

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

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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 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 (Erfteemeijer 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⁻¹ (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⁻¹.

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⁻¹) 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⁻¹ 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⁻¹ 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, 12×9 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 (~ 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 μm), but
152 the median particle varied from 50 to 80 μm at Labrador, from 80 to 100 μm at Hantu and 60 to 100
153 μm 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 μm to 300 μm , and had a median particle size of 60 μm (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⁻¹ (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 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 ± 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 μm 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 O₂ 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 ± 0.13 to -1.52 ± 0.18 $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$; *Pachyseris* respiration rates increased
267 from -0.72 ± 0.07 to -0.78 ± 0.11 $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$; and *Platygyra* respiration rates increased from -1.44
268 ± 0.21 to -1.76 ± 0.25 $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ (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 ± 0.07
277 to -0.19 ± 0.13 $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$; *Pachyseris* declined from 0.25 ± 0.04 to 0.08 ± 0.08 $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$;
278 and *Platygyra* declined from 0.41 ± 0.07 to 0.25 ± 0.14 $\mu\text{mol.cm}^{-2}.\text{hr}^{-1}$ 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 ± 0.11 to 1.18 ± 0.1 and from 1.52 ± 0.14 to 1.24 ± 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 ± 0.02 during the low sediment stress event to 0.95 ± 0.01 during the medium sediment
287 stress event. The P/R ratio fell further during the high sediment stress event (0.93 ± 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 ± 0.01 to 0.56 ± 0.01 ($p = 0.00$) between the low and medium
292 sediment stress events, and from 0.56 ± 0.01 to 0.61 ± 0.02 ($p = 0.01$) between the medium and high
293 sediment stress events, and the yield for *Platygyra* increased from 0.58 ± 0.01 to 0.65 ± 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 ± 0.16) was significantly
300 lower than both *Pachyseris* (1.18 ± 0.16) and *Platygyra* (1.24 ± 0.11), and the maximum
301 photosynthetic yield of *Platygyra* (0.65 ± 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°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⁻².hr⁻¹) 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⁻¹.cm⁻²)
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

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454

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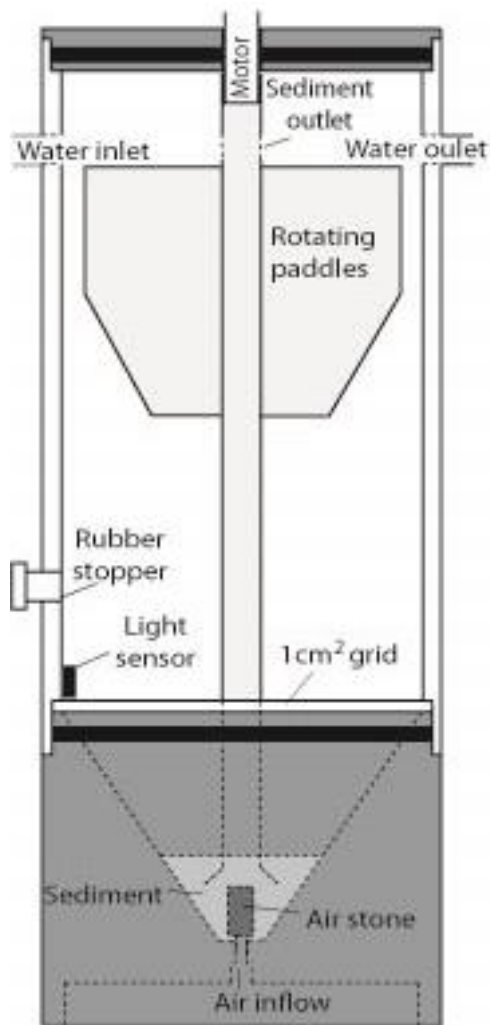
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636 Figure 1: Schematic diagram of the mVORT chamber illustrating position of DC motor, rotating
637 paddles, sediment well, light sensor and the position of the grid on which corals were placed.

