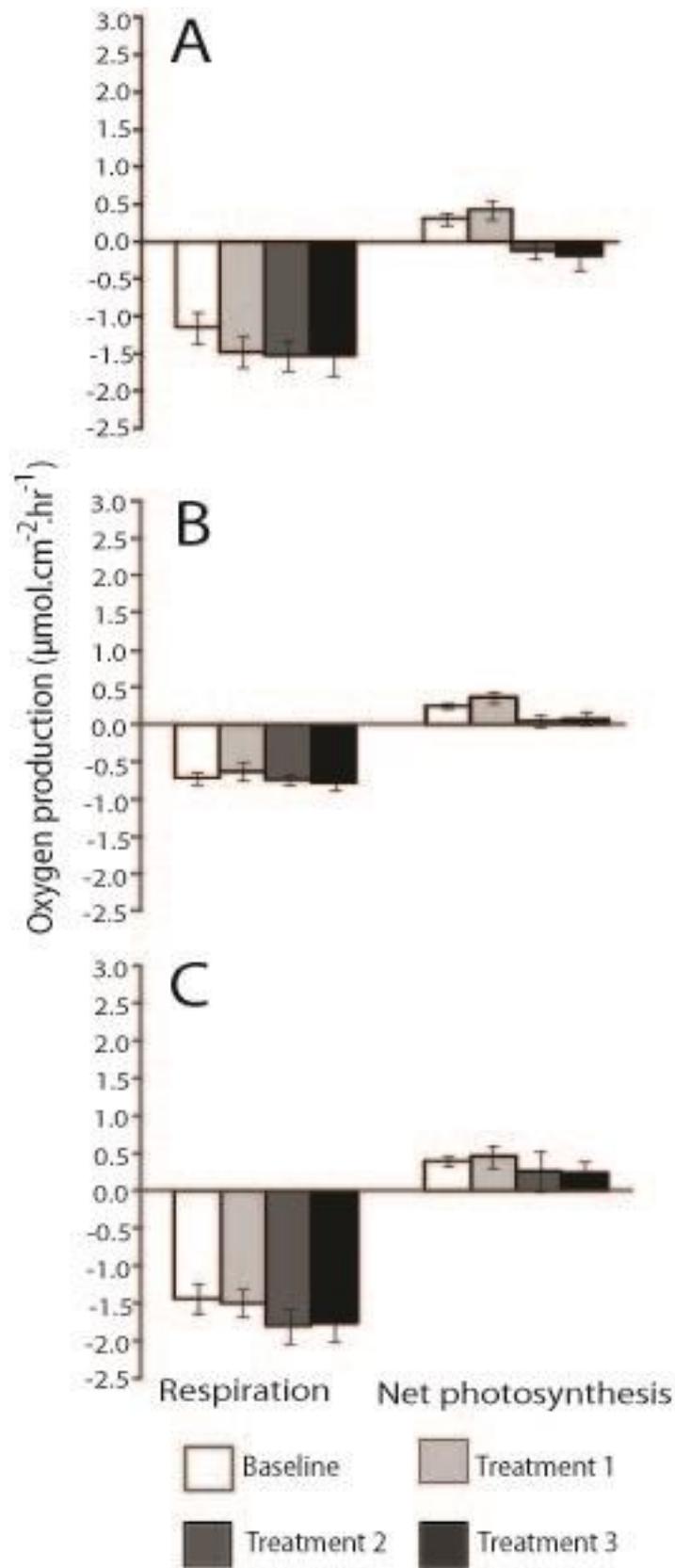
674

675

676

677

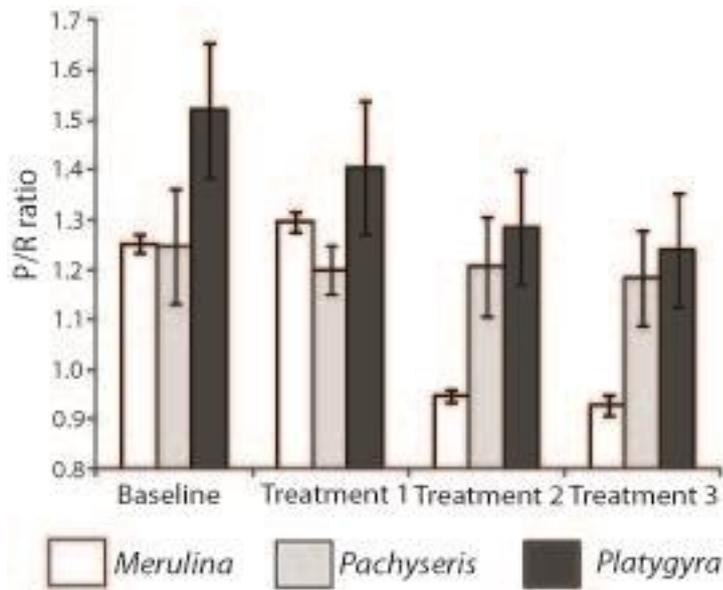
678



679

680 Figure 4: The respiration rate and net photosynthetic rate during all treatments for (A) *Merulina*, (B)

681 *Pachyseris*, and (C) *Platygyra*. Standard errors are represented by error bars (n=24).



682

683

Figure 5: The P/R ratio for all coral species during baseline conditions and all sediment resuspension

684

treatments. Standard errors are represented by error bars (n=24).

685

686

687

688

689

690

691

692

693

694

695

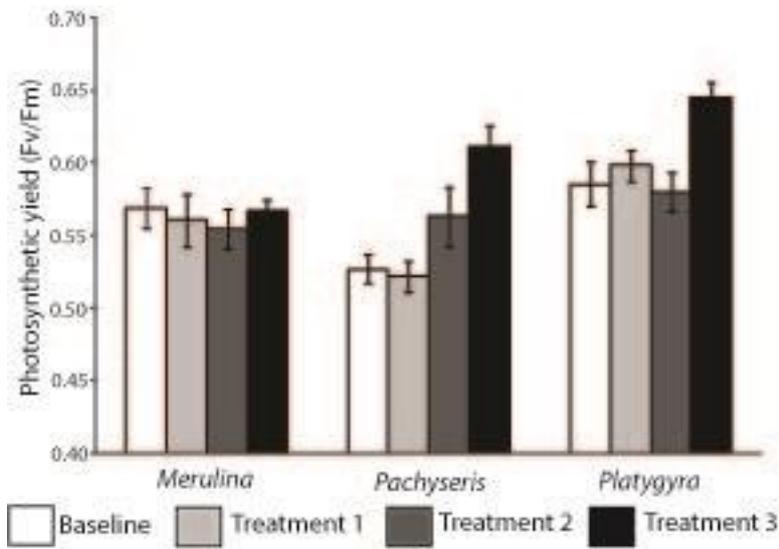
696

697

698

699

700



701

702 Figure 6: The maximum photosynthetic yield (Fv/Fm) for all coral species during baseline conditions

703 and all sediment resuspension treatments. Standard errors are represented by error bars (n=24).

704

705

706

707

708

709

710

711

712

713

714

715

716

717

718

719

720 Table 1: Mean values and standard errors (SE) for respiration, photosynthesis, P/R values and the  
 721 maximum quantum yield for each coral species following two hours of each treatment.

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

722

723

724 Table 2: Results from the Mixed Model with treatment. The type III fixed effects demonstrate if there is a significant effect of treatment on each photo-physiological variable  
 725 (respiration, photosynthesis, P/R ratio, yield) for each species. The estimate of fixed effects demonstrate between which treatments (weeks) the effects were most significant  
 726 e.g. *Merulina* respiration rate following treatment 4 is significantly different (p=0.004) from treatment 1 (baseline conditions) but not treatment 2 and 3. This suggests that the  
 727 respiration rates during all the sediment treatments are significantly different from the baseline, but not significantly different between sediment treatments.

