



# Impacts of Sediments on Coral Energetics: Partitioning the Effects of Turbidity and Settling Particles

Reef K. Junjie<sup>1</sup>, Nicola K. Browne<sup>2\*</sup>, Paul L. A. Erftemeijer<sup>3,4</sup>, Peter A. Todd<sup>1,5</sup>

**1** Experimental Marine and Ecology Laboratory, Department of Biological Sciences, National University of Singapore, Singapore, Singapore, **2** Department of Environment and Agriculture, Curtin University, Perth, Australia, **3** Sinclair Knight Merz (SKM), Perth, Australia, **4** The UWA Oceans Institute, University of Western Australia, Crawley, Australia, **5** Tropical Marine Science Institute, National University of Singapore, Singapore, Singapore

## Abstract

Sediment loads have long been known to be deleterious to corals, but the effects of turbidity and settling particles have not previously been partitioned. This study provides a novel approach using inert silicon carbide powder to partition and quantify the mechanical effects of sediment settling versus reduced light under a chronically high sedimentary regime on two turbid water corals commonly found in Singapore (*Galaxea fascicularis* and *Goniopora somaliensis*). Coral fragments were evenly distributed among three treatments: an open control (30% ambient PAR), a shaded control (15% ambient PAR) and sediment treatment (15% ambient PAR; 26.4 mg cm<sup>-2</sup> day<sup>-1</sup>). The rate of photosynthesis and respiration, and the dark-adapted quantum yield were measured once a week for four weeks. By week four, the photosynthesis to respiration ratio (P/R ratio) and the photosynthetic yield ( $F_v/F_m$ ) had fallen by 14% and 3–17% respectively in the shaded control, contrasting with corals exposed to sediments whose P/R ratio and yield had declined by 21% and 18–34% respectively. The differences in rates between the shaded control and the sediment treatment were attributed to the mechanical effects of sediment deposition. The physiological response to sediment stress differed between species with *G. fascicularis* experiencing a greater decline in the net photosynthetic yield (13%) than *G. somaliensis* (9.5%), but a smaller increase in the respiration rates (*G. fascicularis* = 9.9%, *G. somaliensis* = 14.2%). These different physiological responses were attributed, in part, to coral morphology and highlighted key physiological processes that drive species distribution along high to low turbidity and depositional gradients.

**Citation:** Junjie RK, Browne NK, Erftemeijer PLA, Todd PA (2014) Impacts of Sediments on Coral Energetics: Partitioning the Effects of Turbidity and Settling Particles. PLoS ONE 9(9): e107195. doi:10.1371/journal.pone.0107195

**Editor:** Randi D. Rotjan, New England Aquarium, United States of America

**Received:** June 27, 2013; **Accepted:** August 14, 2014; **Published:** September 8, 2014

**Copyright:** © 2014 Junjie et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** This research was carried out as part of Singapore-Delfte Water Alliance Marine & Coastal Research Program (Theme 2): “Dredging and infrastructure development near critical marine ecosystems” (R-264-001-001-272) with additional support from the National Parks-funded project: “Impacts of ship-wake-induced sediment resuspension on coral reefs and seagrass in Singapore.” The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors confirm that they have the following interests: co-author Nicola Browne is employed at DHI Singapore and Paul Erftemeijer is employed by Sinclair Knight Merz (SKM). There are no patents, products in development or marketed products to declare. This does not alter the authors’ adherence to all the PLOS ONE policies on sharing data and materials.

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

## Introduction

Singapore’s diverse coral reef system hosts 255 hard coral species [1,2] but pressure from coastal reclamation and dredging operations have resulted in the loss of at least 60% of its original coral reef area [3]. It is estimated that poor water quality associated with high sediment loads will further reduce Singapore’s original reef to only 21% by 2030 [4]. Since the 1970s, sedimentation rates have risen from 3.2–5.9 mg cm<sup>-2</sup> d<sup>-1</sup> [5] to 15–30 mg cm<sup>-2</sup> d<sup>-1</sup> [6,7,8] with average visibility reduced from 10 m (1960s) to less than 2 m [9]. Sedimentation rates and turbidity decline with increasing distance from Singapore’s mainland, resulting in spatial variations in coral species composition and reef health [10]. The least threatened and most diverse coral reefs are those furthest to the south (e.g. at Raffles light house which supports 141 hard coral species).

Inshore to offshore changes in coral cover and/or composition observed in numerous coral reef systems, including the Great Barrier Reef, are in part attributed to spatial differences in the sediment regime [11,12,13]. Coral species better adapted or acclimatised to cope with the stress effects of down-welling

sediment are typically more abundant in reef habitats exposed to high sediment loads [14,15,16,17]. Increased sediment deposition can cause coral mortality by smothering and burying [18], limit hard substrate availability and decrease larvae settlement rates, increase energy costs due to active sediment removal [19] and reduce energy available for coral calcification [20,21] and reproduction, and promote tissue infection [22,23,24]. High sediment loads usually result in greater turbidity, limiting light availability and reducing photosynthetic yield by symbiotic zooxanthellae. This results in a decrease in net productivity and lower carbon gain. Anthony and Hoegh-Guldberg [25] showed that it is possible for zooxanthellae to photo-acclimatize by increasing the number and size of chloroplasts. This response varies among species with some corals being better able to photo-acclimate, and thus capable of growing at deeper sites or on turbid reefs typically found close to shore.

Many corals on turbid reefs have developed morphological as well as physiological mechanisms that have enabled them to survive the negative effects of high sediment loads. For example, *Turbinaria* develops a funnel shape which directs sediments to the colony base reducing the area affected by sediment [26] whereas

other corals have developed ways to rapidly remove sediment either through polyp projection (e.g. *Goniopora*), ciliary action (e.g. *Galaxea*) or mucus production [27,28]. However, the removal of sediments comes at an energetic cost to the affected corals [29]. Under chronically high sedimentation and turbidity regimes, or during acute sediment stress events such as dredging operations, corals experience limited light and energy capture coupled with increased energy expenditure, which may exceed coral tolerances and lead to tissue mortality [30]. The point when coral tolerances are exceeded, and the physiological changes that occur within the coral due to both the separate and combined effects of reduced light and sediment smothering, are not fully understood. This uncertainty is due to the number of associated effects of sediments that go beyond shading the coral, most of which are negative: e.g. the sediment barrier prevents gas exchange and waste removal [19], and nutrients and organics in sediment promote rapid increases in bacterial populations in coral mucus [31]. However, sediments may also provide an additional food source through heterotrophic feeding, offsetting the carbon deficit [32]. Coral responses to sediments differ significantly both among and within coral species [27,30], further complicating the analysis.

The balance between sedimentation and sediment resuspension is considered to be a key driver of coral community composition and distribution on turbid coral reefs [33,34,35,36,37,38]. Numerous studies have attempted to understand the biological response of corals to sediment stress by measuring growth rates, photosynthetic yields, the ratio of photosynthesis to respiration (P/R ratio), and tissue mortality. For example, a study by Crabbe and Smith [38] on turbid reefs in south-east Sulawesi, Indonesia, found lower growth rates of both branching and non-branching corals with increased sedimentation, while Weber et al. [39] measured reduced photosynthetic yields within 48 hrs of sediments settling on corals. In the latter study, sediments with higher organic content (>0.5%) caused the largest reductions in the photosynthetic yield (>30% within 48 hrs). Exposure to sediments will also decrease the P/R ratio [30,40,41], however, there are disagreements within the literature as to whether the reduction in the P/R ratio is largely driven by light-limited photosynthesis or increased respiration rates associated with removing settling sediments. If the former is correct, then photo-efficiency together with heterotrophic capacity would drive the partitioning of species between reef habitats characterised by high sediment resuspension rates versus habitats dominated by sediment deposition [42]. However, Anthony and Connolly [43] suggest that energy costs associated with handling sediment stress, e.g. sediment clearing [29] and increased respiration, drive coral sediment tolerances and hence species distribution between resuspension and depositional environments. What remains unclear is how coral physiology is influenced separately by turbidity and limited light penetration versus the physical effects of sediments settling on corals and subsequent sediment clearing.

