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Laboratory-based studies examining the effects of sediments on corals: Executive summary and management implications

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WAMSI Dredging Science Node

Theme 4 Report

Project 4.6

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WAMSI Dredging Science Node

The WAMSI Dredging Science Node is a strategic research initiative that evolved in response to uncertainties in the environmental impact assessment and management of large-scale dredging operations and coastal infrastructure developments. Its goal is to enhance capacity within government and the private sector to predict and manage the environmental impacts of dredging in Western Australia, delivered through a combination of reviews, field studies, laboratory experimentation, relationship testing and development of standardised protocols and guidance for impact prediction, monitoring and management.

Funding Sources

The $20million Dredging Science Node is delivering one of the largest single issue environmental research programs in Australia. This applied research is funded by **Woodside Energy, Chevron Australia, BHP Billiton and the WAMSI Partners** and designed to provide a significant and meaningful improvement in the certainty around the effects, and management, of dredging operations in Western Australia. Although focussed on port and coastal development in Western Australia, the outputs will also be broadly applicable across Australia and globally.

This remarkable **collaboration between industry, government and research** extends beyond the classical funder-provider model. End-users of science in regulator and conservation agencies, and consultant and industry groups are actively involved in the governance of the node, to ensure ongoing focus on applicable science and converting the outputs into fit-for-purpose and usable products. The governance structure includes clear delineation between end-user focussed scoping and the arms-length research activity to ensure it is independent, unbiased and defensible.

And critically, the trusted across-sector collaboration developed through the WAMSI model has allowed the sharing of hundreds of millions of dollars worth of environmental monitoring data, much of it collected by environmental consultants on behalf of industry. By providing access to this usually **confidential data,** the **Industry Partners** are substantially enhancing WAMSI researchers' ability to determine the real-world impacts of dredging projects, and how they can best be managed. Rio Tinto's voluntary data contribution is particularly noteworthy, as it is not one of the funding contributors to the Node.

Funding and critical data **Critical data**

woodside Chevron western australian marine science institution bhpbilliton RioTinto

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Bessell-Browne P, Negri AP, Fisher R, Clode PL, Jones R. Impacts of light limitation on corals and crustose coralline algae. Sci Rep. 2017;7(1):11553. doi: 10.1038/s41598-017-11783-z.

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Bessell-Browne P, Negri AP, Clode PL, Jones R . Cumulative impacts: thermally bleached corals have reduced capacity to clear deposited sediment Sci Rep. 2017;2017(7: 2716 | DOI:10.1038/s41598-017-02810-0).

Duckworth A, Giofre N, Jones R. Coral morphology and sedimentation. Mar Pollut Bull. 2017;125:289–300. doi: https://doi.org/10.1016/j.marpolbul.2017.08.036.

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Front cover images (L-R)

Image 1: Trailing Suction Hopper Dredge *Gateway* in operation during the Fremantle Port Inner Harbour and Channel Deepening Project. (Source: OEPA)

Image 2: WAMSI PhD student Pia Bessell-Browne measuring temperature in a tank during an experiment investigating the impacts of sediment related pressures on corals at the Australian Institute of Marine Science (AIMS) National Sea Simulator (SeaSim) (source AIMS).

Image 3: Dredge Plume at Barrow Island. Image produced with data from the Japan Aerospace Exploration Agency (JAXA) Advanced Land Observing Satellite (ALOS) taken on 29 August 2010.

Image 4: A technician at the SeaSim demonstrating the use of the electronic control system of experimental systems developed to investigate the impacts of dredging related pressures on marine organisms (source AIMS).

Contents

Executive Summary

Dredging and dredging related activities such as dredge material placement (spoil disposal) release sediment into the water column and the resulting turbidity (water cloudiness) can have a significant effect on nearby benthic communities. There is a critical need to improve the ability to make scientifically sound predictions of the likely extent, severity, and persistence of environmental impacts associated with dredging, especially when conducted close to sensitive habitats such as coral reefs. This summary outlines the major findings of a series of 8 individual laboratory-based experiments, written as 5 different reports (Project 4.6.1–4.6.5), which were designed to examine cause-effect pathways, and where possible establish dose response relationships for multiple coral species. The exposure conditions used in these studies were based on the recent detailed studies of spatial and temporal patterns of dredging plumes from several large scale capital dredging projects (Fisher et al. 2015, Jones et al. 2015). The studies were conducted in parallel with, and designed to support and aid in the interpretation of the water quality guidelines developed from an *in situ* investigation of coral health during a capital dredging program (Fisher et al. 2017)(**Text Box 1**).

