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Effects of suspended sediments and nutrient enrichment on juvenile corals

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ABSTRACT

Three to six-month-old juveniles of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta* were experimentally co-exposed to nutrient enrichment and suspended sediments (without light attenuation or sediment deposition) for 40 days. Suspended sediments reduced survivorship of *A. millepora* strongly, proportional to the sediment concentration, but not in *A. tenuis* or *P. acuta* juveniles. However, juvenile growth of the latter two species was reduced to less than half or to zero, respectively. Additionally, suspended sediments increased effective quantum yields of symbionts associated with *A. millepora* and *A. tenuis*, but not those associated with *P. acuta*. Nutrient enrichment did not significantly affect juvenile survivorship, growth or photophysiology for any of the three species, either as a sole stressor or in combination with suspended sediments. Our results indicate that exposure to suspended sediments can be energetically costly for juveniles of some coral species, implying detrimental longer-term but species-specific repercussions for populations and coral cover.

1. Introduction

An estimated 25% of coral reefs globally are threatened by increasing loads of sediments, nutrients and pollutants from terrestrial runoff associated with coastal development, dredging, deforestation and agriculture (Burke et al., 2011). Declining coastal water quality can lead to increases in macroalgal cover (Fabricius, 2005), reductions in coral biodiversity (De'ath and Fabricius, 2010), proliferation of macrobioeroders that weaken the structural integrity of coral reefs (Le Grand and Fabricius, 2011), increases in the frequency and severity of coral diseases (Bruno et al., 2003), and changes in the composition of biofilms that provide conditioned surfaces for larval settlement and metamorphosis of many sessile organisms (Wieczorek and Todd, 1998, Webster et al., 2004, Sawall et al., 2012).

Field and laboratory studies have shown that sediments and nutrients can both negatively affect corals. High concentrations of suspended sediments reduce gamete fertilization success of gametes and larval settlement (Gilmour, 1999, Jones et al., 2015b, Ricardo et al., 2015, Humanes et al., 2017), cause shifts in the dominance of energy acquisition from phototrophy to heterotrophy (Anthony and Fabricius, 2000), alter colony morphology, and cause declines in growth and survivorship (Anthony and Fabricius, 2000, Jones et al., 2016). Suspended sediments can affect adult corals in three major ways (reviewed

by Jones et al. (2016)). Firstly, contact between suspended particles and the coral can cause irritation, disrupt feeding mechanisms, and increase the energy expenditure into tentacle movement and mucus production for self-cleaning. The suspended particles can also attenuate light and change light quality, which affects energy acquisition by the associated *Symbiodinium* symbionts. Finally, settling sediments can smother corals, which again increases cleaning efforts which may be overwhelming, resulting in bleaching and tissue death by anoxia. Elevated concentrations of nutrients also negatively affect all coral life history stages, reducing gamete production (Ward and Harrison, 2000, Loya et al., 2004), fertilization success (Humanes et al., 2016) and calcification rates, as well as increasing the ratio of symbiont to host cells, which can increase the vulnerability of this symbiotic partnership to disruptions (bleaching) associated with high sea temperatures (Marubini and Davies, 1996, Cunning and Baker, 2012, Vega Thurber et al., 2014). Conversely, when co-occurring with conditions that promote shifts from autotrophy to heterotrophy, elevated nutrients can stimulate calcification and growth rates, and increase host tissue protein content and biomass in some coral species (Bongiorni et al., 2003a, Sawall et al., 2011, Ezzat et al., 2015).

In combination, nutrient-enriched sediments in inshore areas influenced by river runoff (Brodie et al., 2012) can exacerbate the already detrimental effects of suspended and deposited sediments on corals,

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further reducing larval settlement success, and adult survivorship and growth rates (Fabricius, 2005, Weber et al., 2006, Humanes et al., 2017). Dissolved inorganic nutrients, especially nitrogen and phosphorus also promote the formation of phytoplankton blooms (Furnas, 2003, Kroon et al., 2012), which transform the dissolved inorganic nutrients and convert them into particulate organic nutrients (Grossart and Ploug, 2001, Brodie et al., 2010). Particulate organic nutrients reduce water clarity and stimulate microbial communities that exude mucopolysaccharides (Angly et al., 2016), form aggregates with sediments that compromise coral juvenile and adult survivorship when deposited on their tissues (Fabricius et al., 2003, Weber et al., 2012), and promote the development of coral diseases (D'Angelo and Wiedenmann, 2014).

The Great Barrier Reef (GBR), the World's largest coral reef system, is located adjacent to tropical catchments along the North Queensland coast of Australia that have been modified by extensive agriculture. At present, rivers discharge an estimated 17 million tonnes of suspended sediments, along with 80,000 t of nitrogen and 16,000 t of phosphorous annually, a 3–8-fold increase compared to pre-European settlement (McCulloch et al., 2003, Kroon et al., 2012). Over 30 major rivers discharge sediments and nutrients into the GBR lagoon during the wet season (December–March), simultaneously introducing dissolved and particulate organic and inorganic nutrients together with fine terrigenous sediments (Fabricius et al., 2014). Fine sediments then undergo repeated cycles of deposition and resuspension at < 20 m bathymetry (Fabricius et al., 2013), until they are eventually deposited either on the deeper seafloor below the reach of storm waves, or in north-facing coastal embayments (Larcombe et al., 1995, Wolanski et al., 2005). Consequently, high concentrations of suspended sediments are commonly found throughout the year in the shallow GBR lagoon, and their effects on the structure and function of these inshore marine ecosystems is of great concern (Schaffelke et al., 2005, Brodie and Waterhouse, 2012).

Although there has been some research on the impacts of organically enriched suspended or deposited sediments on fertilization, larval survivorship and settlement (Humphrey et al., 2008, Humanes et al., 2017), and on juvenile and adult stages of scleractinian corals (Fabricius and Wolanski, 2000, Weber et al., 2006, Weber et al., 2012, Perez et al., 2014, Liu et al., 2015, Moeller et al., 2016), the effects of physical contact of suspended sediments together with nutrient enrichment on key physiological processes of juvenile corals in the months following settlement remain unknown. This represents a significant knowledge gap, particularly as: i) sediment and nutrient discharges into coastal areas are a growing problem worldwide (Syvitski et al., 2005); ii) juvenile growth and survivorship rates play a key role in the maintenance and replenishment of coral populations (Ritson-Williams et al., 2010); iii) early life history stages of corals are typically considered more sensitive to environmental change and pollution than adult stages (Fabricius, 2005); and iv) scleractinian corals are the main ecosystem engineers of coral reefs (Bellwood and Hughes, 2001).

