

1 **Recreating pulsed turbidity events to determine coral sediment thresholds for active**
2 **management**

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22 Abstract

23 Active management of anthropogenically driven sediment resuspension events near coral reefs relies
24 on an accurate assessment of coral thresholds to both suspended and deposited sediments. Yet the
25 range of coral responses to sediments both within and among species has limited our ability to
26 determine representative threshold values. This study reviews information available on coral
27 physiological responses to a range of sediment loads at varying time frames and provides a novel
28 approach to assess coral thresholds to suspended and deposited sediments. The new approach
29 replicates natural turbidity regimes by creating pulsed turbidity events at two environmentally realistic
30 levels (moderate = $\sim 50 \text{ mg.l}^{-1}$, peaks at 100 mg.l^{-1} ; severe = $\sim 100 \text{ mg.l}^{-1}$, peaks at 250 mg.l^{-1}). Corals
31 (*Merulina ampliata*, *Pachyseris speciosa*, *Platygyra sinensis*) were subjected to two exposure
32 regimes: pulsed turbidity events for four weeks followed by two months of recovery (constant regime)
33 or pulsed turbidity events every other week followed by one month of recovery (periodic regime).
34 Coral thresholds were greater than commonly used estimates with little to no effect on corals at
35 moderate sediment levels. At extreme sediment levels, species morphological differences were
36 potentially key determinants of coral survival. The periodic exposure regime was less detrimental to
37 all coral species than the constant exposure regime as demonstrated by elevated yields and lower
38 tissue mortality rates. To improve knowledge on coral-sediment threshold values, research needs to
39 expand to incorporate a broader range of species and exposure regimes. Realistic threshold values
40 combined with modelling efforts would improve prediction of reef health and enable managers to
41 react to declines in health before coral mortality occurs.

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49 **1.0 Introduction**

50 Corals in inshore turbid waters are frequently exposed to pulsed turbidity events created by wind-
51 driven waves or tidal currents that resuspend sea floor sediments and redistribute sediments over coral
52 reefs (Browne et al., 2012). The frequency, severity and duration of these events are highly variable,
53 but peaks in turbidity may reach $>150 \text{ mg l}^{-1}$ and last several hours (Larcombe et al., 2001; Wolanski
54 et al., 2008; Browne et al., 2013a). Turbidity levels may also fluctuate over corals reefs due to
55 anthropogenic activities such as coastal development and dredging, both of which can lead to
56 significant increases in suspended sediment loads and pulses of extreme turbidity ($>500 \text{ mg l}^{-1}$;
57 Wolanski and Gibbs, 1992; Thomas et al., 2003). These pulses of acute sediment exposure that often
58 occur within inshore regions characterised by chronically elevated turbidity regimes may lead to long-
59 term declines in coral cover, diversity and reef stability.

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61 Given the adverse long-term effects of acute pulsed turbidity events on coral reefs, management of
62 activities that result in elevated exposure to sediments is critical. Successful management relies on an
63 adequate understanding of the coral reef ecosystem and how changes in the environment will impact
64 its function. However, coral reefs are complex systems whose physical and biological parameters
65 vary both spatially and temporally (Storlazzi et al., 2010; Browne et al., 2012; Falter et al., 2013).
66 Different coral species have variable responses to the same environmental conditions, and even
67 individuals of the same species on different reefs may respond differently due differences in natural
68 background conditions between reefs (Anthony and Larcombe, 2000). For example, corals frequently
69 exposed to a high natural background turbidity regime typically show elevated tolerances to sediments
70 than their counterparts from clear-water reefs (Anthony, 2000). Coral responses may also vary
71 depending on the presence of additional stressors such as elevated temperatures or nutrients which
72 may lower coral thresholds (Weber et al., 2006; Anthony et al., 2011). At present, poor understanding
73 of coral responses to sediments has resulted in inappropriate management of activities, such as
74 dredging, that resuspended and redistribute sediments. Inadequate management has led to both
75 significant damage to coral reefs due to limited consideration for their health (e.g. Pollock et al.,
76 2014) as well as overly conservative practices resulting in significant delays and project costs

77 (Hanley, 2011). Following a review of the environmental impacts of dredging on corals by
78 Erftemeijer et al (2012), the authors recommend the need for improving current predictions of
79 sediment impacts on corals through both a critical evaluation of previous dredging projects and
80 targeted experimental research.

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82 A central component to improving management of practices that lead to acute sediment events, is a
83 greater understanding of coral physiological and morphological responses to sediments at varying
84 intensities and durations. During acute sediment resuspension events, elevated turbidity levels limit
85 light availability and reduce coral photosynthesis and energy production rates (Anthony and Connolly,
86 2004). Many corals are, however, able to acclimate to low light conditions by increasing the
87 concentration of photosynthetic compounds and/or symbiont densities (Rogers, 1979; Dubinsky et al.,
88 1984) or by switching from autotrophy to heterotrophy (Anthony and Fabricius, 2000), thereby
89 alleviating some of the photophysiological stress associated with reduced light. As sediments settle
90 out of the water column onto corals, coral respiration rates may increase as corals expend energy
91 during active sediment removal. As the ratio of photosynthesis to respiration (P/R ratio) declines,
92 energy availability for growth, reproduction and coral immunity also declines (Telesnicki and
93 Goldberg, 1995; Anthony and Hoegh-Guldberg, 2003). However, the process of sediment removal is
94 crucial for corals to prevent tissue necrosis that occurs underneath deposited sediments (Lasker,
95 1980). The ability of corals to acclimate to low light conditions and/or to rapidly remove sediments
96 varies among coral species and is related to their photo-physiology as well as their morphology
97 (Stafford-Smith, 1993; Riegl, 1995). As such, coral sediment thresholds vary among species and
98 individuals of the same species. Despite extensive research into coral and sediment interactions, there
99 remains a considerable lack of understanding on coral responses to sediments during events of
100 varying intensity and duration, and how species specific sediment tolerances translate through to the
101 community scale.

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103 Coral thresholds to sediments are not static, but will typically decline over the duration of sediment
104 exposure (Philipp and Fabricius, 2003; Piniak, 2007; Negri et al., 2009). Coral responses to

105 sediments have been evaluated both in the field and laboratory using a range of experimental setups.
106 Yet, there have been several inconsistencies between field and laboratory observations with higher
107 thresholds typically observed for longer periods in the laboratory. These inconsistencies may, in part,
108 be due to the fact that in the laboratory all other environmental conditions can be maintained at non-
109 stressful levels. In contrast, coral responses to sediments in situ will potentially change due to
110 fluctuations in temperature, salinity and nutrients. Ex situ studies may, therefore, give a more
111 accurate account of coral responses to sediments, but only if an adequate experimental design has
112 been used and corals are exposed to environmentally realistic conditions (Flores et al., 2012).
113 Inconsistencies may also be due to the limited effort made to recreate pulsed turbidity events, a key
114 characteristic of both natural and anthropogenic turbidity events. These pulses may potentially allow
115 for coral recovery and enable corals to endure greater levels of sediment exposure for longer time
116 periods. Longer recovery periods in between disturbance events are considered vital to the long-term
117 sustainability of reef ecosystems (Nystrom et al., 2000), however, there has been limited research as
118 to how such recovery periods may influence coral sediment thresholds during longer periods of
119 sediment exposure such as during dredging operations that last several weeks.