The effects of sediments from dredging activities on corals has recently been reviewed, and the problems associated with predicting effects of mobilized sediment on corals discussed (see Jones et al. 2016). One of the key points raised was that there are many different mechanisms (cause-effect pathways) whereby sediment could affect corals. These include reduced light availability for photosynthesis of the corals' algal symbionts (by light scattering and absorption in the water column), reduced filtering and feeding as a result of elevated suspended sediment concentrations (SSCs), and increased sediment deposition that could result in tissue smothering. The problem is that these largely physical pressures can act either alone or in combination, which can obscure or confound attempts to relate the various pressures (a physical, chemical or biological change that has the potential to cause environmental change) to the biological responses and to define exposure conditions above which effects could occur (i.e. derive guideline values).

Here we summarise the results of a series of laboratory based experiments designed to explore the three primary cause effect pathways of mobilised sediments on corals. The species used, questions addressed, material and methods, experimental conditions and the results and conclusions are briefly summarized in Tables 1. Some generic approaches that are common to all experiments are itemized below.

All experimental work was conducted at the National Sea Simulator (SeaSim) based at the Australian Institute of Marine Science (AIMS, Townsville, Queensland) using 8 coral species (see Text Box 2). All corals were collected from the central Great Barrier Reef (GBR) and were kept for a ~1 month holding period to recover from the collecting and handling procedures (Figure 1). Experiments were conducted in constant temperature rooms (27°C) in 115 L or 1500 L sized containers (Figure 1, Figure 2) receiving a continuous supply of filtered (0.45 μm) clean seawater (33‰ salinity) at a rate which ensured multiple water changes every day.

Corals were held on a plastic false-bottom floor in the tanks and illuminated by LED lights providing a ~12 h light:dark cycle. Lights were programmed to undergo a diel cycle reaching maximum intensity at noon, and delivering daily light integrals (DLI, or the total summed photosynthetically active radiation [PAR] over the course of the day) from 0 (darkness) to 12 mol quanta m^{-2} d^{-1} depending on the experiments. Corals were exposed to suspended sediments or sediments that were allowed to settle out of suspension, or simply to reductions in light alone, depending on the question being addressed.

Sediments for the studies were collected from an offshore clear-water environment or muddy, turbid reef zone environments at three different locations, and were ground using a rod mill grinder to reach a mean grain size typically in the silt-sized range. Sediments were delivered to the tanks either manually or as aliquots of a concentrated suspension from a stock tank. Turbidity was typically measured using nephelometers in each tank and converted to SSCs using sediment-specific conversion factors. Sediment deposition was measured using SedPods (Field et al. 2012) or sediment deposition meters (Whinney et al. 2017). Lights, nephelometers and solenoid valves between the stock tank and experimental chambers were connected to a programmable logic

controller (PLC). The PLC recorded nephelometrically-derived SSC levels and controlled the opening and controlling of the solenoid vales to inject sediment into the tanks and maintain SSCs at the desired level despite the water exchanges. Depending on the experiment the sediments were kept in suspension using submersible pumps also controlled by the PLC, or allowed to settle out of suspension.

Text Box 1. Laboratory based (*ex situ*) and field based *(in situ* studies)

Guideline or threshold values can be developed from both *ex situ* laboratory-based (i.e. aquarium) studies and/or from *in situ* field-based studies. The advantage of field studies are that they are less artificial, hence ecologically relevant, but this is offset by the fact that it is nearly impossible to repeat a study. It is also more difficult to interpret results because of the combination of pressures operating in unison (as noted above). Field studies can also be susceptible to uncontrollable external anomalies or chance events – such as cyclones or storm damage, or marine heatwaves that cause coral bleaching[1] – which can further confound interpretations.