The present study used a laboratory-based approach to determine the physiological effects of sediment deposition, independent of light, on two coral species (*G. fascicularis*, *G. somaliensis*) commonly found on turbid water reefs in the Indo-Pacific. The experimental setup was designed to deliver sediments at a constant chronic rate over several weeks that resulted in a sedimentation rate typically measured on turbid reefs. Inert silicon carbide powder (10 µm to 300 µm), rather than natural reef material, was used in the study to assess the mechanical effects of down-welling particles on corals without confounding factors such as nutrients, heavy metals and microbes found in natural sediments [44]. The effects of sedimentation on coral physiology were examined and compared with two controls:

open and shaded. The light levels in the shaded control were carefully aligned with the light levels in the sediment exposed treatment, thereby allowing the comparative assessment of reduced light versus reduced light and sedimentation. The physiological response of corals to sediment deposition and light reduction were measured using P/R ratios and photosynthetic yields. The two primary objectives of the study were to: 1) quantify the physiological effects of chronic sedimentation for two common Indo-Pacific corals, and 2) assess the difference in coral physiological response between the mechanical effects of sediment deposition and light reduction.

## Materials and Methods

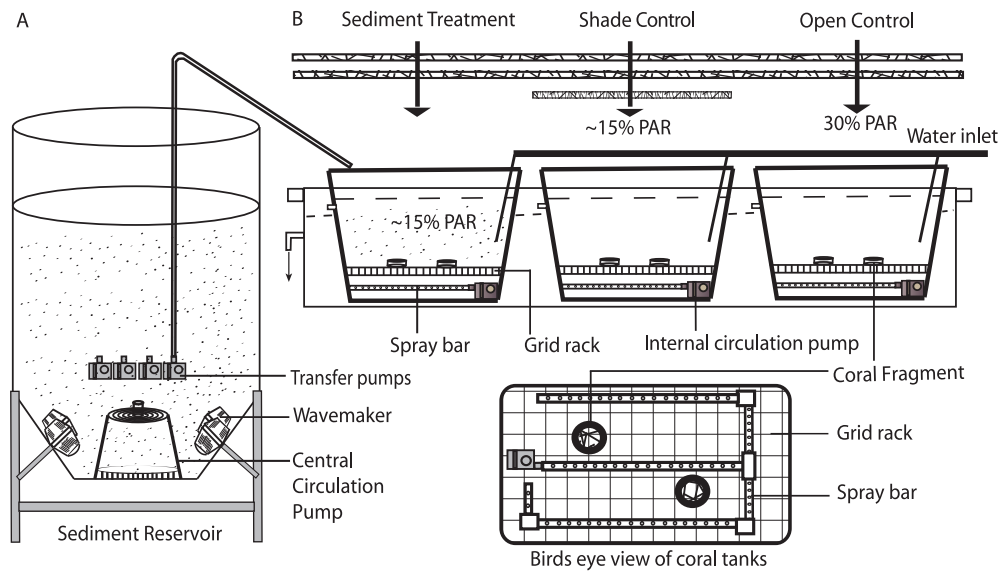
### Study species and sampling design

*Galaxea fascicularis* and *Goniopora somaliensis* are commonly found in sheltered reef environments throughout the Indo-Pacific [45]. *G. fascicularis* grows into domed colonies with cylindrical corallites (<10 mm diameter) linked together by horizontal plates (coenosteum) [45]. In contrast, *G. somaliensis* forms sub-massive colonies with shallow calices and small corallites (3 to 5 mm diameter) with a smooth surface [45]. Both species are hermatypic, meeting the majority of their energy demands through photosynthesis by the zooxanthellae living within their tissues. Research permit (No. NP/RP12-007), that includes permission to collect corals, was granted by the National Parks Board (NParks), a statutory government board in charge of terrestrial and marine parks in Singapore, under the project entitled 'Impacts of ship-wake induced sediment resuspension on corals reefs and sea grass in Singapore.'

In December 2011, fragments (surface area =  $95 \pm 2 \text{ cm}^2$ , determined using the 'aluminium foil' method [46]) were chiselled off 12 colonies of *G. fascicularis* and 12 colonies of *G. somaliensis* found at ~3 m depth at Lowest Astronomical Tide (LAT) at the north-western fringing reef of Pulau Hantu (103.44°E, 1.13°N): an island located 8 km southwest of Singapore's main island. In the mid-1970s much of the reef flat surrounding Pulau Hantu was destroyed following a reclamation project which increased the island's land area from 0.024 to 0.12 km<sup>2</sup> [2]. Today, approximately 2.21 km<sup>2</sup> of intertidal reef flat remains [47]. Sedimentation rates on the reef slope often exceed  $10 \text{ mg cm}^{-2} \text{ d}^{-1}$  [6,48,49], levels considered to be detrimental to the more sensitive species of coral [40]. At 3 m depth (LAT), turbidity typically ranges between 5 and 20 mg l<sup>-1</sup> and light levels vary from 50 to 200 mol photons m<sup>-2</sup> s<sup>-1</sup> [48]. All fragments were maintained in a holding tank supplied with continuous flow of sand-filtered seawater at the Tropical Marine Science Institute research facility on St John's Island, south of mainland Singapore (193.85°E, 1.22°N). Corals were left to acclimatize for three weeks before the experiment commenced in January 2012.

### Experimental setup and design

The experimental setup, adapted from Anthony [50], comprised of 12 tanks (42 L: 45×30×31 cm) with three different treatments: open control, shaded control, and sediment-stressed (Fig. 1). Each tank received a constant supply of fresh sand-filtered seawater through transfer pumps from the sediment reservoir at a rate of ~350 cm<sup>3</sup> min<sup>-1</sup>. An internal convection current at the bottom of each sediment treatment tank prevented immediate settlement of sediment through the use of a spray bar attached to an internal circulation pump (Boyu 1200 L h<sup>-1</sup>, China). The tanks were placed in a fiberglass water bath (1.6×1.5×0.3 m) with continuous water flow to ensure uniform water temperature in all the tanks (~28°C; temperatures typically experienced in Singa-



**Figure 1. Experimental setup.** (A) Sediment reservoir, (B) Coral treatment tanks. Four tanks for each treatment (sediment, shade, open) were placed in a water bath positioned under a shade cloth which reduced ambient light to 30%. Additional shading was placed over the shaded to control which further reduced ambient light levels to 15%, comparable light levels to that of the sediment treatment tanks. doi:10.1371/journal.pone.0107195.g001

pore waters). Following acclimatization, one fragment from each species was randomly selected and placed in the treatment tanks on a plastic grid to prevent accumulation of sediments at the base of each coral fragment. Fragments were rotated between the four corners within each tank once per week for four weeks.

### Sediment preparation and delivery

The grain size distribution of the natural sedimentation profile at Pulau Hantu was analysed by Lui et al. [44] through laser diffraction particle size analyses (Malvern Mastersizer Particle Size Analyser, UK) and matched using a combination of commercially available particle sizes of silicon carbide powder (Kemet Far East Pte Ltd). Silicon carbide, also known as carborundum, is chemically inert and has been previously used in coral sediment rejection studies [19]. The final silicon carbide mix contained particle sizes ranging from 10  $\mu\text{m}$  to 300  $\mu\text{m}$ , and had a median particle size of 60  $\mu\text{m}$  (Fig. 2).

A 250 L tapered bottom cylindrical fibre-glass drum was fabricated and used as the sediment suspension reservoir, providing material to the four sediment-stressed tanks. Silicon carbide in the drum was kept in suspension and homogenized by a central circulation pump and two aquarium wave-makers (Sun Sun 6000 L  $\text{h}^{-1}$ , China; Fig. 1). The sediment-suspension (75 ml) was supplied to the sediment-stress treatment tanks, via four transfer pumps (BOYU 1200 L  $\text{h}^{-1}$ , China), in discrete 3 s pulses every 10 minutes, which resulted in a relatively constant sediment “rain” in the tanks. The sedimentation rate was measured by placing three petri dishes (75 mm diameter) in each sediment-stress tank for 24 h, and the mean sedimentation rates for the four individual tanks were:  $26.6 \pm 0.28$ ,  $26.3 \pm 0.38$ ,  $25.8 \pm 0.55$  and  $27.0 \pm 0.18$   $\text{mg cm}^{-2} \text{day}^{-1}$ .