To improve current understanding of the effects of nutrient-enriched suspended sediments on juvenile corals, we performed a series of controlled laboratory exposure experiments over 40 days. We compare the effects of the physical contact of suspended sediments (in the absence of deposition and light attenuation), with and without nutrient enrichment, on juveniles of three coral species that are common on inshore reefs of the GBR and throughout the tropical Indo-Pacific (*Acropora tenuis*, *A. millepora* and *Pocillopora acuta*). Our data on juvenile survivorship and growth, photochemical efficiency, respiration and photosynthesis provide insights into the vulnerability of coral juveniles to nutrient-enriched suspended sediments commonly associated with runoff events in inshore areas.

2. Materials and methods

2.1. Spawning, gamete collection and larval settlement

Gravid colonies (> 20 cm diameter) of the broadcast spawning corals *Acropora tenuis* (Dana 1846) and *A. millepora* (Ehrenberg, 1834) were collected on the 6th of November 2014 at ~6 m depth, under permit G12/35236.1 issued by the Great Barrier Reef Marine Park Authority; gravid colonies of the brooding coral *Pocillopora acuta* (Lamarck, 1816) were collected in February 2015, from Davies Reef (19° 06'S, 146° 51'E). All three species have branching growth forms and are zooxanthellate corals, meeting much of their energy demands through photosynthesis by endosymbiotic *Symbiodinium* communities. Colonies were transferred to an outdoor flow-through system, with temperature set to the reef conditions on the day of collection (27 °C) in the National Sea Simulator facility (SeaSim) at the Australian Institute of Marine Science (AIMS). Following spawning of 11 colonies of *A. tenuis* and 13 colonies of *A. millepora* (on days 5 and 8 after the November full moon, respectively), egg-sperm bundles were gently scooped from the surface of aquaria. Eggs were separated from sperm using a 100 µm mesh filter and washed five times in FSW (0.2 µm filtered sea water), and then cross-fertilized as described by Negri and Heyward (2000). Larvae were reared in 500 l flow-through tanks using 1 µm-filtered seawater at 27 °C. To collect larvae from the brooding coral *P. acuta*, 15 colonies were isolated in 25 l flow-through tanks with 100 µm mesh collectors positioned at outflows, which collected larvae released between the 22nd and 25th of February 2015. Artificial aragonite substrata (~2 cm in diameter, Oceans Wonders LLC) and overgrown with crustose coralline algae (CCA), were offered to larvae of the three species as settlement substrata. The resulting recruits were reared in flow-through tanks at 27 °C until the beginning of the experiment on 13th May 2015. Their ages at the beginning of the experiment were: 188 days for *A. tenuis*, 185 days for *A. millepora*, and 78 days for *P. acuta*.

2.2. Experimental design and treatment types

Juveniles were exposed for 40 days to eight treatments, consisting of four levels of suspended sediments (0, 10, 30 or 100 mg l⁻¹) and two levels of nutrient enrichment (+ 0 or + 0.6 mg OC l⁻¹ FSW) in a fully crossed experimental design. Treatments mimicked the impact of terrestrial runoff events, wind-driven resuspension events, or dredging activities that simultaneously introduce nutrients and fine-sized particle sediments into inshore reef waters. Sediments and nutrients were collected from the seafloor at 2 m depth at Orpheus Island (18° 36'S, 146° 29'E) and transported to AIMS two weeks before starting exposures. Sediments were wet-sieved to obtain fine particles (average ± sd. particle size: 7.3 ± 1.5 µm, 95% < 20 µm), and kept in 60 l flow-through tanks at 27 °C until experiments commenced. Plankton containing organic and inorganic nutrients were collected with a plankton net (mesh size 100 µm), sieved to remove large fragments (> 26 µm), homogenized with a blender, and frozen in aliquots until use. Natural plankton was used as the nutrient source to maintain a realistic stoichiometric composition of organic and inorganic nutrients and trace elements present in inshore reefs, a method previously used for studying the effects of nutrient enrichment on hard corals (Fabricius et al., 2003, Weber et al., 2012, Humanes et al., 2016, Humanes et al., 2017).

Suspended sediment concentrations (0, 10, 30 and 100 mg l⁻¹) were verified using a nephelometer calibrated with the same sediments (TPS 90FL-T). Experimental suspended sediment concentrations were chosen to represent the range of *in situ* conditions that have been recorded on inshore GBR reefs and in association with dredging projects. Concentrations recorded *in situ* have been up to 5 mg l⁻¹ under calm conditions on inshore reefs (Macdonald et al., 2013), between 5 and 30 mg l⁻¹ after storms and in river plumes, and up to 100 mg l⁻¹ close

to dredging activities (Thomas et al., 2003, Stoddart and Anstee, 2005, Jones et al., 2015a, Ricardo et al., 2015). The nutrient enrichment treatment was prepared by augmenting sediments with 0.6 mg l^{-1} FSW of organic carbon (OC) as plankton (as prepared above). Nutrient concentrations were based on *in situ* water quality measurements of GBR coastal waters (Kroon et al., 2012, Schaffelke et al., 2012, Waters et al., 2014).

2.3. Experimental setup

Eight custom-made 60 l tanks were used to prepare the modified seawater treatments stocks, which were then mixed to produce four levels of suspended sediments (0, 10, 30 or 100 mg l^{-1}), each combined with two levels of nutrient enrichment (+0, or $+0.6 \text{ mg OC l}^{-1}$ FSW). Light intensities in stock treatments were $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ over a 12 h:12 h diurnal cycle (Fig. S1, Supplementary material). Treatments were prepared daily by adding the corresponding amounts of sediments and nutrients to FSW. Air stones were used to maintain sediments in suspension in the stock tanks, and an Eheim 1260 l h^{-1} pump (Eheim 1260: Eheim GmbH, Germany) was used to pulse the modified seawater (for 10 min every 90 min, 2 l in total) into the treatment tanks ($n = 3$ tanks per treatment) via 4 mm hose (6 turnovers per day).

Exposures were conducted in 24 round-bottom glass tanks (4 l) that were positioned below the stock tanks (Fig. S1, Supplementary material). A VorTech MP10 pump, positioned on the bottom in the center of each experimental tank, was used to keep sediments suspended. Aragonite substrata with attached juveniles were fixed vertically ~ 3 cm below the water surface to prevent sediment accumulation on juveniles. Lids of clear PVC helped stabilize temperatures and salinity. Light intensity was adjusted above each tank so all juveniles were exposed to $60 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ over a 12 h:12 h diurnal cycle. This orientation and low light intensity was chosen to mimic conditions in crevices and undersurfaces in the reef, where corals juveniles are usually found (Doropoulos et al., 2016). The number of juveniles per species placed in each replicate tank depended on how many had survived the 3–6-month period post-settlement: 9–10 juveniles per tank for *A. tenuis*, 16–18 for *A. millepora*, and 20–22 for *P. acuta*.