Laboratory-based studies offer some solution to the issue of pressures operating in combination, by allowing isolation and separation (disentanglement) of some of the variables and examining mechanisms individually. For example, it is possible to alter the light levels between tanks so test organisms are exposed to different SSCs but under the same light levels. It is possible to examine some variables in isolation, such as adjusting light intensity in experimental tanks to examine light deprivation. It is also possible to manipulate the experimental conditions to eliminate some variables, such as keeping sediments from settling and so exclude the effects of sediment deposition as a cause-effect pathway. Laboratory-based studies also allow the testing of the relative tolerance of different species or morphologies to different factors, such as sediment types and particle sizes, and allow an examination of the effects of external factors such as water flow on species sensitivity. Laboratory-based studies can eliminate extraneous external factors such as heatwaves and coral bleaching events, but it is also possible to purposefully introduce such variables – e.g. examining whether corals that have been bleached by a period of elevated water temperatures are more of less susceptible to sediments. *All these different types of manipulations and experiments described above were used in the experimental sequence described below*.

The pros and cons of *ex situ* versus *in situ* studies are well known, and guideline development may be most robust when based on a combination of both types of studies (laboratory and field studies, physiological and ecological endpoints and observations) i.e. using a weight of evidence (WoE) approach. If adopting such an approach it is essential that laboratory-based experiments use exposure regimes that are environmentally relevant. If conditions deviate too much from those occurring *in situ*, then laboratory-based studies can produce results that are simply experimental artefacts (Jones et al. 2016). This makes it difficult to assess whether sediments actually pose a risk as opposed to merely being a hazard (Harris et al. 2014). Temporal and spatial changes in water quality during several dredging programs in Western Australia have recently been comprehensively described (see Fisher et al. (2015), Jones et al. (2015), Jones et al. (2016)) and provide valuable information for contextualising laboratory based experiments and helping to define relevant exposure conditions.

[1]Corals contain endosymbiotic dinoflagellate microalgae (*Symbiodinium* spp.) and the chlorophyll and peridinin photosynthetic pigments of the algae predominantly give corals their brown pigmentation. When stressed the symbiosis dissociates and the algae leave the corals which turn progressively white (i.e. bleach) as the coral skeleton becomes more visible through the relatively transparent animal (coral) tissues. Bleaching is a sublethal stress of corals i.e. they could eventually regain the algae, and can occur in corals in response to a range of stresses including elevated water temperatures, high light levels, and chemicals such as copper, cyanide and herbicides as well as to extended periods of light deprivation.

Experiments were conducted over short term periods (i.e. 'acute' studies conducted over several days) or longer term periods (i.e. 'chronic' studies conducted several weeks). A range of lethal and sublethal endpoints were used, including changes in growth, mortality and partial mortality and photochemical efficiency of the endosymbiotic dinoflagellates, changes coral colour, density of the dinoflagellates, chlorophyll *a* and c_2 and

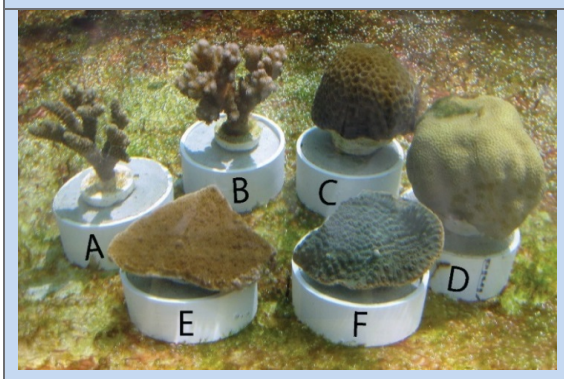
peridinin content of the algae, and changes in lipid content and lipid class.

Experiments followed a logical sequence with treatment levels usually based on previous experimental results and were separated into studies associated with:

- SSCs and light attenuation (Project 4.6.1, 4.6.2 and 4.6.3),
- Sediment deposition (Project 4.6.4), and
- The effects of bleaching[1] from thermal stress on sediment clearance capability (Project 4.6.5).

Text Box 2 . Choice of corals of the laboratory-based studies

All experiments were conducted with explants of multiple coral species selected from a range of different families and representing three primary morphologies (branching, foliose, massive). The coral species used are widely distributed throughout northern Australia and the Indo-Pacific including the Pilbara region of Western Australia (Jones 2016). The selected species represent the range of dominant morphologies (branching, foliose and massive morphologies) and are common and often dominant morphologies in the Pilbara.