### Light measurements and attenuation

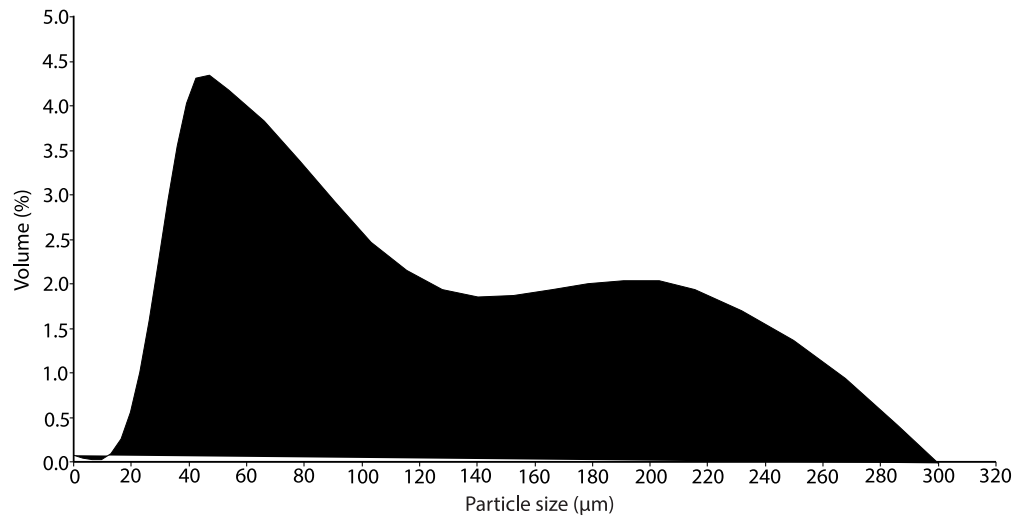
The experiment design was setup outdoors underneath shading nets that reduced solar light penetration to  $\sim 30\%$  of ambient light. In January 2012, the daily surface irradiance in the open control ranged from 600 to 1800  $\text{mol photons m}^{-2} \text{s}^{-1}$  (measured in the

tanks at the level of the coral fragments) between 10 am and 2 pm. Prior to the start of the experiment, light measurements using LI-1400 Data logger (LI-COR, United States) indicated that light levels within the sediment stress tanks further reduced light penetration to  $\sim 50\%$  of surface irradiation. Hence, additional shade netting was added to create the shade control tanks so that they also received  $\sim 15\%$  ambient PAR (Fig. 1).

We acknowledge that when sediments settle on corals at a rate that far exceeds their removal rate (during rapid sediment loading events e.g. dredging) the sediment layer creates an additional barrier to light [51], further limiting photosynthesis. However, in this chronic sedimentary regime, the level of sediment deposition ( $\sim 26 \text{ mg cm}^{-2} \text{day}^{-1}$ ) was well below previous measured rates that may lead to light attenuation at the surface (200  $\text{mg cm}^{-2}$  leads to a 75% light reduction at the surface [29]) and the two coral species were able to remove sediments from their surfaces relatively quickly. Hence, we are confident that light levels at the coral surface in both the shaded control and sediment treatment tanks were comparable.

### Physiological assessment

Two physiological parameters—P/R ratio and photosynthetic yield—were used as quantitative indicators of coral stress. The maximum photosynthetic yield ( $F_v/F_m$ ) for all 24 coral fragments was measured weekly between 1 and 3 pm using a Diving-PAM, Walz Germany [52]. The coral fragments were dark-adapted for 10 min before fluorescence yield measurements were taken [53,54]. The optical-fiber probe was kept at a constant distance of 5 mm from the surface of the coral and the average of five measurements for each coral fragment was calculated.  $F_o$  was measured by applying a pulsed measuring beam of  $<1 \mu\text{mol photon m}^{-2} \text{s}^{-1}$  and the emission  $F_m$  was measured following the application of a saturating pulse of actinic light ( $>1000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ ). The P/R ratio was measured using RESP-EDU software and Loligo Systems respiratory system (Denmark) between 10 am and 12 pm. A circular respirometry chamber (1.5 L) with a circulatory pump and an integrated galvanic cell oxygen probe (Loligo Systems, Denmark), was fabricated to



**Figure 2. The sediment particle profile of the silicon carbide powder.**  
doi:10.1371/journal.pone.0107195.g002

accommodate the size of the fragments. Oxygen consumption/production ( $\text{mg O}_2 \text{ l}^{-1}$ ) within the chamber (after subtracting the volume of coral) was measured every 1 minute for 5 minutes, followed by a 2 min flush period. The net photosynthetic rates were measured after 2 hrs of solar light irradiance ( $295 \pm 10 \text{ mol photons m}^{-2} \text{ s}^{-1}$ ; ambient light under shading) whereas respiratory rates were measured after 10 min incubation in the dark. Oxygen production and respiration rates were normalised to the surface area of live tissue for each coral fragment ( $\mu\text{mol cm}^{-2} \text{ hr}^{-1}$ ), and the P/R ratio was calculated by dividing the gross photosynthetic rate (the net photosynthetic rate added to the respiration rate) by the respiration rate.

### Statistical analyses

All statistical analyses were performed using IBM SPSS Statistics Standard v. 19 (2011), comparing the percentage change in photosynthesis, respiration and yield between treatments over the four weeks. Percentage change, as opposed to absolute values, was used as coral fragments in week 1 had marginally variable baseline photosynthesis, respiration and yield values. Hence, absolute values averaged over replicates could obscure trends. Oxygen production and respiration ( $\mu\text{mol cm}^{-2} \text{ hr}^{-1}$ ) and yield measurements (Fv/Fm) were converted to a percentage change by comparing the rate in weeks 2, 3 and 4, to rates and yields collected in week 1. Negative values of percentage change indicated a decline in the rate and yield. Data were checked for normality and homogeneity of variance using the Shapiro-Wilk test and Levene's test respectively. One-way repeated measures ANOVAs ( $\alpha = 0.05$ ) were performed ( $n = 4$ ), with adjustments made for multiple comparisons using Bonferroni corrections, to assess if and when there was a significant change in rates and yields over the four weeks for each of the controls (open and shaded) and the sediment-stressed treatment. Mauchy's test of sphericity was carried out, and where the assumption was violated, data was adjusted using the Greenhouse Geisser adjustment. Power calculations were also performed in SPSS, by selecting the relevant option during the repeated measures analysis process, to verify differences in samples were representative ( $>0.8$ ) of differences in the population.