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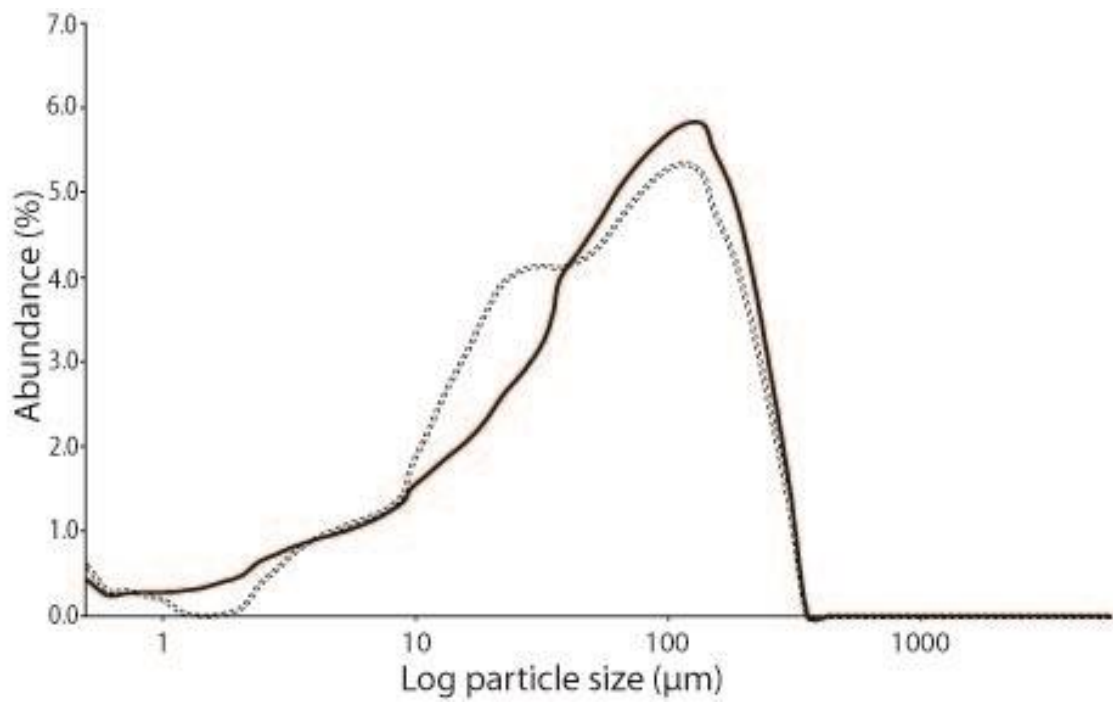
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647 Figure 2: The sediment profile of sediments collected from the sediment trap at Labrador (black line)

648 and the silica carbide profile (dashed line).

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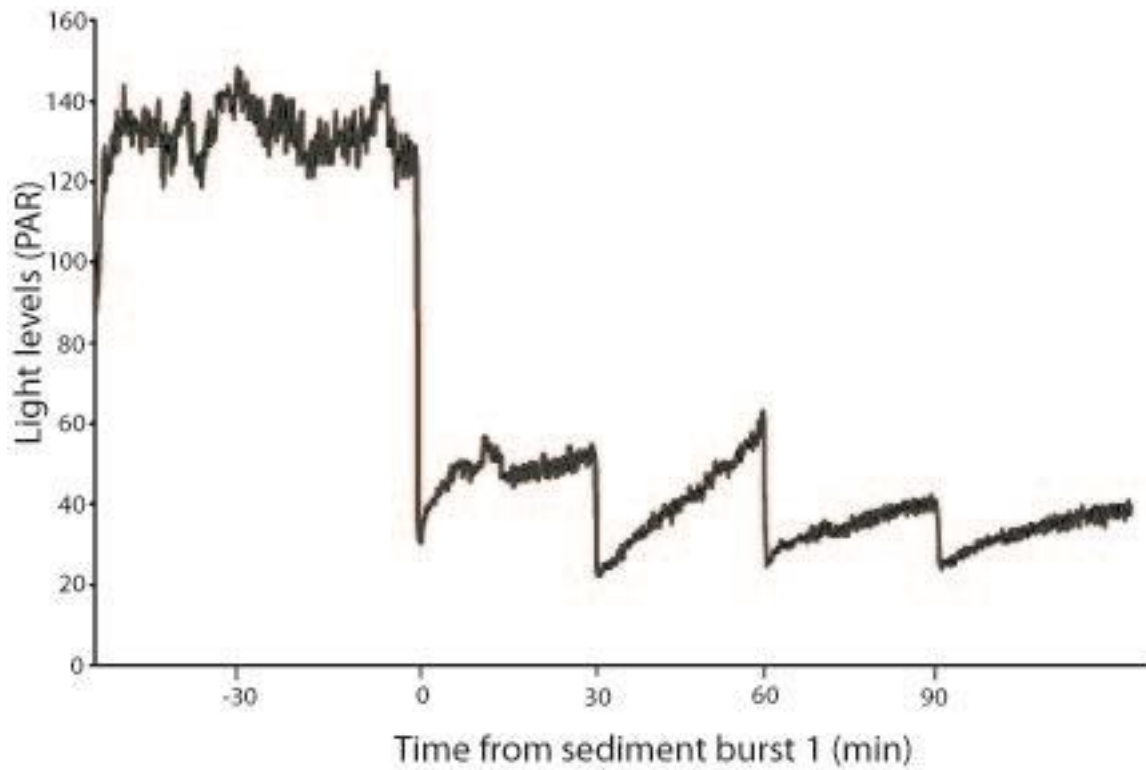
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664 Figure 3: Graphic illustration of the light levels (PAR) inside a chamber during a high turbidity event.