(A) *Acropora millepora* (Ehrenberg 1834);
(B) *Pocillopora damicornis* Linnaeus (1758);
(C) *Goniastrea retiformis* (Lamarck, 1816).
(D) *Porites lutea* (Dana 1846) or *Porites lobata* (Bernard 1896)
(E) *Montipora aequituberculata* (Veron 1995)
(F) *Turbinaria reniformis* (Bernard 1896).

Where A and B are **branching** morphologies, C and D '**massive'** spherical and hemispherical morphologies and E and F **foliose** and **encrusting** morphologies.

[1] Corals contain endosymbiotic dinoflagellate microalgae (*Symbiodinium* spp.) and the chlorophyll and peridinin photosynthetic pigments of the algae predominantly give corals their brown pigmentation. When stressed the symbiosis dissociates and the algae leave the corals which turn progressively white (i.e. bleach) as the coral skeleton becomes more visible through the relatively transparent animal (coral) tissues. Bleaching is a sublethal stress of corals i.e. they could eventually regain the algae, and can occur in corals in response to a range of stresses including elevated water temperatures, high light levels, and chemicals such as copper, cyanide and herbicides as well as to extended periods of light deprivation.

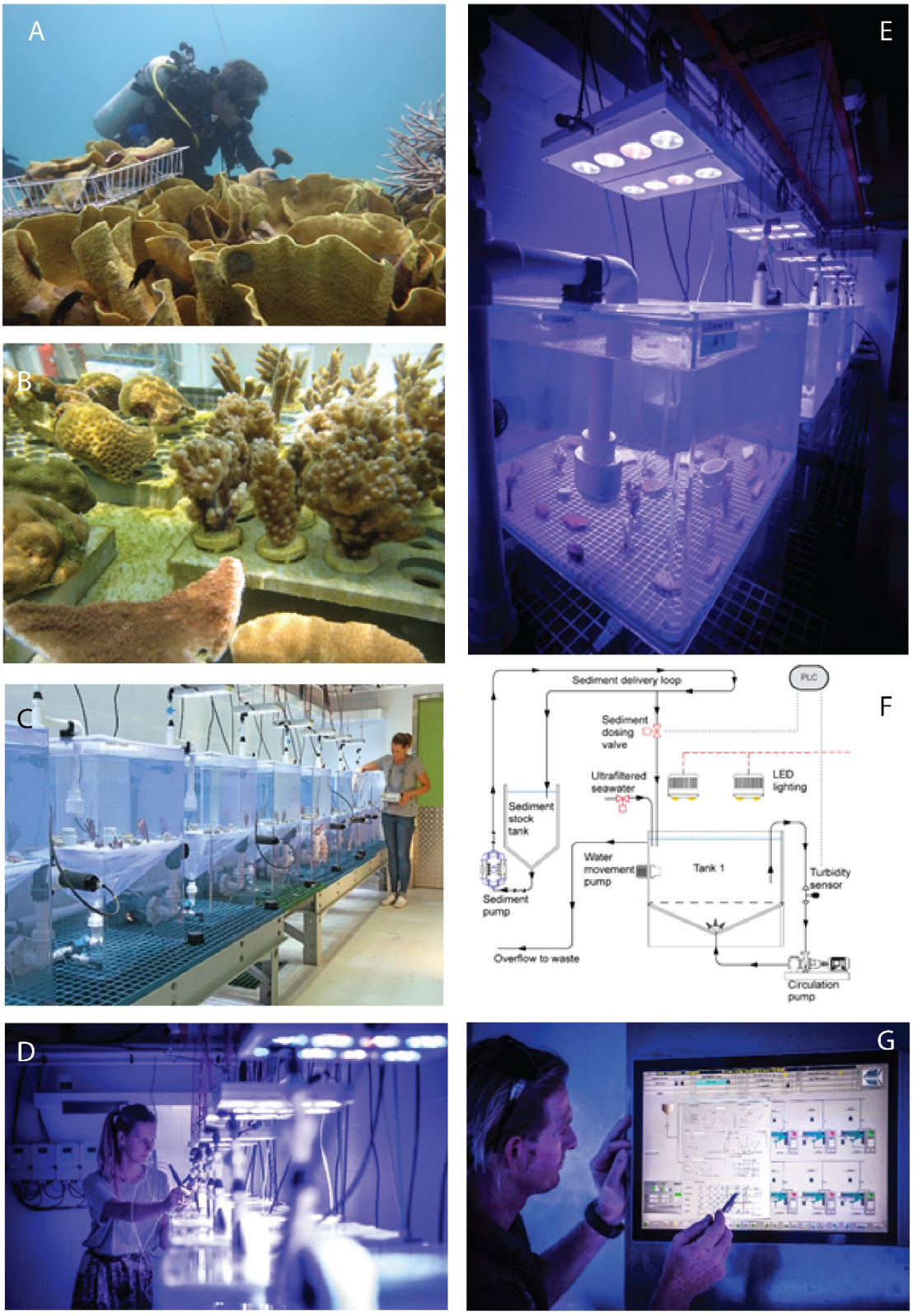


Figure 1. (A) Collection of corals for the laboratory based experiments in the AIMS SeaSim, (B) Corals were fragmented and individually numbered and left in holdings tanks for 1 month prior to the experiments. (C, D, E) explants were then exposed to elevated SSCs, or reduced light, alone and in combination in 18 × 115 L containers, with sediment delivered from concentrated stock tanks through pivoting solenoid valves controlled through a programmable logic controller which also recorded all light and turbidity measurements during the experiments. Image attribution: A, B Alan Duckworth (AIMS), image C, Steve Clarke (AIMS), images D,E,G, Christian Miller.