## Results

### Photosynthesis and respiration

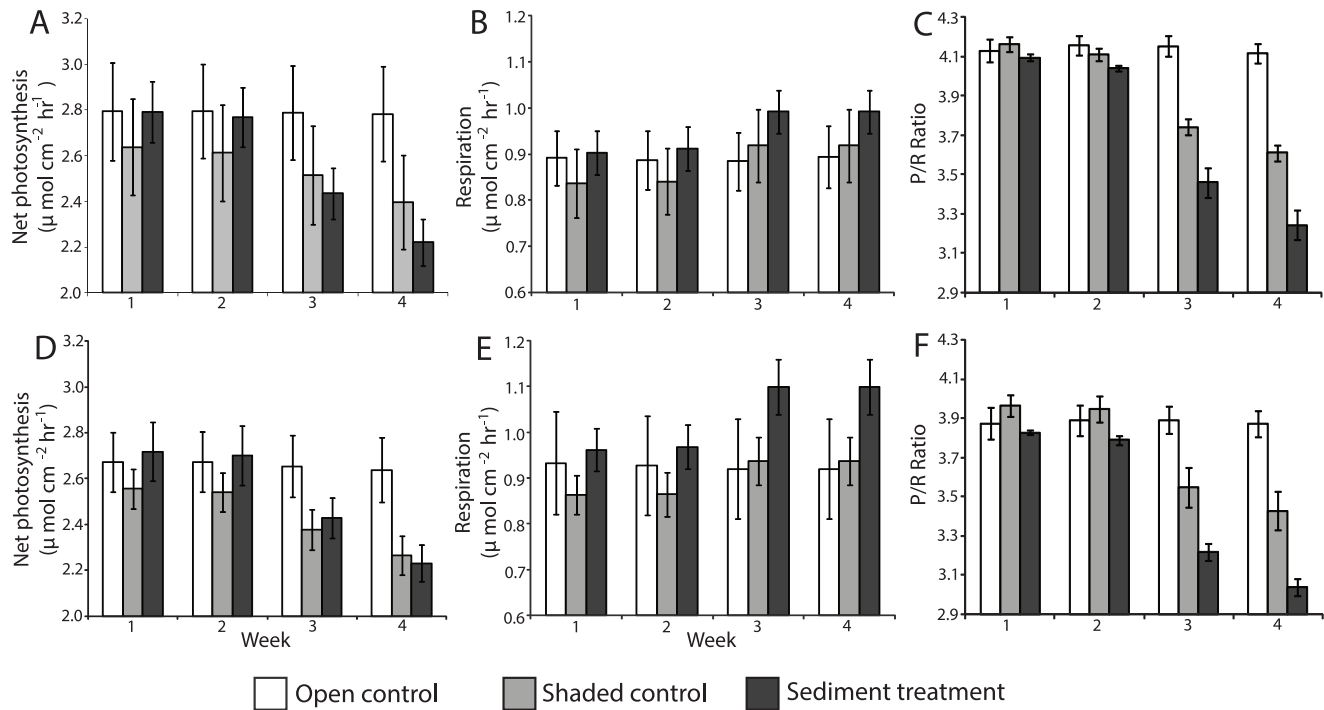
The net photosynthetic rate for *G. fascicularis* and *G. somaliensis* in the shaded control and sediment treatments fell from  $>2.5 \mu\text{mol cm}^{-2} \text{ hr}^{-1}$ , measured at the start of the experiment, to approximately  $2.4 \mu\text{mol cm}^{-2} \text{ hr}^{-1}$  by week 3 and to  $2.2\text{--}2.4 \mu\text{mol cm}^{-2} \text{ hr}^{-1}$  by week 4 (Fig. 3; Table 1). The decline in photosynthesis was significant for both coral species ( $p < 0.022$ ; Table 2), and post hoc analysis revealed that the most significant decline occurred between weeks 3 and 4 ( $p < 0.001$ ; Table 3).

In the shaded control and sediment treatment, the respiration rates increased from  $<0.9$  in week 1 to  $0.9\text{--}1.00 \mu\text{mol cm}^{-2} \text{ hr}^{-1}$  measured in week 4 for *G. fascicularis*, and from  $<0.96$  to  $<1.10 \mu\text{mol cm}^{-2} \text{ hr}^{-1}$  for *G. somaliensis* (Fig. 3; Table 1). The respiration rate was significantly greater by week 3 in both the shaded control and sediment treatment for both coral species ( $p < 0.043$ ; Table 3).

The P/R ratio was greater in *G. fascicularis* (range =  $3.04\text{--}4.11$ ) than in *G. somaliensis* (range =  $2.94\text{--}4.05$ ) in all treatments and over time (Fig. 4). The decline in the P/R ratio by week 4 was comparable between species with a 14% decline occurring in the shaded control and a decline of 21% in the sediment treatment (Table 1). Thus, the mechanical effects of sedimentation resulted in an additional 50% decline in coral physiological function. In contrast, the P/R ratios in the open controls were stable throughout the experiment. Despite similar declines in the P/R ratio, relative causes for the decline differed between species with lower P/R ratios largely due to reduced photosynthesis in *G. fascicularis* but the result of increased respiration in *G. somaliensis*.

### Photosynthetic yield

The photosynthetic yield (Fv/Fm) was consistently greater for *G. somaliensis* (range =  $0.41$  to  $0.62$ ) than for *G. fascicularis* (range =  $0.41$  to  $0.53$ ) within all treatments. There was no significant difference in the quantum yield in both the open and shaded control for *G. somaliensis* over the course of the experiment (Table 2). The quantum yield in the sediment treatment did, however, decline each week and was significantly lower by week 4 ( $0.6$  to  $0.41$ ;  $p < 0.001$ ). In contrast, the quantum



**Figure 3. Net photosynthetic rates, the respiration rates and the P/R values for *G. fascicularis* (A, B, C) and *G. somaliensis* (D, E, F) over four weeks in the open control (white), shaded control (grey) and sediment treatment (black).** The error bars represent standard errors (SE), and  $n=4$ .

doi:10.1371/journal.pone.0107195.g003

yield for *G. fascicularis* in both the shaded control (week 4;  $p=0.013$ ) and sediment treatment declined each week with significant weekly declines in the sediment treatment (Table 3). By the end of the experiment, the quantum yield had declined by 3% and 34% for *G. somaliensis*, and 17% and 19% for *G. fascicularis* in the shaded control and sediment treatment respectively, further illustrating species differences in coral physiological responses to reduced light and sediment stress.

## Discussion

This laboratory study provides the first analysis of the partitioned effects of turbidity and settling sediment on coral energetics during a chronic sedimentary event. The effects of turbidity and sediment settling were separated using a novel experimental setup whereby the effects of shading were compared with the combined effects of shading (turbidity) and settling sediment on two turbid water corals. Given that corals in the shaded control and sediment treatment experienced the same light levels, we were able to demonstrate that chronic sedimentation had a greater negative effect on corals than reduced light levels alone given that the P/R ratios and photosynthetic yield were significantly lower ( $p<0.04$ ) in the sediment treatment (P/R ratio = 3.04–3.24, yield = 0.40–0.41) than both the open (P/R ratio = 3.87–4.11, yield = 0.52–0.67) and shaded controls (P/R ratio = 3.42–3.61, yield = 0.46–0.58). However, coral species responses to reduced light and the deposition of sediments on the coral surface differed, most likely due to coral morphology.

Coral respiration rates in the sediment treatment significantly increased each week, illustrating the increased energy expenditure required to remove sediments as they settle. Corals can actively remove sediments from their surfaces either through the production of mucus or by active ciliary action [41]. These processes are

energetically expensive [19] and will lead to increased respiration rates, but are necessary to prevent tissue mortality under settled sediments [40,55]. Interestingly, there was also a consistent increase in the respiration rate of those coral fragments in the shaded control (Fig. 2). Typically, under low light conditions coral respiration rates are lower than at higher light levels due to decreased energy expenditure [56,57]. However, there have been many exceptions to this trend, with several studies showing a lack of sensitivity to light levels [42,58]. A potential explanation for the unexpected increase in respiration rates is photo-inhibition. Hoogenboom et al. [59] demonstrated that when low light photo-acclimated corals are exposed to increased light levels, respiration increases due to photo-inhibition. In this study, corals in the shaded treatment were exposed to 15% of ambient light (typically 90–200  $\text{mol photons m}^{-2}\text{ s}^{-1}$ ) but respiration of dark adapted corals was measured following a two hour incubation at  $\sim 300$   $\text{mol photons m}^{-2}\text{ s}^{-1}$  for the photosynthetic measurements. The increase in light levels, even though relatively small and for a short time period, may be sufficient to stress the corals resulting in higher respiration rates. Despite this experimental artefact, both the measured respiration rate and increase in the respiration was significantly greater in the sediment treatment than both the open and shaded control ( $p<0.001$ , Table 2).

Previous research has illustrated declines in photosynthesis and the P/R ratio during sediment exposure due to the combined effects of both turbidity and sedimentation [43]. Here, we were able to separate and quantify the effects, and found that low light levels caused a  $\sim 13\%$  decline in the P/R ratio, whereas sediment settling resulted in a further  $\sim 7\%$  reduction in the P/R ratio, largely due to increased respiration rates. Greater reductions in the P/R ratio have been observed during acute sediment stress events where coral photosynthesis and respiration rates declined by 43% to 64% and 13 to 23%, respectively [29]. These declines in

**Table 1.** Absolute means and percentage change values of net photosynthesis, gross photosynthesis, respiration, the P/R ratio and the yield during the course of the experiment for *G. fascicularis* and *G. somaliensis*.