Suspended sediment concentrations in each experimental tank were characterized daily based on turbidity readings (Table S2, Supplementary material). Dissolved organic carbon, particulate organic carbon, total dissolved phosphorus, total particulate phosphorus, dissolved organic nitrogen, total particulate nitrogen, ammonium, nitrate, and nitrite were measured once per week in duplicate subsamples from the stock feeder tanks (Table S3, Supplementary material). Water samples were analyzed by the AIMS Analytical Services laboratory following Schaffelke et al. (2012). Nutrient treatments were designated as ‘low’ and ‘high’ nutrient enrichment, corresponding to the addition of +0 or $+0.6 \text{ mg OC l}^{-1}$ FSW, respectively. The treatment with 0 mg l^{-1} suspended sediments and low concentrations of nutrients was designated as the control.

2.4. Responses of juveniles to nutrient-enriched suspended sediments

2.4.1. Survivorship and growth

Juvenile survivorship was assessed every 3 to 4 days, with mortality defined as the point in time when live tissue was no longer present. Survivorship was expressed as the proportion of colonies within each tank that survived to the end of the experiment (day 40) in relation to the number of juveniles at the beginning of the experiment (day 1). Images of each juvenile were taken at the start of the experiment using a digital camera (Leica MC170) connected to a stereomicroscope. The area of live tissue on each juvenile colony was measured with the program ToupView 3.7. Initial size (S_{t1}) of juveniles varied between species; juveniles of *A. tenuis* and *A. millepora* had a similar size range (1.34 ± 0.84 and $1.49 \pm 1.25 \text{ mm}^2$ respectively; average \pm s.d.),

whereas *P. acuta* juveniles were considerably larger ($18.5 \pm 12.0 \text{ mm}^2$). Growth was estimated as the proportional change in size (ΔS) following a 40-day exposure period (S_{t2}), using the formula $\Delta S = (S_{t2} - S_{t1}) / S_{t1}$.

2.4.2. Photochemical efficiency of symbionts

The quantum yields of *Symbiodinium* communities associated with juvenile corals were measured by pulse amplitude modulation (PAM) fluorometry on day 39 of exposure. Maximum quantum yield of photosystem II (PSII) in dark-adapted samples represents the proportion of available light that can be photochemically quenched. Reductions in this parameter are indicative of photooxidative stress and damage to PSII (Jones et al., 1999). Effective quantum yield, as measured on illuminated samples, was used to estimate the efficiency of photochemical energy conversion within PSII under a given light intensity (Genty et al., 1989). Higher values of effective quantum yield represent more efficient use of incident radiation and, all other factors being equal, higher rates of photosynthesis (Finelli et al., 2005). Quantum yields were measured with a Maxi Imaging PAM Fluorometer (I-PAM, Walz GmbH, Germany), which measures the fluorescence of a selected area of interest in the image (i.e., the juvenile). For the measurements, all surviving juveniles were transferred into a 0.5 l container filled with FSW and dark-adapted for one hour prior to exposure to a saturation light pulse (gain = 2, intensity = 1, saturation pulse = 8). Maximum quantum yield was calculated using the formula $F_v/F_m = (F_m' - F_0)/F_m'$, where F_v = variable fluorescence, F_m' = maximum fluorescence under dark adaption, and F_0 = minimum fluorescence. Effective quantum yields were measured while juveniles were illuminated with an actinic light intensity of $20 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and calculated using the formula $\Delta F/F_m' = (F_m' - F)/F_m'$, where F_m' = maximum fluorescence and F = fluorescence yield, both measured under light conditions (Ralph et al., 2007).

2.4.3. Respiration and net photosynthesis

O_2 microelectrodes were used to measure respiration and photosynthesis in *A. tenuis* juveniles exposed to two suspended sediment treatments with no nutrient enrichment: 1) 0 mg l^{-1} suspended sediments (control), and 2) 100 mg l^{-1} suspended sediments (high suspended sediments). Measurements were performed between 16 and 18 days after the start of exposures for two individuals from the control treatment and two individuals from the high suspended sediment treatment. Each juvenile was placed in a custom-built flow chamber ($25 \times 10 \times 10 \text{ cm}$), through which seawater of each treatment was circulated at a flow velocity of $\sim 1 \text{ cm s}^{-1}$. A light intensity of $60 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ was used for homogeneous, vertical illumination of the juvenile in each treatment. O_2 microelectrodes (tip size: $10 \mu\text{m}$ in diameter; 90% response time (t_{90}) < 1 s) were built as described in (Revsbech, 1989) and calibrated with air-saturated water (100% air-saturation) and N_2 -bubbled water (0% air saturation). Microsensors were mounted on a motor-driven micromanipulator (MM3, Märzhäuser, Wetzlar, Germany) controlled by custom-written profiling software (μ -Profiler, <http://www.microsen-wiki.net/>), which also recorded signals amplified by a data acquisition device (DAQ-Pad 6009, National Instruments).

The micromanipulator was used to place microelectrodes in direct contact with coenosarc tissues (tissue connecting polyps) to minimize the destabilizing influence of polyp movement. In this position, the relative measurements between treatments are made in the same location on the microscale: for example, to test the relationship between respiration rates in the absence and presence of suspended solids (Weber et al., 2012). Positioning of the microelectrode on each juvenile was fine-tuned using the light-dark shift technique (Revsbech and Jorgensen, 1983), i.e., position was adjusted until an instantaneous and clear response in the signal was obtained when the light was turned off. One hour after the microsensors were positioned, light and dark profiles were performed ($n = 4$ –10 replicate profiles per colony) under the

treatment conditions to which juveniles were pre-exposed during the experiment (0 or 100 mg l⁻¹ of suspended sediments). To evaluate the response of juveniles to changes in water quality, measurements were then repeated 1 h after changing treatment conditions (by adding sediments to the tank or adding water to wash the sediments resulting in concentrations of 100 or 0 mg l⁻¹ of suspended sediments, respectively). Methodological restrictions prevented measurements with nutrient-enriched sediments, because it is not possible to add previously incubated nutrient-enriched sediments to a volume of water with non-enriched sediments (i.e. to change treatment conditions from non-enriched sediments to enriched sediments) and maintain suspended sediment concentrations without diluting nutrients. O₂ concentration profiles were measured from the tissue surface upwards into the water column in vertical steps of 50 μm (Fig. S4, Supplementary material). Net O₂ exchange fluxes were calculated from the measured steady-state concentration profiles using Fick's first law of diffusion, with a molecular diffusion coefficient for O₂ of 2.3535 × 10⁻⁵ cm² s⁻¹ (27 °C and salinity 35 psu).