120 Here, a laboratory experiment is devised which recreated pulsed turbidity events at two
121 environmentally realistic intensities (moderate = $\sim 50 \text{ mg.l}^{-1}$, peaks at 100 mg.l^{-1} ; severe = $\sim 100 \text{ mg.l}^{-1}$,
122 peaks at 250 mg.l^{-1}) for four weeks followed by two months of recovery or every other week followed
123 by one month of recovery. It was anticipated that this cycle of weekly periodic exposure at both
124 severity levels would alleviate some of the sediment stress, thereby allowing corals to survive for
125 longer time periods under the same sedimentary regime. During days of sediment exposure, corals
126 were exposed to 6 pulses of turbidity, each lasting approximately 2 hours. Changes in coral photo-
127 physiology (maximum yield, respiration, photosynthesis) and rates in tissue mortality were monitored
128 either weekly or monthly during the 11 week experiment. Specifically, the objectives were to 1).
129 Determine coral thresholds to turbidity and sedimentation under realistic pulsed exposure regimes, 2).
130 Assess differences in coral species physiological responses to sediment stress, and 3). Assess the
131 influence of constant versus periodic sediment exposure on coral responses to sediments.

132

133 **2.0 Materials and methods**

134 **2.1 Study species and sampling sites**

135 Three turbid water corals, common to the Indo-pacific, were selected for the study: *Merulina ampliata*
136 and *Pachyseris speciosa*, two plate corals, and *Platygyra sinensis*, a massive coral. Eight coral
137 colonies from each species were collected from Singapore's inshore turbid water reef slopes at 3 m
138 depth (Labrador Park: N 1.26636, E 103.80015, Kusu Island: N 1.22838, E 103.85525, Palau Hantu:
139 N 1.22640, E 103.74675). Turbidity and light levels on the reef slope (at 3 m LAT) typically range
140 from 1 to 20 mg l⁻¹, peaking at >150 mg l⁻¹ during resuspension events, and <50 to 400 PAR
141 respectively (Browne et al., 2015). Sedimentation rates throughout the year are highly variable, but
142 typically range from 2 to 15 mg cm⁻² day⁻¹ at Kusu Island and Palau Hantu, and from 5 to 40 mg cm⁻²
143 day⁻¹ at Labrador Park (Browne et al., 2015).

144 Three coral fragments (5x5 cm) were obtained from each coral colony (N=24 for each species, N= 72
145 fragments) using a chisel. Each fragment was mounted onto a plastic grid using underwater epoxy
146 resin (Epoxxy, UK) and transported to the aquarium facility at the Tropical Marine Science Institute
147 (TMSI) on St. Johns Island. Fragments were allowed to recover for at least 8 weeks in 200 L indoor
148 flow through tanks prior to the start of the experiment (water temperature ~29°C, salinity 30 ppt,
149 photoperiod 10 hr:14hr light:dark cycle at 120 to 140 μmol photons m⁻² s⁻¹).

150

151 **2.2 Mesocosm chamber**

152 Corals were exposed to a variable sedimentary regime in cylindrical mesocosm chambers (9 L).
153 These chambers are mini versions of the 300 L Vortex resuspension Tank (VoRT) described by
154 Davies et al. (2009), and were successfully used to determine the influence of acute sediment
155 resuspension events on corals by Browne et al. (2014). Water flow in the chamber is driven by a
156 motorised central paddle (~65 revolutions per minute to create a flow rate of 5-10 cm s⁻¹) attached to a
157 hollow vertical shaft. The shaft has holes at the top of the chamber and doubles up as an air-lift to
158 resuspend particulate matter that has collected in the tapered well at the bottom of the chamber. The

159 rotating paddles dissipate sediments through the water column above the coral fragments positioned
160 on a plastic grid directly above the sediment well. The amount of sediment particles forced up the
161 central tube was controlled by the duration (seconds) of air that was pumped through the air lift.

162

163 The mesocosm chambers were placed into 300 L water baths through which sea water flowed at a
164 constant rate of 5 L min⁻¹ (water temperature ~29°C). A light source (four T5 HO aquarium bulbs
165 which provide the essential actinic blue light that corals require) was suspended 75 cm above the
166 corals, and delivered between 120-140 μmol photons m⁻² s⁻¹, equivalent to mean daily PAR measured
167 at collection sites (Browne et al., 2015). In each mVORT, sediment (~25 g) was placed at the bottom
168 of the well, and the tanks were slowly filled with sea water, through the side water inlet valve, from a
169 central reservoir tank. Motors that were used to turn the paddles, were controlled by via
170 programmable pulse width modulation (PWM) from a central microcontroller which enabled the user
171 to set the motor speed between 1 to 65 revolutions per minute (rpm). Previous tests verified that 20
172 rpm within a 20 cm diameter cylindrical tank generated a flow rate of approximately 10 cm s⁻¹, at the
173 midpoint between the centre and outer edge of the tank. Current speeds at reefs sites are typically <5
174 cm s⁻¹, but rise to 10-15 cm s⁻¹ during resuspension events (N.K. Browne, unpublished data).

175

176 ***2.3 Sediment preparation***

177 The grain size distribution of the natural sedimentation profile at Labrador, Pulau Hantu and Kusu
178 was analysed through laser diffraction particle size analyses (Malvern Mastersizer Particle Size
179 Analyser, UK). These sediments had been collected by hand from the substrate surrounding corals.
180 The particulate particle size ranged from 1-300 μm, with a median particle size of 40 to 140 μm,
181 dependent on site and seasonal variations (Browne et al., 2015). The sediment profile was closely
182 matched by combining commercially available particle sizes of silicon carbide powder (Kemet
183 Fareast Pte Ltd) following Lui et al. (2012). The resulting silicon carbide mix contained particle sizes
184 ranging from 1 μm to 300 μm, and had a median particle size of 60 μm. Silicon carbide has been
185 successfully used for this purpose in a number of coral and sediment stress studies (e.g. Stafford-

186 Smith & Ormond 1992, Lui et al. 2012). Browne et al (2014) provides a detailed discussion on the
187 use of silica carbide for this type of study

188 ***2.4 Experimental design***

189 In February 2013, four or five randomly selected coral fragments were placed into one of fifteen
190 cylindrical mesocosm chambers. In each chamber, there was at least one fragment of each coral
191 species. Corals were exposed to one of five treatments for eleven weeks: 1). Control; mean turbidity
192 = $<1 \text{ mg l}^{-1}$; sedimentation rate = $<0.5 \text{ mg cm}^{-2} \text{ day}^{-1}$ (n=4), 2). Moderate sediment stress for four
193 consecutive weeks followed by seven weeks recovery period; mean turbidity = 40 mg l^{-1} ;
194 sedimentation rate = $25 \text{ mg cm}^{-2} \text{ day}^{-1}$ (n=5), 3). Moderate sediment stress for four non-consecutive
195 weeks (one week exposure/one week recovery) followed by three weeks recovery period; mean
196 turbidity = 40 mg l^{-1} ; sedimentation rate = $25 \text{ mg cm}^{-2} \text{ day}^{-1}$ (n=5), 4). Extreme sediment stress for
197 four consecutive weeks followed by seven weeks recovery period; mean turbidity = 90 mg l^{-1} ;
198 sedimentation rate = $65 \text{ mg cm}^{-2} \text{ day}^{-1}$ (n=5) and, 5). Extreme sediment stress for four non-
199 consecutive weeks (one week exposure/one week recovery) followed by three weeks recovery period ;
200 mean turbidity = 90 mg l^{-1} ; sedimentation rate = $65 \text{ mg cm}^{-2} \text{ day}^{-1}$ (n=5).