<b>Absolute values</b>		<b>Week 1</b>			<b>Week 2</b>								
<b>Coral</b>	<b>Treatment</b>	<b>Net photosynthesis (μmol/cm<sup>2</sup>/hr)</b>	<b>Respiration (μmol/cm<sup>2</sup>/hr)</b>	<b>Ratio</b>	<b>Yield</b>	<b>Net photosynthesis (μmol/cm<sup>2</sup>/hr)</b>	<b>Respiration (μmol/cm<sup>2</sup>/hr)</b>	<b>Ratio</b>	<b>Yield</b>				
<i>Galaxea</i>	Open control	2.79	0.89	4.13	0.52	2.80	0.89	4.15	0.50				
	Shaded control	2.64	0.84	4.16	0.55	2.61	0.84	4.11	0.50				
	Sediment	2.79	0.90	4.09	0.51	2.77	0.91	4.04	0.48				
<i>Goniopora</i>	Open control	2.67	0.93	3.87	0.62	2.67	0.93	3.89	0.69				
	Shaded control	2.56	0.86	3.97	0.60	2.54	0.86	3.95	0.57				
	Sediment	2.72	0.96	3.83	0.60	2.70	0.97	3.79	0.54				
		<b>Week 3</b>			<b>Week 4</b>								
<i>Galaxea</i>	Open control	2.79	0.88	4.15	0.50	2.78	0.89	4.11	0.52				
	Shaded control	2.51	0.92	3.74	0.47	2.40	0.92	3.61	0.46				
	Sediment	2.43	0.99	3.46	0.41	2.22	0.99	3.24	0.41				
<i>Goniopora</i>	Open control	2.65	0.92	3.89	0.66	2.64	0.92	3.87	0.67				
	Shaded control	2.38	0.94	3.55	0.54	2.26	0.94	3.43	0.58				
	Sediment	2.43	1.10	3.22	0.51	2.23	1.10	3.04	0.40				
<b>Percentage change</b>		<b>Week 1</b>			<b>Week 2</b>			<b>Week 3</b>			<b>Week 4</b>		
<i>Galaxea</i>	Open control	0.00	0.00	0.00	0.00	0.10	-0.57	0.64	-2.61				
	Shaded control	0.00	0.00	0.00	0.00	-0.95	0.46	-1.15	-10.41				
	Sediment	0.00	0.00	0.00	0.00	-0.76	1.07	-1.37	-5.79				
<i>Goniopora</i>	Open control	0.00	0.00	0.00	0.00	0.08	-0.60	0.47	10.53				
	Shaded control	0.00	0.00	0.00	0.00	-0.63	0.10	-0.45	-4.71				
	Sediment	0.00	0.00	0.00	0.00	-0.64	0.68	-0.97	-11.23				
		<b>Week 3</b>			<b>Week 4</b>								
<i>Galaxea</i>	Open control	-0.16	-0.8	0.6	-4.1	-0.4	0.3	-0.3	1.1				
	Shaded control	-4.66	9.7	-10.1	-15.6	-9.1	9.7	-13.2	-17.7				
	Sediment	-12.77	9.9	-15.5	-18.7	-20.4	9.9	-20.8	-19.0				
<i>Goniopora</i>	Open control	-0.67	-1.4	0.4	6.7	-1.2	-1.4	-0.0	7.1				
	Shaded control	-6.99	8.5	-10.5	-10.2	-11.4	8.5	-13.5	-3.1				
	Sediment	-10.64	14.2	-15.9	-16.3	-17.9	14.2	-20.6	-34.1				

Results are provided for the open control, shaded control and sediment treatment every week for four weeks. A negative value under percentage change indicates a drop in the associated variable compared to week one. doi:10.1371/journal.pone.0107195.t001

**Table 2.** Summary results of one-way repeated measures ANOVA ( $\alpha = 0.05$ ,  $n = 4$ ) to assess if there was a significant difference in the percentage change of photosynthesis, respiration and yield by the end of the experiment (week 4).

Coral	Measure	Open control					Shaded control					Sediment				
		df	MS	F	P value	Obs Pwr	df	MS	F	P value	Obs Pwr	df	MS	F	P value	Obs Pwr
<i>Galaxea</i>	Net Photo	2	0.25	1.12	0.860	0.168	1	136	18.85	<b>0.022</b>	<b>.810</b>	1	726.46	23.90	<b>0.016</b>	<b>.887</b>
	Error	6	0.23				3	7.23			3	31.91				
	Respiration	2	2.05	2.49	0.164	0.324	1	231.83	74.62	<b>0.003</b>	<b>.999</b>	1	215.31	26.41	<b>0.014</b>	<b>.912</b>
	Error	6	0.42				3	3.11			3	8.15				
	Yield	2	29.06	1.64	0.270	0.227	2	58.51	9.74	<b>0.013</b>	<b>.860</b>	2	228.28	31.85	<b>0.001</b>	<b>1.00</b>
	Error	6	17.68				6	6.01			6	7.16				
<i>Goniopora</i>	Net Photo	2	1.95	4.75	0.058	.557	1	233.64	23.39	<b>0.017</b>	<b>.881</b>	2	587.47	161.57	<b>0.001</b>	<b>1.00</b>
	Error	6	0.41				3	10.00			6	3.64				
	Respiration	2	0.79	2.52	0.160	.328	1	187.64	300.94	<b>&lt;0.001</b>	<b>1.00</b>	2	480.62	62.58	<b>0.004</b>	<b>.998</b>
	Error	6	0.31				3	0.62			6	7.68				
	Yield	2	16.98	1.44	0.308	.204	1	93.49	1.25	0.345	.128	2	612.45	14.79	<b>0.005</b>	<b>.964</b>
	Error	6	11.79				3	74.52			6	41.42				

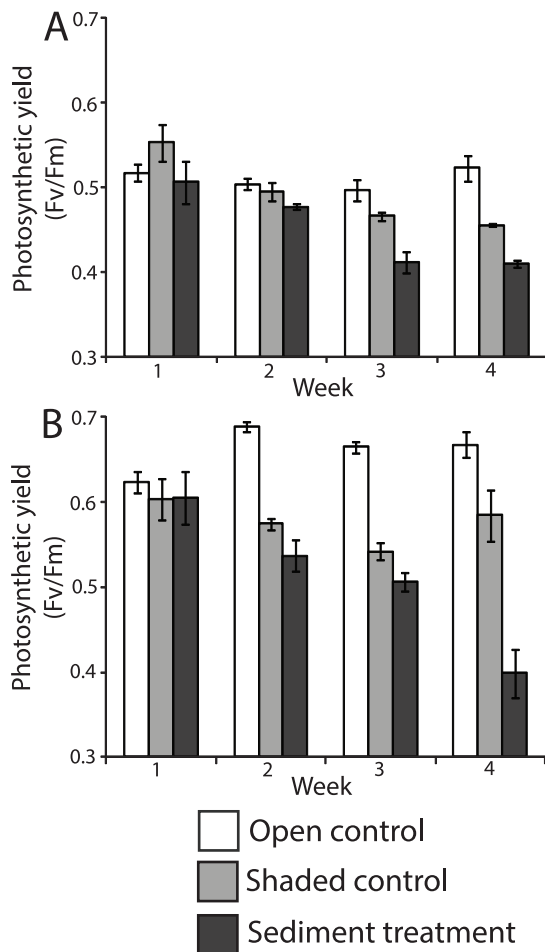
Data were analysed untransformed and numbers in bold indicate  $p < 0.05$ . Mauchly's test of sphericity was violated for the shaded controls and sediment treatment corals, and hence, data was adjusted using the Greenhouse Geisser adjustment.  
doi:10.1371/journal.pone.0107195.t002

**Table 3.** Post-hoc analysis following one-way repeated measures ANOVA to assess when (i.e. either between weeks 2 and 3, weeks 2 and 4, and weeks 3 and 4) there was a significant change in photosynthesis, respiration and yield for the shaded control and sediment treatment.