2.5. Data analysis

Effects of treatments on juvenile survivorship were estimated using the Cox's Proportional Hazard (CPH) model (Cox, 1972), after statistical testing and fulfilling model assumptions (functions `cox.zph` and `coxph` in the package 'survival' of the statistical software R; R Development Core Team, 2016). The effects of suspended sediments and nutrient enrichment on coral responses (growth, effective quantum yield and maximum quantum yield) were analyzed using linear mixed effects models (LME), with suspended sediments (numerical factor: 0, 10, 30 or 100 mg l⁻¹) and nutrient enrichment (categorical factor: low and high enrichment) as fixed factors and tank as a random error term. Effects of different water quality conditions (0 or 100 mg l⁻¹) on the respiration and net photosynthesis of *A. tenuis* of juveniles were analyzed with general linear models (GLM), with suspended sediment concentration (categorical factor) as fixed factor. The functions `anova.lme` with marginal sum of squares (for the LME), `glm` (for the GLM), and `drop1` were used to estimate *P*-values. All LME and GLM analyses were done using the package `lme` in R (Team, 2016).

3. Results

3.1. Survivorship and growth

Survivorship of juveniles varied among species (Fig. 1). After 40 days of exposure, survivorship was high in all treatments for both *A. tenuis* (between 78.1 ± 0.1% and 90.6 ± 0.1%, average ± s.e. per tank) and *P. acuta* (between 93.8 ± 3.3% and 100% per tank), and was unaffected by the suspended sediment and nutrient enrichment treatments (*P* > 0.05 for all treatments and interactions, Table 1, Fig. 1). In contrast, survivorship of *A. millepora* juveniles declined significantly with increasing suspended sediment concentrations (*P* = 0.002, Table 1, Fig. 1), to 64 ± 0.06% when suspended sediments (100 mg l⁻¹) were combined with high nutrient enrichment, and to 82 ± 0.1% when combined with low nutrient enrichment. Although nutrient enrichment intensified the pattern of decreasing juvenile survivorship with increasing suspended sediments, neither nutrient enrichment on its own nor its interaction with sediments had statistically significant impact on *A. millepora* juvenile survivorship (Table 1, Fig. 1).

The effects of elevated levels of suspended sediments and nutrients on growth of juveniles were species-specific. Growth was significantly and detrimentally affected by suspended sediments in *A. tenuis* (*P* = 0.006; Table 2, Figs. 2–3) and *P. acuta* (*P* < 0.001; Table 2, Figs. 2–3), but not in *A. millepora* (*P* > 0.05; Table 2, Figs. 2–3). Nutrient enrichment and its interaction with sediments did not affect growth in any of the three species (all *P* > 0.05; Table 2, Figs. 2–3). At high concentrations of suspended sediments, some juveniles of each

species declined in size (i.e., partial colony mortality) (i.e., *A. tenuis* in both the 30 and 100 mg l⁻¹/low nutrient enrichment treatments; *A. millepora* in the 30 mg l⁻¹/low nutrient enrichment and 100 mg l⁻¹/high nutrient enrichment treatments; *P. acuta* in the 100 mg l⁻¹/high nutrient enrichment treatment; Fig. 2).

3.2. Photochemical efficiency of the symbionts

Maximum quantum yield (F_v/F_m) and effective quantum yield (ΔF/F_m) were consistently greater for *P. acuta* than for either *A. tenuis* or *A. millepora* (Table S5, Supplementary material). After 40 days of exposure, maximum quantum yield was unaffected by any of the treatments in all three species (all *P* > 0.05 Table 2). In contrast, effective quantum yield increased significantly as suspended sediment concentrations increased in both *A. tenuis* (*P* = 0.013; Table 2, Fig. 4) and *A. millepora* (*P* = 0.024; Table 2, Fig. 4), whereas the effects of nutrients and their interaction with sediments were non-significant for both species (all *P* > 0.05; Table 2, Fig. 4). There were no significant effects of suspended sediments, nutrients or their co-occurrence on the effective quantum yield of *P. acuta* (all *P* > 0.05, Table 2).

3.3. O₂ microelectrode characterization of respiration and net photosynthesis

Respiration rates of the four replicate juveniles of *A. tenuis* juveniles varied in response to suspended sediment exposure (Fig. 5a; Fig. S4, Supplementary material). O₂ consumption rates increased significantly (~1.6 to 7.9-fold) in the high suspended sediment (100 mg l⁻¹) compared with the control treatment (0 mg l⁻¹ suspended sediments; *P* < 0.05 for all replicates, Table 3, Fig. 5a). Net photosynthesis was significantly higher in one of the four juveniles (replicate 2, which had not previously been exposed to high suspended sediments) and unaltered in the others (Table 3, Fig. 5b).

4. Discussion

Our study shows that contact with elevated levels of suspended sediments (in the absence of particle deposition and light attenuation) negatively affects three to six-month-old juveniles of common Indo-Pacific inshore coral species in species-specific ways. High (100 mg l⁻¹) levels of suspended sediments significantly reduced survivorship but not the growth of *A. millepora* juveniles, whereas growth but not survivorship was affected in juveniles of *A. tenuis* and *P. acuta*. Furthermore, high levels of suspended sediments increased effective quantum yields in *Symbiodinium* symbionts associated with *A. tenuis* and *A. millepora*. In contrast, 40-days exposures to nutrient enrichment, either in the presence or absence of suspended sediments, had neither positive nor negative effects on any of the physiological variables measured. This latter finding is surprising and sheds light on two important processes. First, any potential scope for nutrient uptake via additional heterotrophy was insufficient to energetically offset stress from suspended sediments in all three species. Second, even prolonged exposure to nutrient enrichment did not significantly enhance the negative effects of suspended sediments on coral juveniles, at least when sediments remain in suspension. These findings contrast with the effects of deposited sediments enriched with nutrients that caused significant mortality in four-week-old coral juveniles within 43 h (Fabricius et al., 2003).

Decreases in survivorship and growth rates (linear extension) of adult coral colonies in response to suspended sediments have been attributed to depletion of available energy, as a consequence of increased energy requirements for respiration, sediment removal and repair of damaged tissues (Dikou, 2009; Flores et al., 2012; Browne et al., 2015b). Our results show species-specific sensitivity to suspended sediments and differences in patterns of energy allocation in response to this stressor; *A. tenuis* and *P. acuta* prioritized survivorship at the