Species	Variable	Type III Fixed Effects						Estimates of Fixed Effects					
		BIC	Source	Numerator df	Denominator df	F	Sig	Parameter	Estimate	SE	df	t	Sig
<i>Merulina</i>	Respiration	137.76	Intercept	1	17	129.015	0.000	Intercept	1.576	0.176	17	-8.893	0
			Treatment	3	17	4.821	<b>0.013</b>	Treatment 1	-0.328	0.1	17	3.297	<b>0.004</b>
			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	0										
	Net photosynthesis	113.44	Intercept	1	17	1.453	0.245	Intercept	-0.194	0.132	17	-1.47	0.16
			Treatment	3	17	7.561	<b>0.002</b>	Treatment 1	0.45	0.151	17	2.98	<b>0.008</b>
			Treatment 2	0.61	0.158	17	3.871	<b>0.001</b>					
			Treatment 3	0.012	0.115	17	0.1	0.921					
	Treatment 4	0	0										
	P/R	77.39	Intercept	1	17	485.214	0.000	Intercept	0.927	0.083	17	11.1	0
			Treatment	3	17	11.92	<b>0.000</b>	Treatment 1	0.323	0.083	17	3.902	<b>0.001</b>
			Treatment 2	0.372	0.124	17	2.995	<b>0.008</b>					
			Treatment 3	0.0097	0.066	17	0.148	0.884					
	Treatment 4	0											
	Yield	-155.79	Intercept	1	17	4791.05	0.000	Intercept	0.5668	0.0094	9	60.55	0
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	0											
<i>Pachyseris</i>	Respiration	99.068	Intercept	1	17	1.113.117	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	0										
	Net photosynthesis	61.46	Intercept	1	17	5.814	0.028	Intercept	0.107	0.083	17	1.282	0.22
			Treatment	3	17	10.82	<b>0.000</b>	Treatment 1	0.16	0.074	17	-0.237	<b>0.04</b>
			Treatment 2	0.298	0.057	17	5.247	<b>0.00</b>					

								Treatment 3	-0.059	0.059	17	-0.992	0.36
								Treatment 4	0	0			
	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				
	Yield	-137	Intercept	1	17	2114.252	0.000	Intercept	0.611	0.0152	9	40.17	0.00
			Treatment	3	17	10.58	<b>0.000</b>	Treatment 1	-0.074	0.0164	15	-4.53	<b>0.00</b>
								Treatment 2	-0.089	0.0179	11	-4.953	<b>0.00</b>
								Treatment 3	-0.047	0.0174	10	-2.73	<b>0.01</b>
								Treatment 4	0	0			
<i>Platygyra</i>	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			
	Net photosynthesis	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	<b>0.00</b>	Treatment 1	-0.05	0.02	15.00	-0.39	<b>0.01</b>
								Treatment 2	-0.05	0.02	11.00	-2.75	<b>0.01</b>
								Treatment 3	-0.07	0.02	10.00	-3.83	<b>0.00</b>
								Treatment 4	0.00	0.00			

728

729

730 Table 3: Results from Mixed Model analysis with species. The type III fixed effects demonstrate if there is a significant difference between coral species responses for each  
 731 of the photo-physiological variables, and the estimates of fixed effects demonstrate between which species effects of the treatments most significant e.g. *Platygyra* respiration  
 732 rate is significantly different from *Pachyseris* (p=0.00) but not *Merulina*.

Variable	Type III Fixed Effects						Estimates of Fixed Effects						
	BIC	Source	Numerator df	Denominator df	F	Sig	Parameter	Estimate	SE	df	t	Sig	
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	<b>0.00</b>	<i>Merulina</i>	0.18	0.23	143.18	0.79	0.43	
								<i>Pachyseris</i>	0.98	0.23	143.18	4.26	<b>0.00</b>
								<i>Platygyra</i>	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	<i>Merulina</i>	-0.44	0.18	148.80	-2.47	<b>0.02</b>	
								<i>Pachyseris</i>	-1.15	0.18	151.22	-0.85	0.40
								<i>Platygyra</i>	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	<i>Merulina</i>	-0.31	0.16	184.45	-1.98	<b>0.05</b>	
								<i>Pachyseris</i>	-0.05	0.16	185.71	-0.32	0.75
								<i>Platygyra</i>	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	<b>0.00</b>	<i>Merulina</i>	-0.08	0.02	172.95	-3.99	<b>0.00</b>	
								<i>Pachyseris</i>	-0.03	0.02	172.95	-1.76	<b>0.08</b>
								<i>Platygyra</i>	0.00	0.00			

733