Coral	Measure	Time	Shaded control				Sediment					
			Week 2	Week 3	Week 4	Week 2	Week 3	Week 4	Week 2	Week 3	Week 4	
<i>Galaxea</i>	Net photosynthesis	Week 2		0.320	<b>0.046</b>	0.137		0.031	<b>&lt;0.001</b>	0.137		0.031
		Week 3	0.320		<b>&lt;0.001</b>	0.137		0.031		<b>&lt;0.001</b>		<b>&lt;0.001</b>
		Week 4	<b>0.046</b>	<b>&lt;0.001</b>		<b>0.043</b>	<b>&lt;0.001</b>					
	Respiration	Week 2	0.010	<b>0.010</b>	<b>0.010</b>	<b>0.043</b>	<b>0.043</b>	<b>0.043</b>	<b>0.043</b>	<b>0.043</b>	<b>0.043</b>	1.000
	Week 3	0.010		1.000	<b>0.043</b>		<b>0.043</b>				1.000	
	Week 4	0.010	1.000		<b>0.043</b>	1.000		<b>0.045</b>			<b>0.002</b>	
	Yield	Week 2	0.277	0.230	0.089	<b>0.045</b>					1.000	
		Week 3	0.277		0.230	<b>0.002</b>					1.000	
		Week 4	0.089	0.230		<b>0.011</b>						
<i>Goniopora</i>	Net photosynthesis	Week 2		0.140	<b>0.034</b>	0.140		<b>0.010</b>	<b>&lt;0.001</b>	0.140		<b>0.002</b>
		Week 3	0.140		<b>&lt;0.001</b>	0.140		<b>0.010</b>		<b>&lt;0.001</b>		<b>&lt;0.001</b>
		Week 4	<b>0.034</b>	<b>&lt;0.001</b>		<b>0.002</b>	<b>&lt;0.001</b>					
	Respiration	Week 2	<b>0.001</b>	<b>0.001</b>	<b>0.001</b>	<b>0.013</b>	<b>0.013</b>	<b>0.013</b>	<b>0.013</b>	<b>0.013</b>	<b>0.013</b>	1.000
	Week 3	<b>0.001</b>		1.000	<b>0.013</b>		<b>0.013</b>				1.000	
	Week 4	<b>0.001</b>	1.000		<b>0.013</b>	1.000					1.000	
	Yield	Week 2	0.284	0.284	1.000	0.680		0.680		0.680	0.078	
		Week 3	0.284		1.000	0.680		0.680		0.680	0.060	
		Week 4	1.000	1.000	1.000	0.078		0.060		0.060		

There was no significant difference in measured variables for corals held within the open control treatment. Numbers in bold indicate  $p < 0.05$ . doi:10.1371/journal.pone.0107195.t003





**Figure 4. The photosynthetic yield for *G.fascicularis* (A, C) and *G.somaliensis* (B, D) over four weeks in the open control (white), shaded control (grey) and sediment treatment (black).** The error bars represent standard errors (SE), and n=4. doi:10.1371/journal.pone.0107195.g004

respiration rates contrast with our chronic sediment exposure study and illustrate the significance of exposure time and sediment load on coral physiological responses. Sedimentary experimental conditions created here represent chronic sediment regimes on reefs in nearshore turbid reef environments and suggest that under these conditions reduced light accounts for 66% of the decline in P/R and sediment settling accounts of 33% of the decline. Future experiments that separate and quantify the effects of light and sedimentation on corals can be replicated for acute sediment stress events where corals are exposed to greater quantities of sediment for shorter time periods.

The influence of sediments on coral energetics varied between the two coral species, with *G. fascicularis* suffering from a greater decline in net photosynthesis than *G. somaliensis*. The decline in the photosynthesis in the sediment treatment was due to reductions in the maximum quantum yield. The maximum quantum yield is a measure of the photosynthetic efficiency of the photosystem II (PS II), hence a decline in the yield may limit the rate of photosynthesis at low light [25]. Note that the fluorescence yield and oxygen production can become decoupled, however, this typically occurs at high light levels (>300 PAR), whereas a positive linear relationship has been found at lower light intensities [60]. *G. fascicularis* had a lower maximum yield (0.51)

than *G. somaliensis* (0.60) at the start of the experiment, so was less acclimated to low light conditions resulting in a greater decline in photosynthesis in the sediment treatment. Reductions in the maximum quantum yield due to sediment stress have also been measured in *Montipora* and *Porites*, where the decline in the yield was a function of sediment type and time of exposure [61]. Fine sediments were found to have the greatest influence, reducing the maximum yield by approximately 25% in 20 hours. Conversely, low light levels are known to increase the maximum quantum yield as corals photo-acclimate and increase their efficiency at utilising what light is available [25,62,63]. There was no significant change in the maximum yield of *G. somaliensis* in the shaded control although a decline in the yield was observed up until week 3 of the experiment, followed by an increase in week 4. The increase in yield in week 4 suggests that corals were photo-acclimating to the low light conditions by the end of the experiment. The maximum quantum yield of *G. fascicularis* in the shaded control also declined during the experiment, but by week 4 the yield had stabilised. If the experiment had continued we might have observed an increase in the yield (as with *G. somaliensis* in week 4) indicating that *G. fascicularis* was photo-acclimating to the low light conditions.

Greater respiration rates observed for *G. somaliensis* may, in part, be attributed to differences in coral morphology. Coral growth form, tissue angle, and polyp form all influence coral sediment tolerances [19], and some coral morphologies (e.g. those with tall polyps and convex colonies) substantially reduce the need for active removal thereby reducing energy expenditure [64]. A recent review of 77 published studies found that coral tolerances to turbidity and sedimentation were significantly related to growth form but not calyx size [30]. The morphology of *G. somaliensis* is characterised by many shallow calices (<5 mm) that form a relatively smooth surface [45]. Sediments are rapidly removed from its surface by active modification of the boundary layer through the projection of polyps above the colony surface and ciliary action [27]. Our results suggest that this combined sediment clearance method although effective in that it limits the amount of reduced light penetration by settled sediments, does cause a significant increase in respiration. In contrast, *G. fascicularis* has corallites (~7 mm) that are cylindrical tubes linked via the coenosteum [45], and sediments are removed mainly through ciliary mechanisms [27]. Respiration rates for *G. fascicularis* in the sediment treatment were lower than for *G. somaliensis* and not significantly different from the shaded control, which suggests that less energy is required for ciliary action than polyp projection. Despite elevated respiration rates and associated sediment clearing, the yield of *G. somaliensis* was comparable to *G. fascicularis* by week 4 suggesting that both corals were experiencing photo-physiological stress.

In turbid reef environments spatial variations in rates of sediment resuspension and deposition are driven by local variations in hydrodynamics, with sheltered habitats typically dominated by sediment deposition and exposed habitats dominated by sediment resuspension [65]. These spatial variations in the sedimentary regime will drive coral species distributions depending on coral tolerances to sediments [16,17]. Anthony and Connolly [43] attribute such species partitioning to increases in respiration rates with rising sediment load, which contrasts with an earlier study by Anthony and Fabricius [42] who stated that photosynthetic rates and heterotrophy were key drivers in habitat distribution of corals. Based on our results we postulate that coral species distributions along gradients of turbidity and sedimentation will depend on the interplay of individual tolerances to both sedimentation and light reduction. Coral tolerances to sediments

are largely driven by their efficiency at sediment removal and how quickly they can photo-acclimate and/or switch to heterotrophy [32,42]. Those corals that can remove sediments with minimum energy use (e.g. *G. fascicularis*) may be more suited to depositional environments whereas those coral species that can both rapidly remove sediments and photo-acclimate (e.g. *G. somaliensis*) may be more suited to reef habitats dominated by sediment resuspension. Such patterns of distributions of these two species are indeed confirmed by observations from inshore turbid reefs in Singapore [2] and on inshore reefs on the Great Barrier Reef [16,36,38,66], emphasising the important balance between sediment deposition and resuspension in driving coral species distributions.