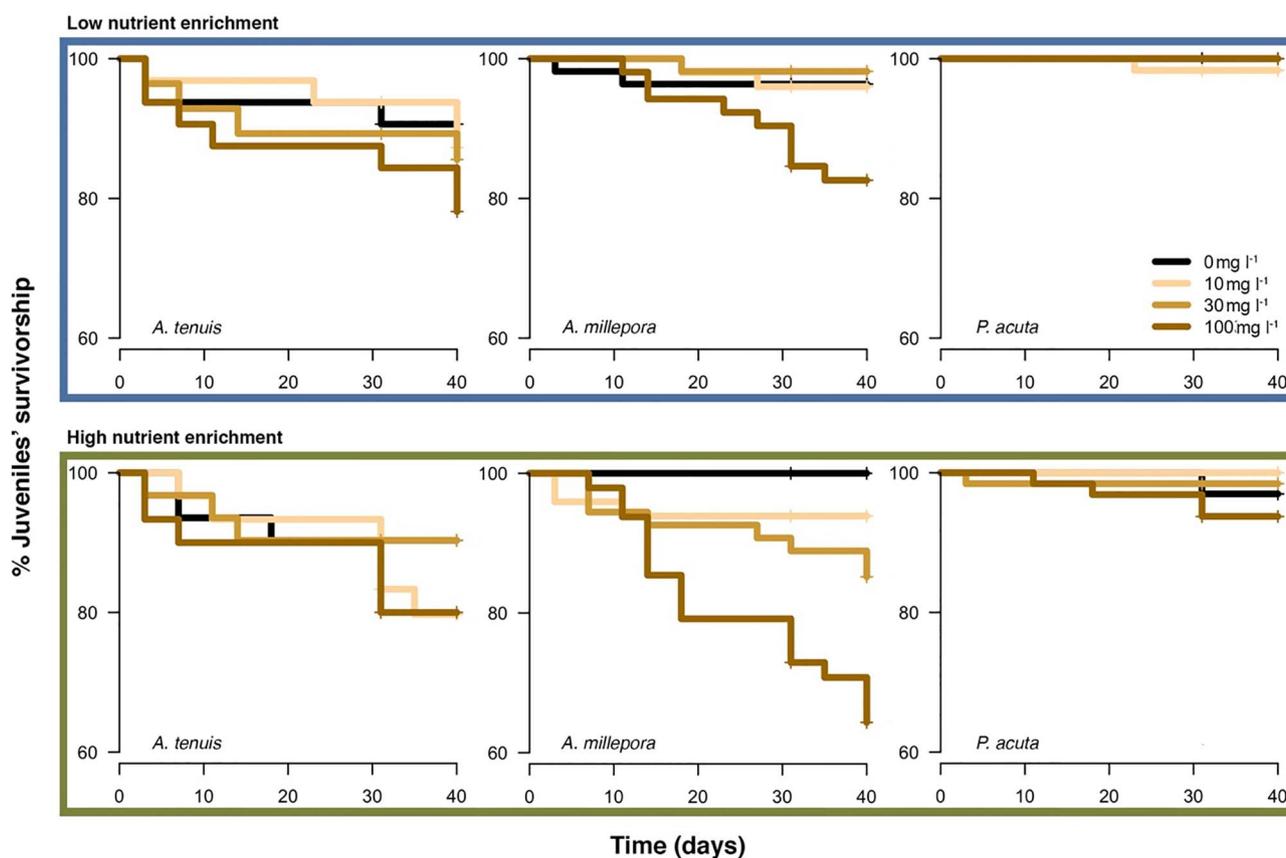


Fig. 1. Survivorship rates of *Acropora tenuis* (n = 27–32 juveniles per experimental treatment), *A. millepora* (n = 47–54 juveniles per experimental treatment) and *Pocillopora acuta* (n = 58–66 juveniles per experimental treatment) exposed to four suspended sediment treatments (SS: 0, 10, 30 or 100 mg l⁻¹) and nutrient enrichment (low [blue box], or high [green box]). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Effects of suspended sediments (SS) and nutrient enrichment (Nut) on the survivorship of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta* juveniles (Fig. 1). Results of Cox hazard regression analysis, with SS and Nut as fixed factors and tanks as random error term. Significance at P < 0.05 is shown in bold.

Factor	<i>A. tenuis</i>		<i>A. millepora</i>		<i>P. acuta</i>	
	z-Value	P-value	z-Value	P-value	z-Value	P-value
SS	1.415	0.157	3.002	0.002	-0.530	0.596
Nut	0.318	0.750	0.984	0.325	0.419	0.675
SS × Nut	-0.356	0.722	0.359	0.719	0.768	0.442

expense of growth as water quality declined, whereas *A. millepora* did not appear to have this capacity for such acclimatization. The impacts of light attenuation and suspended sediments are confounded in turbid

Table 2
Effects of suspended sediments (SS) and nutrient enrichment (Nut) on growth (Fig. 2) and *Symbiodinium* photophysiology [maximum quantum yield (Fig. 4) and effective quantum yield (Table S5, Supplementary material)] in juveniles of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta*. Results of linear mixed models (LME) with SS and Nut as fixed factors and tanks as random error term.

Variable	Factor	<i>A. tenuis</i>			<i>A. millepora</i>			<i>P. acuta</i>		
		Df	F-value	P-value	Df	F-value	P-value	Df	F-value	P-value
Growth	SS	1	9.089	0.006	1	3.294	0.084	1	15.913	< 0.001
	Nut	1	1.157	0.294	1	1.325	0.263	1	1.190	0.288
	SS × Nut	1	0.026	0.873	1	1.343	0.260	1	0.028	0.867
Maximum quantum yield (F _v /F _m)	SS	1	1.037	0.320	1	2.026	0.171	1	1.698	0.207
	Nut	1	1.060	0.315	1	1.471	0.240	1	1.460	0.240
	SS × Nut	1	1.288	0.269	1	0.006	0.938	1	1.634	0.215
Effective quantum yield (ΔF/F _m)	SS	1	5.940	0.013	1	5.969	0.024	1	1.650	0.213
	Nut	1	0.768	0.391	1	0.314	0.581	1	3.094	0.093
	SS × Nut	1	0.255	0.874	1	0.004	0.946	1	1.563	0.225