201

202 During the sediment exposure weeks, corals were exposed to six pulsed turbidity events each day
203 (9.00 am, 12 pm, 3 pm, 6 pm, 9 pm, 12 am). Each turbidity event lasted for approximately 2 hr and
204 light levels within the chambers (next to the corals) were recorded every 5 s using a modified mini
205 ambient light sensor (DHI, Denmark), connected to the central control box. The light sensor
206 measured light levels between 350-680 nm and was been calibrated with a LI-COR light sensor (Li-
207 192) to provide the linear calibration co-efficient with which to convert internal engineering units to
208 PAR. Prior to the experiment, turbidity in the chambers had been calibrated with light levels during
209 the sediment resuspension events. Water samples (20 ml) were also collected every day at random
210 intervals from each chamber using a syringe from the side inlet, and were suction filtered through
211 Whatman filters (5 μm particle retention) to confirm the suspended sediment concentrations (SSC).
212 During the 2 h sediment resuspension event, sediments were resuspended via the air burst lift every 40

213 min to provide a pulsed and variable sedimentary regime. The level of sediments resuspended during
214 each pulse was controlled by the length of the airburst (sec), which had previously been calibrated
215 with sediment resuspension levels. The length of each airburst and timing of airbursts were controlled
216 by automated timers. Sedimentation rates ($\text{mg cm}^2 \text{ day}^{-1}$) were calculated every other day for each
217 chamber from a 4 cm diameter plastic disc placed on the plastic grid next to the coral fragments.

218

219 **2.5 Coral condition**

220 Coral condition over the eleven weeks was monitored either weekly (maximum photosynthetic yield
221 and tissue percentage mortality) or monthly (net photosynthesis rate, respiration rate).

222

223 *2.5.1 Maximum photosynthetic yield*

224 The maximum photosynthetic yield (F_v/F_m) was measured using a Diving-PAM (Walz, Germany)
225 between the hours of 10 am and 12 pm. Coral colonies were covered for 20 min in order to maximise
226 the frequency of the open photosystem II reaction centres (Winters et al., 2003). The fluorometer's
227 optical-fibre probe was kept at a constant distance of 5 mm from the surface of the coral and the
228 average of five measurements for each coral fragment was calculated. F_o was measured by applying a
229 pulsed measuring beam of $<1 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ and the emission F_m was measured following the
230 application of a saturating pulse of actinic light ($>1000 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$).

231 *2.5.2 Tissue mortality rate*

232 The tissue mortality rate was calculated from photographs. Coral fragments were photographed with
233 a scale and the surface area (cm^2) was analysed using CPCe software (NOVA, USA). The dead tissue
234 area was calculated as a percentage area of total fragment size.

235

236 *2.5.3 Net photosynthesis and respiration rates*

237 Assessment of the net photosynthesis and the respiration rate were conducted prior to the sediment
238 stress events, and at 4 and 8 weeks following one of the four sediment exposure regimes. The RESP-
239 EDU from Loligo systems respiratory system and software (AUTO-RESP, Denmark) were used to

240 determine rates of oxygen production and removal. A circular respirometry chamber (1.5 L) was
241 fabricated to accommodate the size of the fragments and equipped with a flush pump and a circulatory
242 pump to maintain continuous water flow. The chamber was submerged in a 50 L water bath with
243 running sea water, and temperature and oxygen were recorded every 5 s on a data logger (DAQ-M,
244 Loligo Systems). Light levels outside the chamber were monitored using a cosine-corrected LI-COR
245 probe (Li-192S) connected to a Li-1000 data logger. Oxygen consumption/production rate ($\text{mg O}_2 \text{ l}^{-1}$)
246 within the chamber volume (after subtracting the volume of coral) was measured continuously for 5
247 min using a galvanic cell oxygen probe (Loligo Systems), followed by a 2 min flush period. Net
248 photosynthetic (NP) rates were measured at $\sim 150 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and respiratory rates (R) and
249 the maximum photosynthetic yield were measured after 20 min incubation in the dark. Net oxygen
250 production and respiration rates were normalised to the surface area of live tissue for each coral
251 fragment ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$).

252

253

254 **2.6 Statistical analysis**

255 Data on coral responses (net photosynthesis, respiration, yield) and the sedimentary regime (turbidity
256 and sedimentation rates) were statistically analysed in RStudio (version 0.98.507). Data were tested
257 for normality and homogeneity of variance using Shapiro-Wilk test and Levene's test respectively.
258 One-way repeated measures ANOVA were performed for each coral species to assess: 1) if there was
259 a significant difference in coral response over time within each treatment, 2). if there was a significant
260 difference in coral response between treatments at key time points and, 3). If there was a significant
261 difference in turbidity and sedimentation rates between treatments. Mauchy's test of sphericity was
262 carried out and, where the assumption was violated, data was adjusted using the Greenhouse Geisser
263 adjustment. Post hoc analysis using Bonferroni corrections indicated during which time points and in
264 which treatments coral responses were significantly different.

265

266 **3.0 Results**

267 **3.1 Sedimentary regime**

268 The mean turbidity and sedimentation rate over the 11 weeks was $35.8 \pm 2.3 \text{ mg l}^{-1}$ (peaks at $\sim 100 \text{ mg}$
269 l^{-1}) and $27.8 \pm 1.9 \text{ mg cm}^{-2} \text{ day}^{-1}$, respectively in the moderate sediment treatments, and $92.4 \pm 4.6 \text{ mg}$
270 l^{-1} (peaks at $\sim 250 \text{ mg l}^{-1}$) and $73.1 \pm 3.8 \text{ mg cm}^{-2} \text{ day}^{-1}$, respectively in the extreme sediment
271 treatments (Fig. 1). There was no significant difference between weeks in turbidity and sedimentation
272 rates within each treatment ($p > 0.05$), but turbidity and sedimentation rates in the moderate sediment
273 treatments were significantly lower than rates in the extreme sediment treatments ($p < 0.05$, Table 1).
274 During the pulsed events, light levels in the chambers dropped from ~ 140 to 90-110 PAR in the
275 moderate sediment treatments, and 60-80 PAR in the extreme sediment treatments.

276

277 **3.2 Coral condition**

278 *3.2.1 Net photosynthesis and respiration rate*

279 The mean net photosynthesis rate prior to sediment exposure was 0.59 ± 0.04 , 0.45 ± 0.04 and $1.08 \pm$
280 $0.03 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ for *Merulina*, *Pachyseris* and *Platygyra*, respectively. There was no significant
281 change in net photosynthesis by week 4 and 8 in both moderate sediment treatments (constant and
282 periodic exposure regimes) for all three coral species (Fig. 2). However, net photosynthesis in the
283 extreme sediment treatments saw significant declines (Table 2). Under constant sediment pressure,
284 net photosynthesis rates fell for all coral species following 4 weeks, and saw further significant drops
285 to below $0 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ by week 8 despite 4 weeks of recovery. A similar trend was observed in
286 the periodic sediment exposure although rates for all coral species were significantly lower by week 4
287 ($p < 0.014$).