Figure 2. Images of the 10 × 1500 L tanks used in the longer-term sediment dosing experiments. Each tank received filtered (0.4 µm) seawater at 27 °C at a rate of 1 L min^{-1}. Water movement within each tank was controlled using submersible pumps controlled by a programmable logic controller (PLC). Each tank automatically received pulses of elevated SSCs from a concentrated 500 L reservoir via solenoid valves connected to a PLC. Turbidity, light and sediment deposition rates were recorded continuously by the PLC.

Effects of SSCs and light attenuation (Projects 4.6.1–4.6.3)

Three experiments explored the effects of both elevated SSCs and associated light attenuation on coral health, in the absence of any sedimentation effects (see Table 1). In Project 4.6.1 the relative effect of SSCs and loss of light on coral health were isolated by exposing corals to varying SSC treatments whilst simultaneously correcting light levels for the associated attenuation. Results indicated that there were no negative effects on corals after 28 days at any sediment concentration (up to 100 mg L^{-1}) providing light levels were sufficient. However, all corals in the lowest light treatments lost Chl *a* and discoloured (bleached) after one week. Coral mortality only occurred in the two lowest light treatments (0 and 1.1 mol photons m^{-2} d^{-1}) and was higher when corals were simultaneously exposed to elevated SSCs (Table 1).

Based on Project 4.6.1, the effects of long term exposure to low light (including darkness) was examined to develop a dose-response relationship over a chronic time period (Project 4.6.2, Table 1). Exposure to very low light caused the corals to bleach, by the symbiosis dissociating, yielding 30 d EI_{10} thresholds (irradiance which results in a 10% change in colour) of 1.2–1.9 mol photons m^{-2} d^{-1} (Table 1). The crustose coralline alga (CCA) *Porolithon onkodes* which was included in these experiments was more sensitive than the corals (adult or juveniles). The CCA was high light adapted and exposure to ≤0.1 mol photons m^{-2} resulted in bleaching, with sections of pale tissue and sections of bone white skeleton where tissue had been lost.