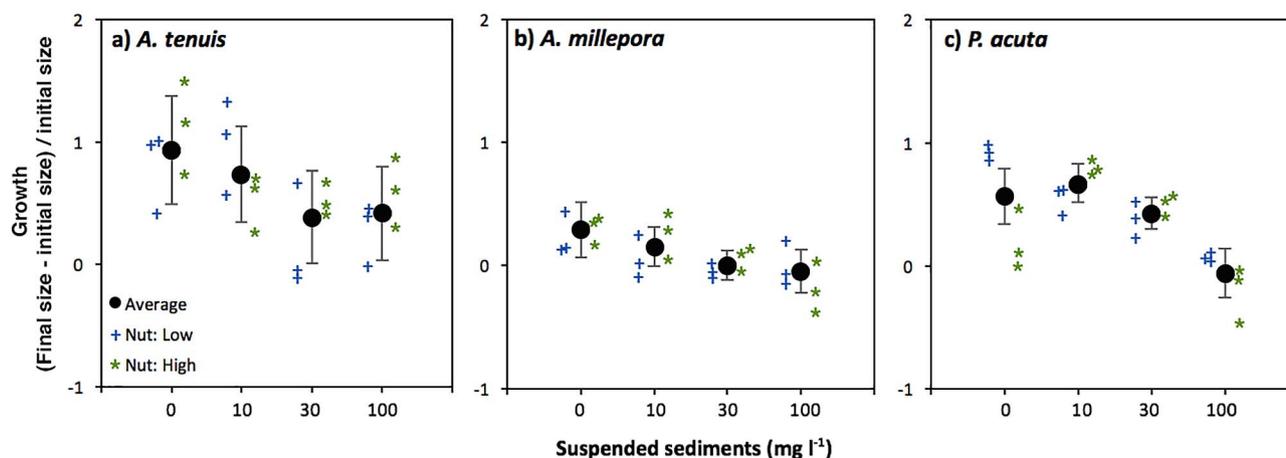


Fig. 2. Growth (proportional to initial size; average \pm s.e.) of *Acropora tenuis* ($n = 9$ – 10 juveniles per replicate tank, $n = 27$ – 32 per experimental treatment), *A. millepora* ($n = 16$ – 18 juveniles per replicate tank, $n = 47$ – 54 per experimental treatment) and *Pocillopora acuta* ($n = 20$ – 22 juveniles per replicate tank, $n = 58$ – 66 per experimental treatment), which had been exposed to four suspended sediment treatments [SS: 0, 10, 30 or 100 mg l^{-1} (circles in shades of brown)] and nutrient enrichment [Nut: low (blue cross) or high (green star), represent values of each tank replicate]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

suspended particles can be heavily colonized by microbial communities that are key in the formation and decomposition of organic matter, depleting oxygen and producing metabolic compounds like CO_2 , ammonium, toxic substances or act as “seed banks” for pathogens that can affect coral health (Simon et al., 2002, Carlos et al., 2013, Cárdenas et al., 2015).

The negative responses to suspended particles described here may be even more severe when coupled with light attenuation by suspended particles (Bessell-Browne et al., 2017b). Specifically, the additional impacts of light attenuation by turbidity *in situ* will change the quantity, quality, and spectral composition of available light, reducing the energy produced by photosynthesis which can provide up to 90% of the coral's daily energy requirements (Muscatine, 1990). Prolonged light attenuation will produce a negative energy balance reducing growth (Richmond, 1993), and can lead to the dissociation of coral-algal symbiosis (bleaching) (Glynn, 1996, DeSalvo et al., 2012). Sediment deposition is also likely to increase the effect of suspended sediments on upward-facing juveniles due to smothering and tissue necrosis in comparison with the vertically positioned colonies in this study. Smothering of juveniles occurs when ciliary movement, hydrostatic inflation, mucus entanglement and tentacle movement is insufficient to remove deposited sediments (Jones et al., 2016), and the resulting build-up of sediments causes bleaching and partial tissue necrosis as a consequence of hypoxia (Fabricius, 2005, Weber et al., 2006, Weber et al., 2012). Further studies that specifically compare the main cause-effect pathways of sediment stress on coral juveniles are clearly warranted.

Increased respiration rates of *A. tenuis* juveniles under high levels of suspended sediments suggest the activation of processes that increase energy expenditure, as has been demonstrated in for adult corals (Telesnicki and Goldberg, 1995, Browne et al., 2014). Corals are both autotrophs and heterotrophs, and many studies have demonstrated their ability to gain at least a portion of energy heterotrophically by suspension feeding (Houlbreque and Ferrier-Pagès, 2009). Ingestion of sediments has been observed in several coral species (Stafford-Smith, 1993, Anthony, 2000) through active capture via tentacle movements (Jones et al., 2016). Although capture of sediments and associated organic matter provides nutritional benefits to some coral species (Anthony, 1999, Anthony and Fabricius, 2000), sediments also represents an energetic cost to the colony as a consequence of the need for clearance activity to remove deposited sediments from tissue surfaces. Production of mucus (Bessell-Browne et al., 2017a) and the increased ciliary and tentacle activity that corals exhibit under high turbidity conditions are energy demanding processes (Abdel-Salam et al., 1988) and thus elevate respiration rates, which in turn, decreases energy

available for processes like growth and survival. Such energetic costs may potentially overcome the benefits of heterotrophic feeding. Relative to zooplankton, suspended sediments represent a poor-quality food source (Anthony, 1999), and energy costs associated with maintenance and repair of damaged tissues are higher when corals are exposed to this stressor. Such energetic costs are likely to impact other important parameters, such as growth or survival of the colony, supporting our results and results from studies of adult colonies (Anthony and Fabricius, 2000, Anthony and Connolly, 2004, Browne et al., 2015b). Our results show that declining water quality incurs energy costs (i.e., high respiration rates), which will have long-term repercussions for coral growth, population size structures and consequently for coral cover.

The consistently high maximum quantum yields (F_v/F_m') observed across all treatments indicates that photosystem II of *Symbiodinium* symbionts is robust to levels of suspended sediment levels up to 100 mg l^{-1} . The absence of an effect of suspended sediments and nutrient enrichment, as individual stressor or when combined, on maximum quantum yields, is corroborated by results found for adult corals exposed to suspended sediments (Sofonia and Anthony, 2008, Flores et al., 2012, Browne et al., 2015a, Liu et al., 2015, Bessell-Browne et al., 2017b). In contrast, reductions in F_v/F_m' have been recorded when sediments accumulate on corals, causing tissue damage by smothering (Philipp and Fabricius, 2003, Weber et al., 2006, Piniak, 2007). In our study, sediments did not accumulate on coral tissues, thus symbionts had sufficient light to alleviate stress from potential shading and prevent damage to photosystem II. Increases in effective quantum yield with increasing levels of suspended sediment suggest that symbionts associated with coral juveniles compensated for rising turbidity by increasing their photochemical efficiency, as has been found for adult corals in field studies (Piniak and Storlazzi, 2008, Sawall et al., 2011). Effective quantum yields have been reported to increase when food is abundant (i.e., high concentrations of sediments or nutrients) and heterotrophy favoured (Borell and Bischof, 2008, Ferrier-Pagès et al., 2010). Under such circumstances, *Symbiodinium* can take up ammonium produced by host cells as a nitrogen source (Piniak et al., 2003), a process that could also be augmented in corals exposed to high concentrations of some sediment types and which could positively affect the photochemical efficiency of chlorophyll (Ferrier-Pagès et al., 2010). There were apparent changes in colour associated with the sediment and nutrient treatments (Fig. 3), indicating possible effects on the symbiosis, including dissociation of the symbionts (bleaching). However, the small size of many of the juveniles, along with the large variation in coloration from the mouth of the polyp to the coenosarc