288

289 *Pachyseris* had the lowest baseline respiration rate ($0.46 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) prior to sediment
290 exposure, whereas the respiration rates of *Merulina* ($0.99 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) and *Platygyra* ($0.85 \text{ } \mu\text{mol}$
291 $\text{O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) were comparable (Fig. 2). There was no significant difference over time in the respiration
292 rate of the control fragments, and no significant difference between treatments at the start of the
293 experiment ($p > 0.05$; Table 2). The respiration rate of *Merulina* and *Pachyseris* did not increase
294 significantly during both the moderate sediment treatments, but did increase significantly after 8
295 weeks of periodic exposure for *Platygyra* ($p = 0.01$). In the extreme sediment treatments, *Platygyra*'s

296 respiration rate was significantly greater than the baseline rate by week 8 following four consecutive
297 weeks of sediment exposure ($p=0.02$), and by week 4 following four weeks of periodic exposure
298 ($p=0.002$). In contrast, the respiration rate of both *Merulina* and *Pachyseris* was only significantly
299 higher than the baseline by week 8 following both periodic and constant sediment exposure ($p<0.04$).
300 There was a significant difference between treatments for *Platygyra* ($p=0.02$) by week 4, and by week
301 8 for *Merulina* and *Pachyseris* ($p<0.06$; Table 3).

302

303 3.2.2 Yield

304 The mean maximum photosynthetic yield prior to sediment exposure was 0.59 ± 0.02 for *Merulina*,
305 0.55 ± 0.01 for *Pachyseris* and 0.64 ± 0.01 for *Platygyra*. The response in yield to the varying
306 sediment regimes varied between species, however, there was no significant difference in the controls
307 over time for all three coral species (Table 2). *Merulina* yields declined significantly in the moderate
308 constant exposure ($p = 0.001$) and both extreme sediment exposures by week 8 ($p < 0.01$; Table 2).
309 The yield also gradually declined in the moderate periodic exposure but recovered to pre-exposure
310 levels during the final recovery week (Fig. 3). In contrast, the yield of *Pachyseris* fragments
311 increased during all sediment exposure regimes, and yields for both the extreme sediment exposure
312 regimes were significantly greater than pre-exposure levels by week 4 ($p<0.01$). However, yields
313 declined following 2-3 weeks of no sediment exposure and fell below baseline levels by the end of the
314 recovery period. The yield for *Platygyra* fragments were typically greater than *Merulina* and
315 *Pachyseris*, and were more stable over the course of the experiment. Yields only fluctuated
316 significantly over time in the extreme constant exposure regime where rates were significantly lower
317 than the baseline by week 4 ($p<0.001$; Table 2). Yield was only significantly different between
318 treatments for *Pachyseris* during weeks 4,8 and 11 ($p<0.04$; Table 3).

319

320 3.2.3 Tissue mortality

321 Tissue necrosis was only observed for the foliose corals, *Merulina* and *Pachyseris*, exposed to
322 sediments (Fig. 4). The tissue mortality rate was highly variable both between and within the
323 different treatments and also among these two coral species. *Merulina* tissue mortality rates ($>1\%$)

324 were first observed in week 5 in both the moderate and extreme constant sediment regimes. By week
325 6, tissue necrosis was evident in all sediment treatments (2-5%) and gradually increased following
326 weeks 6 to 8. There may have been some recovery by week 11, but due to great variability between
327 fragments, these declines were not significant. In *Pachyseris*, there was limited tissue necrosis
328 observed in the moderate sediment regimes (<2.5%) over the 8 weeks of sediment exposure, but rates
329 in the extreme sediment constant exposure regime, first observed following 2 weeks (3%), increased
330 up to a maximum of 17% following 5 weeks. There was some tissue necrosis observed in the extreme
331 periodic exposure from week 4, but rates remained comparatively low (<5%). There did appear to be
332 some recovery by week 11 with the level of tissue necrosis falling from 17% to 11% and 5% to 2.5%
333 in the extreme constant and periodic exposure regimes, respectively.

334

335 **4.0 Discussion**

336

337 This was the first laboratory study that assessed the influence of pulsed turbidity events on the health
338 of inshore turbid water corals. The severity and duration of these pulsed turbidity events were
339 comparable to moderate (~50 mg.l⁻¹, peaks at 100 mg.l⁻¹) and extreme (~100 mg.l⁻¹, peaks at 250 mg.l⁻¹)
340 spikes in turbidity that corals experience on reefs during both natural and anthropogenically driven
341 turbidity events. Little to no change in coral health was observed following one month of moderate
342 sediment exposure. However, respirations rates increased and photosynthesis rates declined when
343 exposed to extreme sediment levels suggesting coral stress and reduced health. Furthermore, by
344 evaluating the difference between two different exposure regimes, it was found that corals exposed to
345 periodic exposures of pulsed turbidity events displayed reduced signs of coral stress than those
346 exposed to constant sediment exposure. In addition, tissue mortality rates, although highly variable,
347 were first observed in the constant sediment exposure regimes further demonstrating the potential
348 benefits of exposure-recovery regimes for coral long-term health and survival.

349

350 Little to no change in coral health at the moderate sediment exposure concentrations illustrates high
351 chronic sediment thresholds for inshore turbid water corals. *Merulina* and *Pachyseris* photo-

352 physiology was stable throughout the experiment, and although *Platygyra* respiration rates increased,
353 net photosynthesis and, therefore, energy availability did not decline. In comparison, significant
354 declines in net photosynthesis of clear-water corals (*Dichocoenia* and *Meandrina*) have been observed
355 when exposed to turbidity regimes $<50 \text{ mg.l}^{-1}$ within two weeks of exposure (Telesnicki and
356 Goldberg, 1995). These clear-water corals are less tolerant to sediments most likely due to
357 differences in natural background turbidity conditions. Declines in photosynthesis of inshore turbid
358 water corals in response have also been observed (Reigl and Branch, 1995), but rates tested (200
359 mg.cm^2) far exceed those tested here and are very rarely recorded on reefs for extended periods of
360 time. High rates of sediment accumulation typically lead to tissue mortality when rates of sediments
361 settling exceed coral sediment clearance abilities (Stafford-Smith, 1993). Between 0-5% tissue
362 mortality was observed during the moderate sediment exposures, although typically during that latter
363 weeks of sediment exposure suggesting that these corals were able to effectively remove sediments at
364 this rate of exposure. Partial mortality rates in the foliaceous coral, *Montipora* sp., ranged from 0 to
365 50% due to sediment deposition when exposed to 30 mg.l^{-1} SSC (Flores et al., 2012). The rates of
366 tissue mortality were greater than observed here, possibly due to species differences, but more likely
367 the result of lower sediment tolerances in offshore corals. These data suggest that corals in inshore
368 waters, where the background turbidity ranges from 2 to 5 mg.l^{-1} (Browne et al., 2015), can tolerate
369 pulsed turbidity events of $30\text{-}40 \text{ mg.l}^{-1}$ and sediment accumulation rates of $\sim 30 \text{ mg.cm}^2.\text{day}$ for
370 several weeks with little to no negative effects. These conditions are far greater than previous
371 sediment threshold levels of 10 mg.l^{-1} and $10 \text{ mg.cm}^2.\text{day}^{-1}$ as suggested by Rogers (1990).