A central component of the present study was the silicon carbide mixture which provided an improved medium with which to test the direct (sedimentation) and indirect (reduced light) negative effects on corals without the additional confounding factors typically associated with natural sediments (e.g. nutrients, organics, and bacteria). However, the authors acknowledge that there may be some potential concerns when (a) substituting artificial for natural sediments, and (b) comparing the effects of reduced light from shading versus turbidity. Even though the silicon carbide powder used is inert, there may still be some scope for these sediments to act as vectors for microbes and, as such, future studies may consider it appropriate to pass sediments through ozone gas as a means of eliminating microbial contamination. There will also be differences in the surface integrity of the sediments and particle shapes between natural sediments and silicon carbide. However, given the fine particle sizes used in the study, comparable to that of silicon carbide powder used in previous sediment stress studies [19], particle shape and surface integrity are considered to be less important than ensuring that sediments are free of bacteria and nutrients, factors known to significantly influence coral physiology [31,42]. A secondary experimental component is that light levels in the shaded control and sediment treatment were comparable. Light levels were controlled for, but there may have been some differences in the spectral composition of light, a key driver of photosynthesis [67], between the shaded and sediment treatments. The spectral composition of light has only relatively recently become a concern, and consequently has been assessed in a limited number of studies concerning corals and turbidity [68,69,70]. However, Telesnicki and Goldberg [70] found that there was no significant difference in the light spectral quality at low to high turbidity concentrations when using fine sediments composed of marl, a naturally occurring carbonate. These data would suggest that fine silicon carbide sediments, at low turbidity concentrations, would have a limited influence on the light quality and hence, light

spectral quality would be comparable between the shaded control and sediment treatment.

Chronic sediment stress from increased sediment loading is a major threat to coral reef health, particularly for those reefs located close to shore. Managing coral reef health requires quantitative data on coral tolerances to sediments, both suspended and deposited, to generate predictive tools that can determine the impacts of increased sediment loading on coral reefs. This experiment successfully partitioned the effects of turbidity and sedimentation on coral energetics in chronic sedimentary conditions. All coral fragments survived the four week experiment, and no tissue mortality was observed, suggesting that these two coral species can tolerate the physical impacts of a chronic sedimentary regime of  $<27.4 \text{ mg cm}^{-2} \text{ d}^{-1}$  for at least one month. We found that under these sedimentary conditions, reduced light and sediment settling were responsible for 66% and 33% of the associated decline in the P/R ratio, respectively. In contrast, the response in yield to reduced light and sediments varied between species, most likely due to morphological differences, with either reduced light having a comparatively greater negative influence on yield and photo-physiological (*G. fascicularis*) or sediment settling alone resulting in significant physiological stress (*G. somaliensis*). Natural sediments, however, exert negative (e.g. bacteria) and positive (e.g. heterotrophy) pressures on corals, and direct comparisons between artificial and natural sediments would allow the additional assessment of the interplay between the physical and biological impacts of sediments on corals.

## Acknowledgments

Special thanks to Wincent Setiawan for his work on the sediment delivery system prototype and to Rosa Poquita for extensive field assistance. Thanks also to Jani Tanzil, Gerald Lui, Tjeerd Bouma, and the team from the Experimental Marine Ecology Lab for their technical support. All work was conducted with kind permission at the Tropical Marine Science Institute, National University of Singapore. The research permit (No. NP/RP12-007), that includes permission to collect corals, was granted by the National Parks Board (NParks), a statutory government board in charge of terrestrial and marine parks in Singapore, under the project entitled 'Impacts of ship-wake induced sediment resuspension on corals reefs and sea grass in Singapore.'

## Author Contributions

Conceived and designed the experiments: RKJ PAT PLAE. Performed the experiments: RKJ. Analyzed the data: RKJ NKB. Contributed reagents/materials/analysis tools: RKJ PAT NKB. Wrote the paper: RKJ NKB PAT PLAE.

## References

- Huang D (2009) An inventory of zooxanthellate scleractinian corals in Singapore, including 33 new records. *Raffles Bulletin of Zoology* 22: 69–80.
- Tun KPP (2012) Optimisation of reef survey methods and application of reef metrics and biocriteria for the monitoring of sediment-impacted reefs. PhD thesis. Singapore: National University of Singapore. 208 p.
- Chou L (2006) Marine habitats in one of the world's busiest harbours. In: Wolanski E, editor. *The environment in Asia Pacific harbours*. Netherlands: Springer. pp. 377–391.
- Hilton MJ, Manning SS (1995) Conversion of coastal habitats in Singapore: Indications of unsustainable development. *Environ Conserv* 22: 307–322.
- Chan LT (1980) A preliminary study of the effects of land reclamation on the marine fauna of Singapore, with particular reference to the hard corals (Scleractinians). Honours thesis. Singapore: National University of Singapore.
- Lane DJW (1991) Growth of scleractinian corals on sediment-stressed reefs at Singapore. In: Alcalá AG, editor; *Regional Symposium on Living Resources in Coastal Areas*. Marine Science Institute, University of the Philippines, Manila, Philippines. pp. 97–106.
- Todd PA, Sidle RC, Lewin-Koh NJI (2003) An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals. *J Exp Mar Bio Ecol* 299: 97–113.
- Low JKY, Chou LM (1994) Sedimentation rates in Singapore waters. *Proc 3rd ASEAN-Aust Symp Living Coral Resources* 2: 697–701.
- Chou LM (1996) Response of Singapore reefs to land reclamation. *Galaxea* 13: 85–92.
- Low JKY, Chou LM (1995) Environmental status of Singapore's coastal wetlands. Second workshop of the EAS-35 project: Integrated management of watersheds in relation to the coastal and marine environment. Bangkok. United Nations Environment Programme.
- Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. *Coral Reefs* 30: 521–531.
- Fabricius KE, De'ath G, Puotinen M, Done TJ, Cooper TF, et al. (2008) Disturbance gradients on inshore and offshore coral reefs caused by severe tropical cyclone. *Limnol Oceanogr* 53: 690–704.
- DeVantier LM, De'ath G, Turak E, Done T, Fabricius KE (2006) Species richness and community structure of reef building corals on the near shore reefs of the Great Barrier Reef. *Coral Reefs* 25: 329–340.
- Sofonia JJ (2006) Sediment responses of corals from inshore reefs, Great Barrier Reef. Masters thesis. Townsville: James Cook University. 77 p.