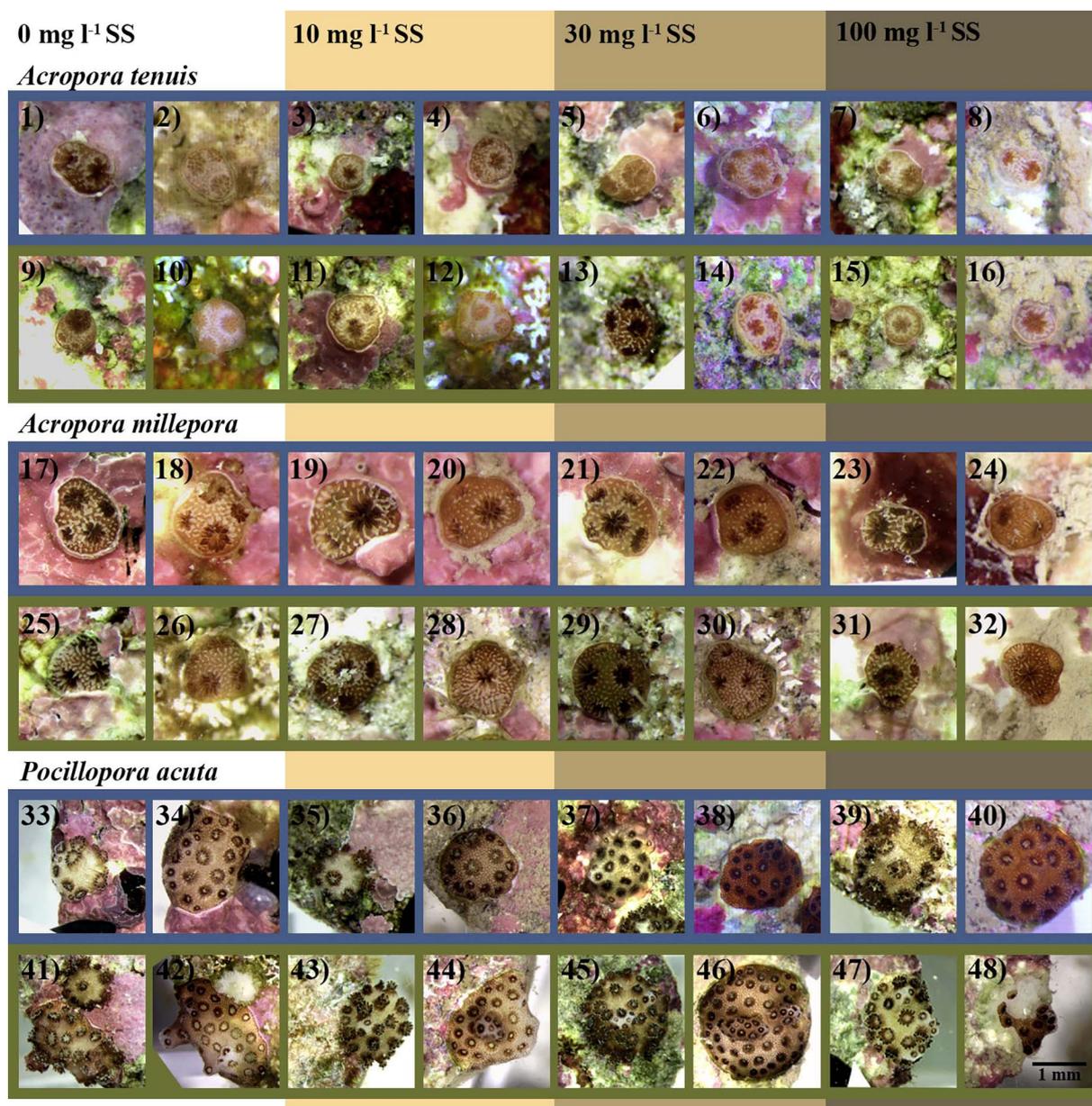


Fig. 3. Paired images of representative juveniles of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta* comparing their macroscopic appearances on day 1 (odd numbers) and day 40 (even numbers) of treatment exposure. Treatments consisted of four suspended sediment concentrations (0, 10, 30 or 100 mg l⁻¹) and two levels of nutrient enrichment (low [blue boxes], or high [green boxes]). Control treatment: low nutrient enrichment and suspended sediment concentration = 0 mg l⁻¹. Medium or large sized colonies showing an average response for the respective treatment were selected for this figure to clearly highlight changes in colonies over 40 days. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

precluded the reliable counting of symbionts, Chl *a* measurements or direct colour comparisons. Further research is needed to address the mechanisms of action of suspended sediments on the associated zooxanthellae of juveniles.

Increases in respiration rates, together with depletions in growth and survivorship rates of juveniles may be linked to the irritation caused by contact with suspended sediments (or their associated chemistry and microbiology). Our results show that the physical presence of suspended particles, without changes in light availability or by sediment deposition on the colony tissue, is sensed by the juveniles producing instant physiological response. The production of mucus under turbid conditions has been described as a response to deposited sediments in adult corals (Bessell-Browne et al., 2017a), and to suspended sediments in coral embryos and larvae (Ricardo et al., 2016). Mucus production may also help explain the increasing respiration rates and representing a cost in the energy budget of the juvenile colonies. As

a protective reflex response, it is functionally analogous to a human sneezing generated under the presence of dust (Bessell-Browne et al., 2017a). Further research is required to study this physiological response in juveniles, and whether it is analogous to the phenomena observed in larvae and adult colonies exposed to suspended sediments. The lack of an effect of nutrient enrichment on the physiological variables measured in all three species during a 40-day exposure period (either as an energy source or as a stressor), raises uncertainties about the direct role of nutrient enrichment in coral reef declines. The view that nutrient enrichment is responsible for coral reef declines has been challenged by evidence that some corals thrive in high-nutrient turbid waters, and by several experimental studies that did not find clear negative impacts on the physiology of adult corals (Bongiorni et al., 2003b, Fabricius, 2005, Rasher et al., 2012). However, our results should be interpreted with caution, as we did not assess the effects of sediment deposition (Perez et al., 2014, Moeller et al., 2016), a factor