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.

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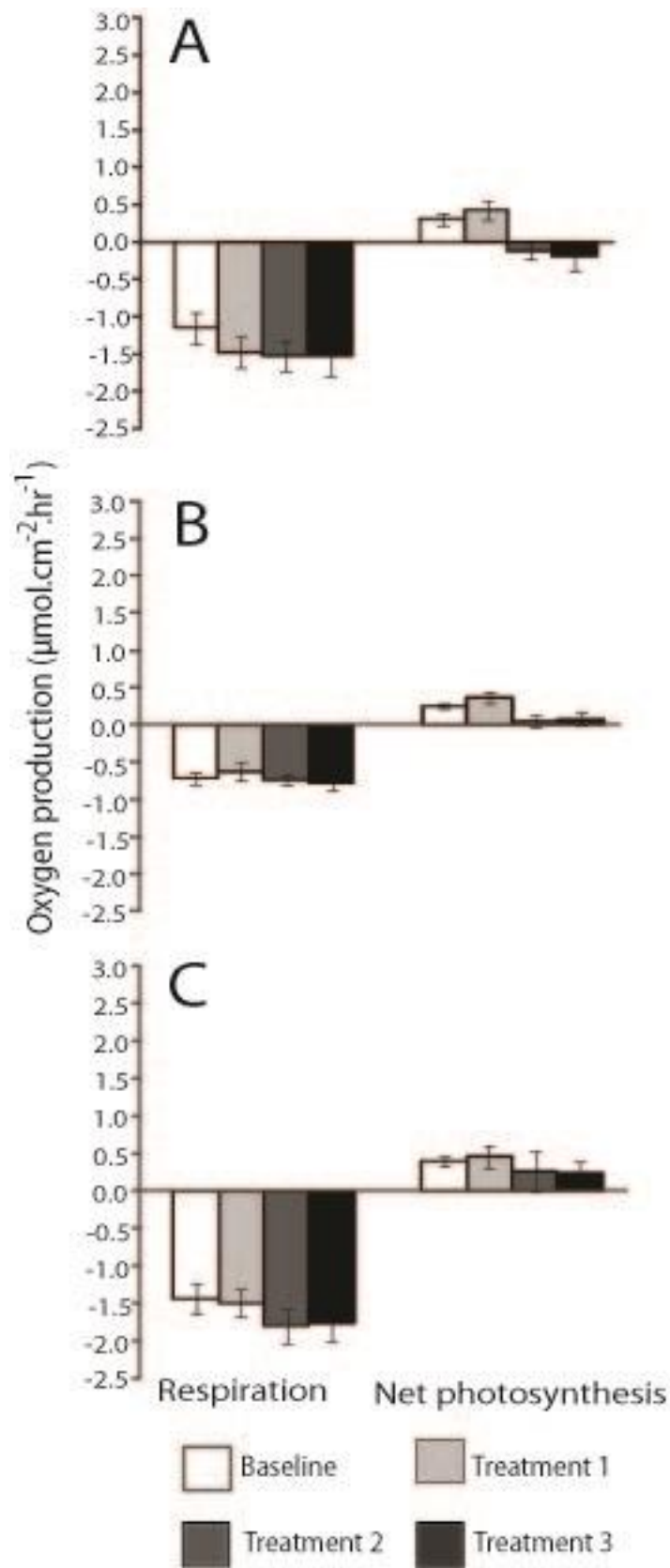
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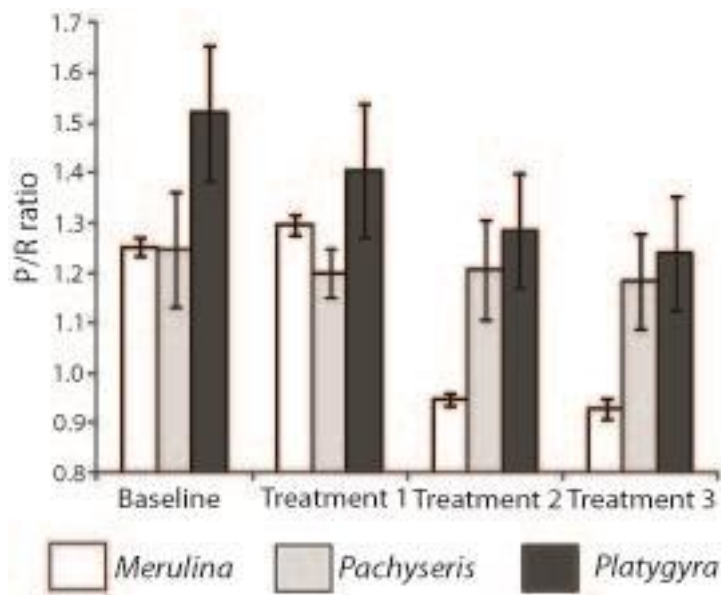
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680 Figure 4: The respiration rate and net photosynthetic rate during all treatments for (A) *Merulina*, (B)