In Project 4.6.3, corals were exposed for 42 d to one of six combinations of elevated SSCs and light reduction, with light adjusted to levels corals would experience under similar SSCs on a shallow (5–6 m) reef. Corals in the middle turbidity treatment showed darkening (caused by photoadaptation involving an increase in algal density and/or algal pigment concentration – Chl *a* and peridinin), whereas in the higher turbidity treatments bleaching occurred, caused by the dissociation of the symbiosis (Table 1). There were no marked effects on the

photochemical efficiency of the algal symbionts. Lipid concentrations were depleted at the high turbidity treatments, and changes in the lipid ratios suggest mobilization of energy stores to combat light limitation. Most corals grew over the 42 days; however, growth rates were much lower in the higher turbidity treatments. The most sensitive species were the branching ones *P. damicornis* > *A. millepora*, followed by the massive *Porites* spp. The turbid water specialist *T. reniformis* was the most tolerant. Together these studies suggest that:

- Light reduction associated with elevated SSCs poses a proportionally greater risk to corals than effects of elevated SSCs alone, i.e. when light levels are experimentally manipulated to avoid light limitation, corals were very resilient to a combination of intensity (100 mg L^{-1}) and duration (28 d) that is many times higher than levels measured at a distance of ~1 km from a large scale (capital) dredging project.
- When elevated SSCs led to reduced light conditions (<1.2–1.9 mol photons m^{-2} d^{-1}) corals were shown to bleach, deplete lipid stores, and show reduced growth rates.
- Light reduction alone constitutes a clear risk to coral reefs from dredging. There were clear differences in the tolerance levels between species and tolerance levels appear positively related to the lipid reserves.
- Overall, most corals were able to adapt to a 3 fold decrease in light levels and a combination of 10 mg L^{-1} and 2.3 mol photons m^{-2} d^{-1} over a period of 42 d (7 weeks) was tolerated by most corals.

Effects of sediment deposition (Project 4.6.4)

Elevated sedimentation is one of the key cause-effect pathways that can damage corals at sites close to dredging activities. If the deposition rates exceed the self-cleaning (sediment rejection) ability of corals, then smothering can result which can lead to tissue mortality (lesion formation).

In Project 4.6.4 the sediment rejection ability of 8 coral species from 5 families and 3 morphologies were assessed in three short term exposure tests that included different sediment types (carbonate sediment from an offshore clear-water environment and mixed carbonate/siliciclastic sediments from 2 different inshore environments), particle sizes (median (D_{50}) PSD of 30 μm (range 0.5–140 μm), flow regimes (0, 2–3 and 9–17 cm s^{-1}), and sediment deposition rate (ranging from 0.5–40 mg cm^{-2} d^{-1}). A longer-term study examining the effects of sediment covering for 16 d (with a 42 d post smothering observation period) was also conducted (Table 1). Overall, the combined studies found that:

- The branching species, *P. damicornis* and *A. millepora* were very capable of self-cleaning and removing sediments compared to the foliose and massive morphologies. At the highest SedPod accumulation rate tested (235 mg cm^{-2} d^{-1}) the amount of sediment accumulation on the branching *A. millepora* was ~3× less than on the foliose *T. reniformis*, 8× less than on the massive *Porites* spp. and 22× less than on the foliose *M. capricornis*.
- Increasing flow rates significantly affected the sediment clearing ability of the corals and compared to static conditions, the amount of sediment settling under a flow of 9–17 cm s^{-1} was ~5× lower on live *Montipora* and *Turbinaria* (and 10–30 × lower based on percent cover);
- Under a deposition level of 20 mg cm^{-2} d^{-1} there was no significant difference in the sediment rejection ability of the corals between fine silt and coarse silt, but under much higher deposition levels (235 mg cm^{-2} d^{-1}) coarse silt was removed on average 3× more efficiently than fine silt;
- Corals cleared siliciclastic sediments from their surfaces faster than carbonate or mixed (carbonate/siliciclastic) sediments. For the foliose species, *M. aequituberculata* and *T. reniformis*, this was 3× and 10× faster respectively;
- The species tested were capable (under a slight flow of <3 cm s^{-1}) of removing all sediment up to 20 mg cm^{-2} d^{-1} leaving only slight residual deposits typically less than a few percent of the surface area. The massive (dome shaped corals) morphologies could do the same up to 40 mg cm^{-2} d^{-1} and the branching species *A. millepora* managed to clear a sedimentation rate (under static conditions) of up to 235 mg cm^{-2} d^{-1}.
- Once corals were smothered in sediments bleaching of the tissues under the sediment occurred in as little as 4 days, but no mortality was observed, even after 6 weeks following this smothering event.

Interactions between sedimentation and bleaching (Project 4.6.5).