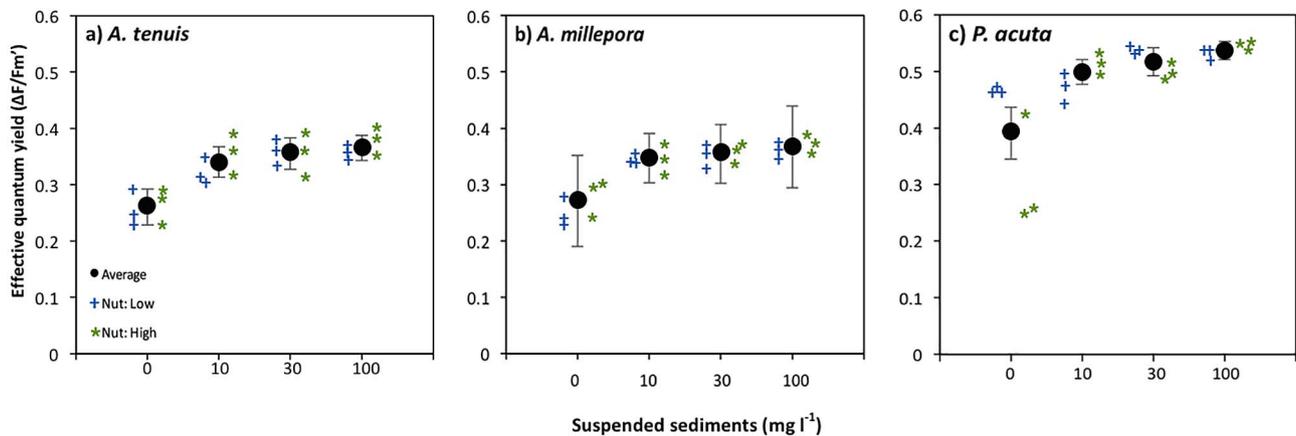


Fig. 4. Effective quantum yield ($\Delta F/F_m'$, average \pm s.e.) of *Symbiodinium* associated with juveniles of *Acropora tenuis* ($n = 9-10$ juveniles per replicate tank, $n = 27-32$ per experimental treatment), *A. millepora* ($n = 16-18$ juveniles per replicate tank, $n = 47-54$ per experimental treatment) and *Pocillopora acuta* ($n = 20-22$ juveniles per replicate tank, $n = 58-66$ per experimental treatment), which had been exposed to four suspended sediment treatments [SS: 0, 10, 30 or 100 mg l^{-1} (black circles)] and two nutrient enrichment treatments [Nut: low (blue cross) or high (green star), each symbol represents a tank replicate ($n = 3$ tanks)]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that when co-occurring with nutrient enrichment is known to have large impacts on both juvenile survivorship (Fabricius et al., 2003) and adult physiology (Weber et al., 2012). Also, the co-occurrence of many other factors (e.g., proliferation of competitors, predators) were not addressed in the present study, but are known to have negative effects on coral communities under scenarios of high turbidity and nutrient enrichment (Bruno et al., 2003, Le Grand and Fabricius, 2011, Liu et al., 2015).

The energetics of corals and their ability to sustain growth and survivorship in differing turbidity regimes are functions of their capacity to tolerate and utilise sediments, and their strategies to cope with stress conditions. This study suggests that, although stress-related responses affecting growth and survivorship vary among coral juveniles of the three species, impacts on both processes will negatively affect populations, either via a reduction in the numbers of new individuals reaching reproductive size classes due to increased mortality, or reductions in growth rates of juveniles. Whereas morphological differences among species have been shown to be determinants of adult coral survivorship under sediment stress conditions (Stafford-Smith, 1993, Huang et al., 2011, Flores et al., 2012, Junjie et al., 2014), physiological

Table 3

Summary of the effects of experimental treatments on 4-month-old juveniles of *Acropora tenuis* on rates of dark respiration (R_D) and net photosynthesis (P_N) based on general linear models (GLM) with suspended sediment concentration (categorical factor) as fixed factor. Water quality changes were performed from 0 mg l^{-1} and low nutrient enrichment to 100 mg l^{-1} with low nutrient enrichment or conversely. Replicates 1 and 2 were acclimatized to control treatment (0 mg l^{-1} and low nutrient enrichment), while replicates 3 and 4 were acclimatized to the high suspended sediment treatment (100 mg l^{-1} low nutrient enrichment).

Original treatment	Replicate	R_D			P_N		
		Df	F-value	P-value	Df	F-value	P-value
SS: 0 mg l^{-1} , Nut: low	1	1	7.56	0.018	1	0.18	0.674
	2	1	132.43	< 0.001	1	30.01	< 0.001
SS: 100 mg l^{-1} , Nut: low	1	1	208.48	< 0.001	1	4.10	0.070
	2	1	9.32	0.018	1	0.89	0.381

differences play a more important role in the capacity of small-sized individuals that have not yet developed adult growth forms to cope with sediment in suspension stress. Ongoing development of coastal zones will likely lead to further increases in suspended sediments and

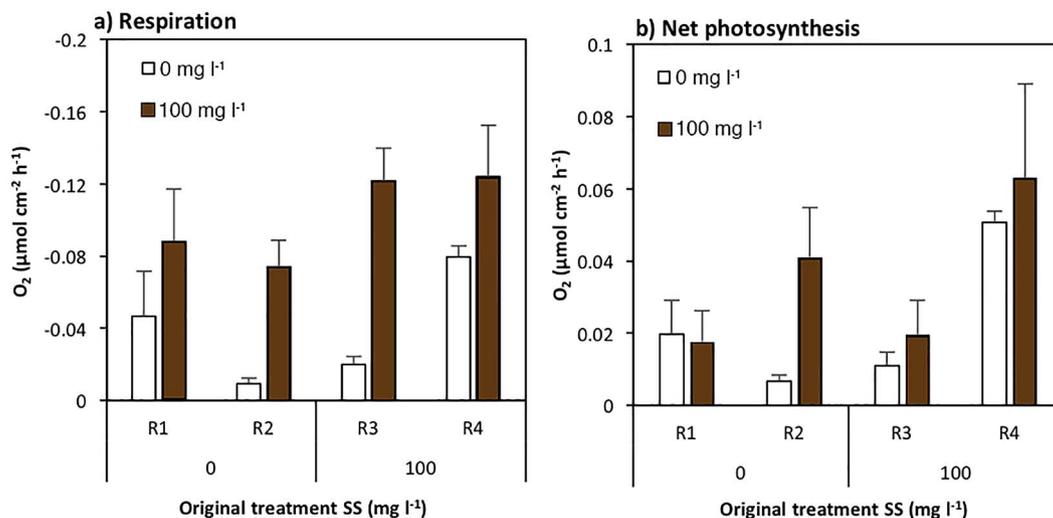


Fig. 5. Rates of a) Respiration in the dark (R_D), and b) Net photosynthesis in the light (P_N) of *Acropora tenuis* juveniles measured by O_2 microelectrodes at the end of 18 days of exposure to two suspended sediment (SS) treatments (SS: 0 mg l^{-1} or 100 mg l^{-1} SS in FSW, $n =$ two replicate juveniles per treatment). White bars: 0 mg l^{-1} SS; brown bars: 100 mg l^{-1} SS. Values are averages \pm s.d. ($n = 4-10$ measurements per juvenile under each suspended sediment condition). R1 to R4 = replicate juveniles. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

nutrients in coastal marine ecosystems. Studies on how early life history stages (i.e. gametes, larvae, recruits, juveniles and adult colonies) and processes (fecundity, fertilization, embryo development, colony growth and survivorship) respond to these stressors are critical for understanding long-term effects of degraded water quality on the population dynamics of inshore coral reef species. Management strategies and plans need to consider the different life history stages of corals and their unique thresholds for processes that are essential for the maintenance and replenishment of coral populations. Although adults of some coral species have moderately high tolerances to suspended sediments and nutrients, it is important to recognise that species thresholds might be determined by the susceptibility of early life history stages to these stressors.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.marpolbul.2017.08.003>.

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