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



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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).

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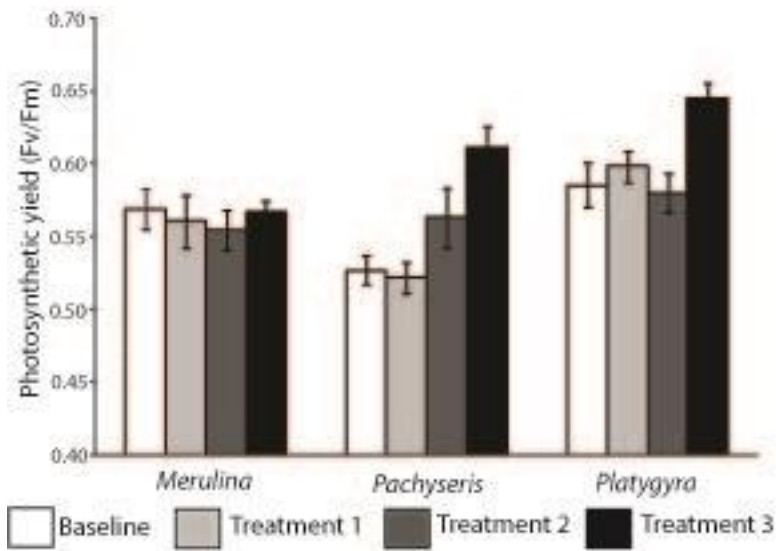
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702 Figure 6: The maximum photosynthetic yield (Fv/Fm) for all coral species during baseline conditions

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

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

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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	0.013	Treatment 1	-0.328	0.1	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	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	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	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	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											
	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	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	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	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	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	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			

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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	0.00	<i>Merulina</i>	0.18	0.23	143.18	0.79	0.43	
								<i>Pachyseris</i>	0.98	0.23	143.18	4.26	0.00
								<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	0.02	
								<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	0.05	
								<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	0.00	<i>Merulina</i>	-0.08	0.02	172.95	-3.99	0.00	
								<i>Pachyseris</i>	-0.03	0.02	172.95	-1.76	0.08
								<i>Platygyra</i>	0.00	0.00			

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