372

373 Variable responses in coral photosynthetic yields between constant and periodic exposure regimes at
374 the same sediment concentrations demonstrate the importance of short recovery periods following
375 sediment exposure for coral health and survival. Maximum photosynthetic yields of *Merulina* and
376 *Pachyseris* only returned to pre-exposure levels in the periodic moderate exposure regime. In
377 contrast, although *Platygyra* yield levels remained high (>0.60), only corals exposed to the constant
378 extreme sediment levels were below pre-experiment yields by week 11. Declines in photosynthetic
379 yield following sediment exposure have previously been documented: Philip and Fabricius (2003)

380 exposed turbid water *Montipora* to a range of sediment accumulation rates ($1-6 \text{ g cm}^{-2} \text{ hr}^{-1}$) and
381 observed declines in yield from 0.65 to <0.1 . Similar rapid declines for *Montipora* sp. were also
382 observed by Piniak (2007), although recovery occurred within 2-3 days following 1-2 days of
383 sediment exposure ($<30 \text{ g cm}^{-1} \text{ hr}^{-1}$). Both these studies illustrate the detrimental impact of short,
384 acute sediment stress events on corals but at levels that rarely occur in the field. A comparable study
385 in terms of sediment exposure (4-16 weeks) and severity ($10-100 \text{ mg l}^{-1}$) found that yield levels of
386 *Acropora* and *Montipora* were relatively stable declining by <0.01 by week 4 and by 0.1 by week 12
387 (Flores et al., 2012). The variable responses to both sediment levels and exposure regimes here
388 demonstrate the important interaction between sediment severity, duration and species specific
389 responses, which confound the establishment of coral sediment threshold levels. These data suggest
390 that the combination of periodic exposure at moderate sediment levels was least detrimental to corals
391 given that yield levels under these conditions either remained high or returned to pre-baseline levels in
392 week 11, and that constant exposure at extreme sediment levels was most detrimental to corals given
393 reduced yields observed in week 11.

394

395 Variability in coral species specific thresholds to sediments was evident under extreme sediment
396 concentrations. *Platygyra* was found to be most tolerant to extreme levels of turbidity given limited
397 declines in its photosynthetic yield, and sedimentation as no tissue mortality was observed. The lack
398 of tissue mortality was most likely due to the corals ability to rapidly remove sediments from its
399 surface by actively inflating polyps (Stafford-Smith and Ormond, 1992; Riegl, 1995). This active
400 sediment removal requires energy, which would explain the significant increase in respiration rates
401 ($\sim 2.5 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ hr}^{-1}$) observed in both extreme sediment treatments. Respiration rates of *Merulina*
402 also increased to $>2 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ hr}^{-1}$. These foliaceous corals also use active sediment removal
403 mechanisms, however smaller polyp size (2-3 mm) typically reduces the efficiency of sediment
404 clearing rates (Stafford-Smith, 1993; Riegl, 1995). As such, between 1-10% tissue mortality was
405 observed from week 5 of the experiment. Highest rates of tissue mortality ($\sim 15\%$) were observed for
406 *Pachyseris* in the constant exposure to extreme sediment concentrations. *Pachyseris* respiration rates
407 were comparatively low ($<1.5 \text{ } \mu\text{mol O}_2 \text{ cm}^{-2} \text{ hr}^{-1}$) which may suggest that less energy was utilised for

408 sediment clearing and that these corals are less efficient at removing sediments. Interestingly,
409 *Pachyseris* yields increased in both extreme sediment treatments during the exposure periods which
410 suggest a greater capacity to accommodate reduced light levels than high rates of sedimentation.
411 Varying responses to sediment resuspension and deposition are reflected in the distribution of
412 *Pachyseris* on reefs: these corals are typically found in higher energy environments on turbid reefs
413 where sediments are periodically resuspended (Browne et al., 2012). In contrast, *Platygyra* has a
414 broader distribution and is found both in high and low energy environments, such as the reef flat and
415 back reef, where sediments are deposited (Done, 1982). Species partitioning along sediment gradients
416 will influence ecological distributions and reef growth and development.

417

418 It has been argued that the balance between sediment deposition and sediment resuspension is more
419 important than the rate of sediment supply on coral reef health (Larcombe and Woolfe, 1999; Orpin
420 and Woolfe, 1999). The negative impacts of sediment deposition are considered to have greater
421 detrimental impacts on coral health than increased turbidity due to coral acclimation mechanisms to
422 low light (Anthony, 2000; Anthony, 2006). However, reduced light levels will limit photosynthesis
423 and reduce energy available for active sediment removal mechanisms (Browne et al., 2014).

424 Sediment clearing rates are not only dependent on calice size, but also on coral morphology. Recent
425 research suggests that coral morphology is more important than calice size in determining coral
426 tolerance to sedimentation: corals with a columnar or plate (folioceous) growth form are more
427 sensitive to sedimentation than massive and branching corals (Sanders and Baron-Szabo, 2005;
428 Erfteimeijer et al., 2012). Previous thresholds to sedimentation range from $10 \text{ mg cm}^{-2} \text{ day}^{-1}$, where
429 coral growth and reproduction rates are reduced and coral diversity declines (Lasker, 1980; Rogers,
430 1990), to $50 \text{ mg cm}^{-2} \text{ day}^{-1}$ where most corals are excluded and many colonies die (Pastorok and
431 Bilyard, 1985). This study suggests, however, that even sensitive folioceous corals can potentially
432 survive sedimentation rates of $30 \text{ mg cm}^{-2} \text{ day}^{-1}$ for over a month with limited influence on coral
433 health, and more tolerant massive corals such as *Platygyra* could survive up to $70 \text{ mg cm}^{-2} \text{ day}^{-1}$ for
434 over a month.

435

436 These increased threshold levels may in part be due to the experimental design which replicated
437 pulsed turbidity events as opposed to constant sediment exposure. In the field, corals are subjected to
438 pulses of sediments that result in a constant flux in turbidity, light and sedimentation (Browne et al.,
439 2013a). To determine realistic sediment thresholds to turbidity and sedimentation, great care was
440 taken to ensure sediment exposure regimes were of environmental relevance. Furthermore, the
441 sediment profile closely matched that found on Singapore inshore turbid reefs as well as inshore reefs
442 on the Great Barrier Reef (Browne et al., 2013b). The results agree with previous findings that many
443 corals can survive at turbidity concentrations that far exceed previous estimates, in many cases for
444 several months due to acclimation processes (Table 4). However, the negative effects of sediment
445 deposition are typically more detrimental to corals, and may be more so than estimated in this study
446 due to the combined negative effects of nutrients and/or contaminants, known to exacerbate the
447 impacts of sediments on corals (Fabricius, 2005). It is therefore recommended that future research
448 into the coral-sediment relationship combine the influence of pulsed turbidity events with additional
449 stressors such as nutrients and contaminants, as well as elevated temperatures and declining in pH to
450 assess the combined effect of multiple stressors on corals and coral reefs.