15. Sweatman H, Thompson A, Delean S, Davidson L, Neale S (2007) Status of nearshore reefs of the Great Barrier Reef 2004. Australian Institute of Marine Science, Townsville.
16. Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95–107.
17. Done T (1986) Zonation and disturbances in coral communities on fringing reefs. In: Baldwin CL, editor. Fringing reef workshop science, industry and management. Great Barrier Reef Marine Park Authority Workshop Series No. 9, p34–38.
18. Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull Mar Sci* 26: 450–466.
19. Stafford-Smith MG, Ormond RFG (1992) Sediment rejection mechanisms of 42 scleractinian corals. *Australian Journal of Marine and Freshwater Sciences* 43: 638–705.
20. Bak RPM (1978) Lethal and sublethal effects of dredging on reef corals. *Mar Pollut Bull* 9: 14–16.
21. Walker DI, Ormond RFG (1982) Coral death from sewage and phosphate pollution at Aqaba, Red Sea. *Mar Pollut Bull* 13: 21–25.
22. Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. *Ecol Lett* 6: 1056–1061.
23. Nugues MM, Roberts CM (2003) Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs* 22: 507–516.
24. Fabricius KE (2005) Effects of terrestrial run of on the ecology of corals and coral reefs: review and synthesis. *Mar Pollut Bull* 50: 125–146.
25. Anthony KRN, Hoegh-Guldberg O (2003) Kinetics of photoacclimatization in corals. *Oecologia* 134: 23–31.
26. Sofonia JJ, Anthony KRN (2008) High-sediment tolerance in the reef coral *Turbinaria mesenterina* from the inner Great Barrier Reef lagoon (Australia). *Estuar Coast Shelf Sci* 78: 748–752.
27. Stafford-Smith MG (1993) Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Mar Biol* 115: 229–243.
28. Hubbard JAEB, Pocock YP (1972) Sediment rejection by recent scleractinian corals: a key to paleo-environmental reconstruction. *Geol Rundsch* 61: 598–626.
29. Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *J Exp Mar Bio Ecol* 186: 259–275.
30. Erfteimeijer PLA, Riegl B, Hoeksema BW, Todd P (2012) Environmental impacts of dredging and other sediment disturbances on corals: A review. *Mar Pollut Bull* 64: 1737–1765.
31. Weber M, Lott C, Fabricius KE (2006) Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. *J Exp Mar Bio Ecol* 336: 18–32.
32. Anthony KRN (2000) Enhanced particle feeding capacity of corals on turbid reefs (Great Barrier Reef). *Coral Reefs* 19: 50–67.
33. Larcombe P, Woolfe KJ (1999) Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. *Coral Reefs* 18: 163–169.
34. Orpin AR, Ridd PV, Stewart LK (1999) Assessment of the relative importance of major sediment-transport mechanisms in the central Great Barrier Reef lagoon. *Australian Journal of Earth Sciences* 46: 883–896.
35. Woolfe KJ, Larcombe P (1999) Terrigenous sedimentation and coral reef growth: a conceptual frame work. *Mar Geol* 155: 331–345.
36. Browne NK, Smithers SG, Perry CT (2010) Geomorphology and community structure of Middle Reef, central Great Barrier Reef, Australia: an inner-shelf turbid zone reef subjected to episodic mortality events. *Coral Reefs* 29: 683–689.
37. Crabbe JC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. *Coral Reefs* 24: 437–441.
38. Browne NK, Smithers SG, Perry CT (2013) Spatial and temporal variations in turbidity on two inshore turbid reefs on the Great Barrier Reef, Australia. *Coral Reefs* 32: 195–210.
39. Weber M, de Beer D, Lott C, Polerecky L, Kohls K, et al. (2012) Mechanisms of damage to corals exposed to sedimentation. *PNAS* 109: E1558–E1567.
40. Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Mar Ecol Prog Ser* 62: 185–202.
41. Abdel-Salam H, Porter JW (1988) Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. Proceedings of the Sixth International Coral Reef Symposium Australia, pp. 285–292.
42. Anthony KRN, Fabricius K (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *J Exp Mar Bio Ecol* 252:221–253
43. Anthony KRN, Connolly SR (2004) Environmental limits to growth: Physiological niche boundaries of corals along turbidity:light gradients. *Oecologia* 141: 373–384.
44. Lui GCY, Setiawan W, Todd P, Erfteimeijer PLA (2012) Among genotype variation for sediment rejection in the reef building coral *Diploastrea Heliopora* (Lamarck, 1816). *The Raffles Bulletin of Zoology* 60: 525–531.
45. Veron JEN (2000) *Corals of the World*; Stafford-Smith DM, editor. Townsville, Australia: Australian Institute of Marine Science (AIMS).
46. Naumann MS, Niggel W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification-evaluation of established techniques by comparison with computer tomography. *Coral Reefs* 28: 109–117.
47. Dikou A, van Woessik R (2006) Survival under chronic stress from sediment load: Spatial patterns of hard coral communities in the southern islands of Singapore. *Mar Pollut Bull* 52: 1340–1354.
48. Todd P, Ladle RJ, Lewin-Koh NJI, Chou L (2004) Genotype × environment interactions in transplanted clones of the massive corals *Favia speciosa* and *Diploastrea heliopora*. *Mar Ecol Prog Ser* 271: 167–182.
49. Chou LM (1988) Community structure of sediment stressed reefs in Singapore. *Galaxea* 7: 101–111.
50. Anthony KRN (1999) A tank system for studying benthic aquatic organisms at predictable levels of turbidity and sedimentation: case study examining coral growth. *Limnol Oceanogr* 44: 1415–1422.
51. Falkowski PG, Jokiel PL, Kinzie RA (1990) Irradiance and corals. In: Dubinsky Z, editor. *Ecosystems of the World 25: Coral Reefs*. Amsterdam: Elsevier. pp. 89–107.
52. Beer S, Vilenkin B, Weil A, Veste M, Susel, et al. (1988) Measuring photosynthetic rates in seagrasses by pulse amplitude modulated (PAM) fluorometry. *Mar Ecol Prog Ser* 174: 293–300.
53. Schreiber U (2004) Pulse-amplitude-modulation (PAM) fluorometry and saturation pulse method: an overview. In: Govindjee P, editor. *Chlorophyll fluorescence: A signature of photosynthesis*. Dordrecht: Kluwer Academic Publishers. pp. 279–319.
54. Hill R, Ralph PJ (2008) Dark-induced reduction of the plastoquinone pool in zooxanthellae of scleractinian corals and implications for measurements of chlorophyll *a* fluorescence. *Symbiosis* 46: 45–56.
55. Fabricius KE, Wolanski E (2000) Rapid smothering of coral reef organisms by muddy marine snow. *Estuar Coast Shelf Sci* 50: 115–120.
56. Rodolfo-Metalpa R, Huot Y, Ferrier-Pagès C (2008) Photosynthetic response of the Mediterranean zooxanthellate coral *Cladocora caespitosa* to the natural range of light and temperature. *Journal of Experimental Biology* 211: 1579–1586.
57. Al-Horani FA, Al-Moghrabi SM, de Beer D (2003) The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Mar Biol* 142: 419–426.
58. Stambler N (1988) Effects of light intensity and ammonium enrichment on the hermatypic coral *Stylophora pistillata* and its zooxanthellae. *Symbiosis* 24: 127–146.
59. Hoogenboom MO, Anthony KRN, Connolly SR (2006) Energetic cost of photoinhibition in corals. *Mar Ecol Prog Ser* 313: 1–12.
60. Ulstrup K, Ralph P, Larkum A, Kühl M (2006) Intra-colonial variability in light acclimation of zooxanthellae in coral tissues of *Pocillopora damicornis*. *Marine Biology* 149:1325–1335.
61. Piniak GA (2007) Effects of two sediment types on the fluorescence yield of two Hawaiian scleractinian corals. *Mar Environ Res* 64: 456–468.
62. Piniak GA, Storlazzi CD (2008) Diurnal variability in turbidity and coral fluorescence on a fringing reef flat: Southern Molokai, Hawaii. *Estuar Coast Shelf Sci* 77: 56–64.
63. Lesser MP, Gorbunov MY (2001) Diurnal and bathymetric changes in chlorophyll fluorescence yields of reef corals measured in situ with a fast repetition rate fluorometer. *Mar Ecol Prog Ser* 212: 69–77.
64. Lasker HR (1980) Sediment rejection by reef corals: The roles of behavior and morphology in *Montastrea cavernosa* (Linnaeus). *J Exp Mar Bio Ecol* 47: 77–87.
65. Browne NK, Smithers SG, Perry CT (2012) Coral reefs of the turbid inner Great Barrier Reef: an environmental and geological perspective on occurrence, composition and growth. *Earth Science Reviews* 115: 1–20.
66. Fabricius KE, De'ath G, McCook L, Turak E, Williams D (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar Pollut Bull* 51: 384–398.
67. Mass T, Kline DI, Roopin M, Veal CJ, Cohen S, et al. (2010) The spectral quality of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata* colonies from different depths in the Red Sea. *Journal of Experimental Biology* 213: 4084–4091.
68. Anthony KRN, Ridd PV, Orpin AR, Larcombe P, Lough J (2004) Temporal variation of light availability in coastal benthic habitats: Effects of clouds, turbidity, and tides. *Limnol Oceanogr* 49: 2201–2211.
69. Hennige SJ, Smith DJ, Walsh SJ, McGinley MP, Warner ME, et al. (2010) Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. *J Exp Mar Bio Ecol* 391: 143–152.
70. Telesnicki GJ, Goldberg WM (1995) Effects of turbidity of photosynthesis and respiration of two South Florida reef coral species. *Bull Mar Sci* 57: 527–539.