A well cited model for the current poor condition of many coral reefs worldwide is the interaction between local anthropogenic factors (e.g. coastal development, poor water shed management, pollution and overfishing) and larger scale regional and global factors (e.g. rising seawater temperatures and ocean acidification). The local and global interaction can manifest itself in many ways, and is typified by situations where dredging projects happen to coincide with 'natural' warm-water coral bleaching events. How to conserve reefs in the face of predicted increases in seawater temperatures associated with climate change and the pernicious threat of coral bleaching is a significant challenge to regulatory agencies. Project 4.6.5 examined the sediment clearance capabilities of three coral species (*Acropora millepora, Turbinaria reniformis, Porites* spp.) that were experimentally induced to bleach by exposing them before hand to a temperature of 31°C for 21 d. Studies were conducted across a range of sediment deposition levels (0, 11, 22 and 40 mg cm^{-2} d^{-1}) using carbonate sediment from an offshore clear-water environment (median sediment particle sizes of 9–53 μm), and over repeated sediment deposition events (1 to 7 daily successive sedimentation events).

The results indicated that:

- Bleached corals were less capable of removing sediments from their surfaces, with sediment accumulating 3–4 fold more on bleached compared to normally-pigmented corals;
- Repeated deposition resulted in a ~3 fold increase in the amount of sediment remaining on the corals, regardless of bleaching status, indicating a reduction in self-cleaning capability of colonies with time; and
- Coral bleaching reduces the ability of corals to remove sediments from their surfaces (to self-clean) and the loss of sediment rejection capability makes them much more vulnerable to sediment smothering if dredging happens to coincide with warm-water bleaching events.

Table 1. Summary effects of growth and health of the branching, foliose and massive corals among the SSC, light and deposition experiments. SSC – suspended sediment concentration (units, mg L^{-1}); SD – sediment deposition (units, mg cm^{-2} day^{-1}); DLI – daily light integral (units, mol photons m^{-2} d^{-1}); PSD – Particle Size Distribution (units, μm); BS – bleaching status (bleached or normally-pigmented); WF – water flow (units, cm s^{-1}); F_v/F_m – photochemical efficiency of the algal symbionts (F_v/F_m); Chl *a* – Chlorophyll a (pg $cell^{-1}$ or μg cm^{-2})

SSC/Light crossed (Project 4.6.1)	**Darkness and low light (Project 4.6.2)**	**SSC/light combined (Project 4.6.3)**	**Clearance rates (Project 4.6.4)**	**Smothering (Project 4.6.4)**	**Clearance rates and bleaching (Project 4.6.5)**
DLIs of 0, 1.1, 8.6, crossed with SSCs of 0, 30, 100	DLIs of 0, 0.02, 0.1, 0.4, 1.1, 4.3	SSC and DLI of 0 & 12.6, 2 & 10.1, 5 & 6.3, 10 & 2.3, 30 & 0.3, 100 & 0	SD: 0.5, 1, 2, 5, 10, 20 40 WF: 0, 2–3, 9–17 PSD: coarse and fine (8–50)	PSD: fine and coarse silt SD: 235 mg cm–2	SD: 0, 11, 22 and 40 Coral health: bleached / not-bleached
Offshore (clear water) reef	None	Offshore (clear water) reef	Offshore (clear water) and 2 nearshore (turbid water) reefs	Offshore (clear water) reef	Offshore (clear water) reef
28 d	28 d	42 d	Single deposition for 1 d	Single deposition for 1–16 d followed by 6 w observation	Daily deposition for 7 d
Acropora millepora Ehrenberg 1834 (Branching)					
All survived • Partial mortality at ≤1 DLI with SSC ≥30 • Bleached at 0 DLI • < Fv/Fm at 0 DLI • < Chl a per cm2 at 0 DLI	All survived • No partial mortality • Bleaching at ≤0.1 DLI • < Fv/Fm at ≤0.1 DLI • < Chl a conc. Per m2 at ≤0.4 DLI;	All survived • Partial mortality at SSC of 100 • <growth at SSC ≥30 mg L^{-1} with DLI of .3 DLI) • <zooxanthellae at ≥30 mg L^{-1} • <lipids at ≥30 mg L^{-1} • Some bleaching at ≥30 mg L^{-1} • Few effects at ≤10 mg L^{-1}	<5% cover at SD ≤40 • Water flow (to 17 cm s^{-1}) did not affect CR • Onslow silt cleared fastest • Fine and coarse silt cleared at same rate	All survived • No partial mortality • <1% smothered tissue • Quickly cleared sediment • No short or long term effects	All survived • No partial mortality • < Fv/Fm and Chl a conc. for bleached corals • Decrease in Fv/Fm for bleached corals as sedimentation level increased • Colour and Chl a not affected by sedimentation level • Bleached corals removed less sediment
Pocillopora damicornis (Linnaeus 1758) *Pocillopora acuta* (Lamarck 1816) (Branching)					
	All survived • Partial mortality at ≤0.1 DLI • < Fv/Fm at ≤0.4 DLI • < Chl a conc. at ≤0.4 DLI	All survived • Partial mortality at 30 mg L^{-1} (0.3 DLI) • < growth at ≥30 mg L^{-1} • < zooxanthellae at ≥30 mg L^{-1} • < lipids at ≥30 mg L^{-1} • Some bleaching at ≥30 mg L^{-1} • Few effects at ≤10 mg L^{-1}	<1% cover at ≤40 mg/cm • Water flow did not affect CR • Onslow silt cleared fastest • Clearance rates similar for fine and coarse silt		