451

452 Active management of anthropogenically driven sediment resuspension events (e.g. dredging) near
453 coral reefs have relied heavily on the use of trigger values (PIANC, 2010). Setting realistic trigger
454 values based on coral sediment thresholds is a current challenge given that sediment responses of only
455 10% of coral species have been evaluated (Erfteimeijer et al., 2012). The limited understanding of the
456 coral-sediment relationship is further complicated as many individuals of the same species are
457 observed to have different tolerances due to differences in natural background conditions between reef
458 environments (Anthony and Fabricius, 2000). Coral sediment thresholds within individual colonies
459 may also fluctuate temporally due to seasonal variations in environmental conditions, which may
460 stress corals and reduce thresholds (Pisapia et al., 2014). Threshold values and, therefore, realistic
461 trigger values, should not be static but vary according to coral species composition, natural sediment
462 exposure regimes and environmental conditions. A review of over 30 papers (see Table 6) illustrates
463 the variability in coral responses and thresholds to sediments over a range of timeframes (hours to one

464 year) and sediment levels (10-1000 mg l⁻¹, 10 to 600 mg cm⁻² day⁻¹; Table 4 and 5). Coral responses
465 to elevated turbidity range from no effect to mucus production, some tissue damage or coral mortality.
466 The latter is typically not observed until turbidity reaches 500 mg l⁻¹ for 1-2 days or >90 mg l⁻¹ for one
467 month (Table 4) illustrating that most corals of varying morphology show some ability to acclimate to
468 low light conditions above previous known thresholds. However, coral responses to sedimentation
469 are less uniform i.e. *Pocillopora* and *Porites* experience coral mortality after two weeks at 30 mg cm⁻²
470 day⁻¹ (Hodgson, 1990), while no negative effect of sedimentation was observed for *Turbinaria* corals
471 after 1 month exposure to 100 mg cm⁻² day⁻¹ (Sofonia and Anthony, 2008). These variable
472 differences may in part be due to inconsistencies in sediment types used to test for thresholds, but it is
473 most likely due to differences in coral morphology and/or calice sizes (Stafford-Smith, 1993;
474 Erftemeijer et al., 2012). To improve current trigger values, which at present are little more than
475 estimates, research needs to expand to incorporate a broader range of species and exposure regimes.
476 Realistic trigger values combined with modelling efforts would predict reef health before, during and
477 following exposure to sediments, and enable managers to react to declines in health before coral
478 mortality occurs.

479

480 This study provides improved estimates of coral thresholds to sediments for three common inshore
481 turbid water coral species. Thresholds to both turbidity and sedimentation rates were greater than
482 commonly used estimates with little to no effect on corals at moderate sediment exposure levels. At
483 extreme exposure levels, species morphological differences are potentially key determinants of coral
484 survival. The periodic exposure regime was less detrimental to all coral species as demonstrated by
485 elevated yields and lower tissue mortality rates. However, the balance between sediment resuspension
486 and deposition, and sediment flux is potentially critical to coral survival in coastal regions that
487 experience elevated sediment loads, driven by natural and/or anthropogenic causes. Active
488 management of anthropogenic activities that result in increased sediment loadings in coastal waters
489 need to determine trigger values based on coral community thresholds as well as background natural
490 conditions. These trigger values must also change seasonally to accommodate additional stressors

491 that may lower thresholds as well as fluctuations in the hydrodynamic regime that influences the
 492 balance between sediment deposition and resuspension.

493

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632

Table 1: One-way repeated measures ANOVA comparing turbidity and sedimentation rates between treatments (MC= moderate constant exposure, MP= moderate periodic exposure, EC=extreme constant exposure, EP= extreme periodic exposure). Results indicate that turbidity and sedimentation rates in the moderate regimes were significantly lower than the extreme regimes during all four weeks of sediment exposure (n=9).

		Exposure weeks			
		1.0	2.0	3.0	4.0
Turbidity (mg l⁻¹)	df	3.0	1.7	1.3	3.0
	MS	20493	13109	21255	9951
	F	20.3	5.0	7.2	21.9
	P value	<0.001	0.03	0.02	<0.001
	Posthoc		MC, MP < EC, EP		
Sedimentation (mg cm⁻² day⁻¹)	df	3.0	1.5	1.3	3.0
	MS	12518	11093	12210	5754
	F	23.7	6.2	6.4	19.7
	P value	<0.001	0.02	0.03	<0.001
	Posthoc		MC, MP < EC, EP		

Table 2: One-way repeated measures ANOVA assessing if there are significant differences between weeks for each treatment (MC= moderate constant exposure, MP= moderate periodic exposure, EC=extreme constant exposure, EP= extreme periodic exposure) and parameter of coral health (net photosynthesis, respiration and yield). Post hoc analysis using Bonferroni corrections indicate between which weeks coral responses were significantly different.

Species	Treatment	Net photosynthesis					Respiration					Yield				
		df	MS	F	p value	Post hoc	df	MS	F	p value	Post hoc	df	MS	F	p value	Post hoc
<i>Merulina</i>	Control	2	0.012	0.136	0.836		2	0.026	0.234	0.801		1.386	0	0.07	0.874	
	MC	2	0.009	0.056	0.946		2	0.51	4.388	0.055		3	0.01	13.72	0.001	0,4>8,11
	MP	2	0.016	0.862	0.488		2	0.023	0.053	0.949		1.026	0.033	8.77	0.057	
	EC	1.062	6.547	15.092	0.015	0>4>8	2	2.55	9.89	0.013	0,4>8	3	0.011	14.05	0.001	0,4>8,11
	EP	2	8.492	15.042	0.014	0>4>8	2	4.172	20.127	0.002	0,4>8	3	0.003	7.271	0.005	0,4>8,11
<i>Pachyseris</i>	Control	2	0.055	2.322	0.301		2	0.002	0.019	0.981		3	0	0.786	0.531	
	MC	2	0.024	0.888	0.479		2	0.008	0.63	0.565		1.776	0.016	6.414	0.067	
	MP	2	0.043	1.004	0.421		2	0.031	0.27	0.776		1.474	0.005	3.126	0.183	
	EC	1.023	3.523	10.613	0.046	0,4>8	2	1.146	5.898	0.037	0,4>8	3	0.004	32.07	<0.001	4>8,11
	EP	2	0.937	21.679	0.002	0>4>8	1	1.755	72.827	0.013	0,4>8	3	0.003	7.27	0.005	4>0,8,11
<i>Platygyra</i>	Control	2	0.193	1.39	0.348		2	0.077	4.85	0.673		3	0	0.61	0.625	
	MC	2	0.263	3.149	0.116		2	1.366	8.334	0.098		1.11	0.009	6	0.123	
	MP	2	0.128	1.24	0.381		2	1.366	8.33	0.011	0,4>8	3	0.001	0.95	0.457	
	EC	2	6.515	30.255	<0.001	0,4>8	1.055	5.892	12.384	0.022	0,4>8	3	0.009	147	<0.001	0>4>11
	EP	2	4.985	28.718	0.001	0>4>8	2	2.66	15.615	0.002	0>4>8	1.106	0.044	1.97	0.293	

Table 3: One-way repeated measures ANOVA assessing if there are significant differences between treatments at 0 (prior to exposure), 4, 8 and 11 weeks (MC= moderate constant exposure, MP= moderate periodic exposure, EC=extreme constant exposure, EP= extreme periodic exposure).

Species	Week	Net photosynthesis				Respiration				Yield			
		df	MS	F	<i>p</i> value	df	MS	F	<i>p</i> value	df	MS	F	<i>p</i> value
<i>Merulina</i>	0	4	0.098	0.59	0.68	4	0.098	0.59	0.68	1.672	0	0.109	0.87
	4	4	0.184	1.464	0.27	4	0.184	1.464	0.27	1.985	0.001	0.252	0.78
	8	4	2.073	3.676	0.05	4	2.073	3.676	0.06	2.218	0.006	1.177	0.37
	11									1.8	0.002	1.71	0.26
<i>Pachyseris</i>	0	4	0.016	0.246	0.90	4	0.027	0.882	0.50	1	0.005	3.379	0.32
	4	4	0.401	27.48	<0.001	4	0.006	0.062	0.99	1.53	0.013	6.974	0.03
	8	4	1.725	21.09	0.01	4	0.34	10.569	0.02	1.49	0.01	3.289	0.04
	11									1.864	0.03	7.279	0.02
<i>Platygyra</i>	0	4	0.038	0.439	0.78	4	0.071	1.11	0.40	1.871	0	0.125	0.87
	4	4	0.792	4.112	0.03	4	0.813	4.188	0.02	1.357	0.005	2.314	0.21
	8	4	6.197	56.867	<0.001	4	1.482	3.2	0.08	2.39	0.002	0.774	0.51
	11									1.49	0.04	2.388	0.18

Table 4: Review of coral responses to varying turbidity concentrations at time-scales ranging from a few hours to 3 months. Coral responses range from acclimation processes (e.g. increase yields and heterotrophy) to reduced growth rates and tissue mortality. Note that these responses occur when all other factors are non-limiting, and studies used a range of sediment types. Numbered references are provided in Table 6 and results from this study are denoted by *.

Time	Turbidity (mg l ⁻¹)												
	10	20	30	40	50	90	100	150	200	300	500	1000	
Hours	<i>Acropora</i> ^{1,2}	<i>Acropora</i> ^{1,2} <i>Montipora</i> ¹ <i>Pocillopora</i> ¹ <i>Porites</i> ³	<i>Acropora</i> ^{1,2}					<i>Merulina</i> ⁶ <i>Pachyseris</i> ⁶ <i>Platygyra</i> ⁶	<i>Acropora</i> ⁸	<i>Pachyseris</i> ⁶ <i>Platygyra</i> ⁶			
< 1 day			<i>Acropora</i> ¹²						<i>Merulina</i> ⁶				<i>Porites</i> ²⁸ <i>Dichocoenia</i> ²⁷
1-2 days	<i>Acropora</i> ²⁷	<i>Acropora</i> ²⁷	<i>Acropora</i> ²⁷		<i>Acropora</i> ¹⁹ <i>Agaricia</i> ²⁷ <i>Dichocoenia</i> ²⁷ <i>Montastrea</i> ²⁷ <i>Porites</i> ²⁷			<i>Acropora</i> ²⁷ <i>Agaricia</i> ²⁷ <i>Montastrea</i> ²⁷ <i>Porites</i> ²⁷			<i>Acropora</i> ²⁷ <i>Agaricia</i> ²⁷ <i>Dichocoenia</i> ²⁷ <i>Montastrea</i> ²⁷ <i>Porites</i> ²⁷	<i>Acropora</i> ²⁸ <i>Agaricia</i> ²⁸ <i>Montastrea</i> ²⁸	
2-5 days								<i>Dichocoenia</i> ²⁷					
2 weeks					<i>Manacini</i> ¹⁷		<i>Manacini</i> ¹⁷	<i>Manacini</i> ¹²	<i>Manacini</i> ¹⁷	<i>Scolymia</i> ¹⁶ <i>Solenastrea</i> ¹⁶ <i>Siderastrea</i> ¹⁶			
3 weeks	<i>Dichocoenia</i> ²⁶	<i>Dichocoenia</i> ²⁶	<i>Dichocoenia</i> ²⁶		<i>Manacini</i> ¹⁷		<i>Manacini</i> ¹⁷	<i>Manacini</i> ¹²	<i>Manacini</i> ¹⁷				
1 month		<i>Porites</i> ¹	<i>Montipora</i> ^{11,15}	<i>Platygyra</i> [*]	<i>Meandrina</i> ²⁶	<i>Platygyra</i> [*]	<i>Montastrea</i> ²⁵						
			<i>Acropora</i> ^{11,15}	<i>Pachyseris</i> [*]		<i>Pachyseris</i> [*] <i>Merulina</i> [*]	<i>Galaxea</i> ¹³	<i>Galaxea</i> ¹³					
2 months		<i>Goniastrea</i> ³	<i>Goniastrea</i> ³				<i>Acropora</i> ^{11,15}						
3 months							<i>Acropora</i> ^{11,15}				<i>Porites</i> ⁵		
Coral response	No effect	High yield/ chlorophyll a	Mucus/polyp protraction	Shift from auto to heterotrophy			Reduction in P/R or reduced growth	Limited larval settlement or reproduction			Bleaching or partial mortality	Mortality	

Table 5: Review of coral responses to varying sediment accumulation rates at time-scales ranging from a few hours to 1 year. Coral responses range from acclimation processes (e.g. increase yields and heterotrophy) to reduced growth rates and tissue mortality. Note that these responses occur when all other factors are non-limiting, and studies used a range of sediment types. Numbered references are provided in Table 6 and results from this study are denoted by *, and refer to Table 5 for colour code.

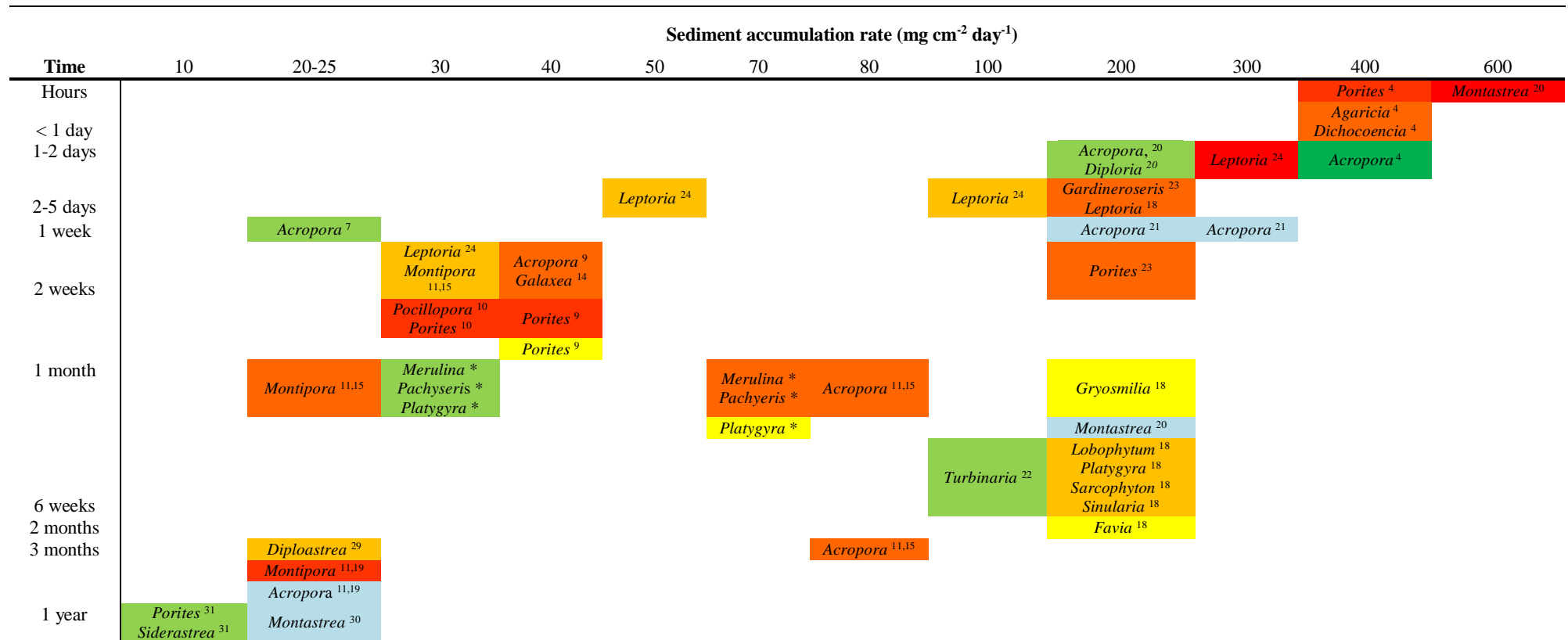


Table 4: Review of coral responses to varying turbidity concentrations at time-scales ranging from a few hours to 3 months. Coral responses range from acclimation processes (e.g. increase yields and heterotrophy) to reduced growth rates and tissue mortality. Note that these responses occur when all other factors are non-limiting, and studies used a range of sediment types. Numbered references are provided in Table 6 and results from this study are denoted by *.

Time	Turbidity (mg l ⁻¹)												
	10	20	30	40	50	90	100	150	200	300	500	1000	
Hours	<i>Acropora</i> ^{1,2}	<i>Acropora</i> ^{1,2} <i>Montipora</i> ¹ <i>Pocillopora</i> ¹ <i>Porites</i> ³	<i>Acropora</i> ^{1,2}					<i>Merulina</i> ⁶ <i>Pachyseris</i> ⁶ <i>Platygyra</i> ⁶	<i>Acropora</i> ⁸	<i>Pachyseris</i> ⁶ <i>Platygyra</i> ⁶			
< 1 day			<i>Acropora</i> ¹²							<i>Merulina</i> ⁶			<i>Porites</i> ²⁸ <i>Dichocoenia</i> ²⁷
1-2 days	<i>Acropora</i> ²⁷	<i>Acropora</i> ²⁷	<i>Acropora</i> ²⁷		<i>Acropora</i> ¹⁹ <i>Agaricia</i> ²⁷ <i>Dichocoenia</i> ²⁷ <i>Montastrea</i> ²⁷ <i>Porites</i> ²⁷			<i>Acropora</i> ²⁷ <i>Agaricia</i> ²⁷ <i>Montastrea</i> ²⁷ <i>Porites</i> ²⁷			<i>Acropora</i> ²⁷ <i>Agaricia</i> ²⁷ <i>Dichocoenia</i> ²⁷ <i>Montastrea</i> ²⁷ <i>Porites</i> ²⁷	<i>Acropora</i> ²⁸ <i>Agaricia</i> ²⁸ <i>Montastrea</i> ²⁸	
2-5 days								<i>Dichocoenia</i> ²⁷					
2 weeks					<i>Manacini</i> ¹⁷		<i>Manacini</i> ¹⁷	<i>Manacini</i> ¹²	<i>Manacini</i> ¹⁷	<i>Scolymia</i> ¹⁶ <i>Solenastrea</i> ¹⁶ <i>Siderastrea</i> ¹⁶			
3 weeks	<i>Dichocoenia</i> ²⁶	<i>Dichocoenia</i> ²⁶	<i>Dichocoenia</i> ²⁶		<i>Manacini</i> ¹⁷		<i>Manacini</i> ¹⁷	<i>Manacini</i> ¹²	<i>Manacini</i> ¹⁷				
1 month		<i>Porites</i> ¹	<i>Montipora</i> ^{11,15}	<i>Platygyra</i> [*]	<i>Meandrina</i> ²⁶	<i>Platygyra</i> [*]	<i>Montastrea</i> ²⁵						
			<i>Acropora</i> ^{11,15}	<i>Pachyseris</i> [*]		<i>Pachyseris</i> [*] <i>Merulina</i> [*]	<i>Galaxea</i> ¹³	<i>Galaxea</i> ¹³					
2 months		<i>Goniastrea</i> ³	<i>Goniastrea</i> ³				<i>Acropora</i> ^{11,15}						
3 months											<i>Porites</i> ⁵		
Coral response	No effect	High yield/ chlorophyll a	Mucus/polyp protraction	Shift from auto to heterotrophy			Reduction in P/R or reduced growth		Limited larval settlement or reproduction		Bleaching or partial mortality		Mortality

Table 6: References for Table 4 and 5.

No.	Reference	No.	Reference
1	Anthony 1999	17	Rice & Hunter 1992
2	Anthony 2000	18	Riegl et al. 1995
3	Anthony & Fabricius 2000	19	Rogers 1979
4	Bak & Elgershuizen 1976	20	Rogers 1990
5	Brown et al. 1990	21	Simpson 1988
6	Browne et al. 2014	22	Sofonia & Anthony 2008
7	Chansang et al. 1992	23	Stafford-Smith 1993
8	Fabricius & Wolanski 2000	24	Stafford-Smith & Ormond 1992
9	Fabricius et al. 2007	25	Szmant-Froelich et al. 1981
10	Hodgson 1990	26	Telesnicki & Goldberg 1995
11	Flores et al. 2011	27	Thompson 1980
12	Kendall 1985	28	Thompson & Bright 1980
13	Larcombe et al. 2001	29	Todd et al. 2004
14	McClanahan & Obura 1997	30	Torres 1998
15	Negri et al 2009	31	Torres & Morelock 2002
16	Rice 1984		

Figure Legends

Figure 1: Mean (\pm SE) turbidity and sediment accumulation rates during each exposure week. In weeks 1 and 3 corals in both sediment regimes were exposed (n=6) at either moderate or extreme sediment loads. In weeks 2 and 4 only corals in the constant (C) sediment regime were exposed (n=3) and in weeks 5 and 7, only corals in the periodic (P) sediment regime were exposed to sediments (n=3).

Figure 2: Mean (\pm SE) net photosynthesis and respiration rates for *Merulina* (A,B), *Pachyseris* (C, D) and, *Platygyra* (E, F) in the four different exposure regimes (MC= moderate constant exposure, MP= moderate periodic exposure, EC=extreme constant exposure, EP= extreme periodic exposure), at three time points (n=5).

Figure 3: Mean (\pm SE) maximum photosynthetic yields for A. *Merulina*, B *Pachyseris* and, C *Platygyra* for each week under one of four treatments (MC= moderate constant exposure, MP= moderate periodic exposure, EC=extreme constant exposure, EP= extreme periodic exposure).

Figure 4: Mean (\pm SE) tissue mortality rates for A. *Merulina* and B. *Pachyseris* for each treatment (MC= moderate constant exposure, MP= moderate periodic exposure, EC=extreme constant exposure, EP= extreme periodic exposure). No tissue mortality was observed for *Platygyra* (n=5).