Montipora aequituberculata (Veron 1995) *Montipora capricornis* Bernard 1897 (Foliose)				
All survived • Partial mortality at ≤1.1 DLI with SSC ≥30 • Bleached at ≤1.1 DLI • < Fv/Fm at 0 DLI • < Chl a at 0 DLI		<12% cover at ≤20 mg cm^{-2} d–1 • >30% cover at 40 mg cm^{-2} • Water flow promoted CR • Onslow silt cleared fastest • Clearance rates similar for fine and coarse silt at 20 mg cm^{-2}	All survived • Low partial mortality at 16 d smothered • >50% cover for fine silt • <20% cover for coarse silt • Could not clear sediment after day 1 • < Fv/Fm for fine silt • Bleached tissue recovered within 6 weeks	
Turbinaria reniformis (Bernard 1896)				
	All survived • partial mortality • < growth at SSC ≥10 mg L^{-1} • < lipids at ≥10 mg L^{-1} • < zooxanthellae at ≥30 mg L^{-1} • Few effects at ≤5 mg L^{-1}	<8% cover at ≤40 mg cm^{-2} d^{-1} • Onslow silt cleared fastest • Clearance rates similar for fine and coarse silt at 20 mg cm^{-2}	All survived • No partial mortality • 2% cover of fine and coarse silt • < Fv/Fm for fine silt • All recovered within 6 weeks	All survived • Partial mortality for 1 bleached fragment at 22 mg cm^{-2} day^{-1} • < Fv/Fm and Chl a conc. for bleached corals • < Fv/Fm for bleached corals as sedimentation level increased • Colour and Chl a not affected by sedimentation level • Bleached corals removed less sediment
Porites lutea (Dana 1846) *Porites lobata* (Bernard 1896) (Massive)				
All survived • Partial mortality at 1.1 DLI with SSC 100 • Bleached at 1.1 DLI • < Fv/Fm at 0 DLI • < Chl a at 0 DLI	All survived • No partial mortality • < growth at ≥10 mg L^{-1} • < lipids at ≥30 mg L^{-1} • < zooxanthellae at ≥30 mg L^{-1} • bleached at ≥30 mg L^{-1} • Few effects at ≤5 mg L^{-1}	<5% cover at ≤40 mg cm^{-2} d^{-1} • Water flow not examined • Sediment type/size not examined	All survived • No partial mortality • 21% cover of fine and coarse silt • All recovered within 6 weeks	All survived • Partial mortality for 1 bleached fragment at 11 mg cm^{-2} day^{-1} • < Fv/Fm and Chl a conc. for bleached corals • Decrease of Fv/Fm for bleached corals as sedimentation level increased • Colour and Chl a not affected by sedimentation level • Bleached corals removed less sediment
Goniastrea retiformis (Lamarck, 1816) (Massive)				
		<3% cover at ≤40 mg cm^{-2} d^{-1} • Water flow not examined • Sediment type/size not examined		

Implications for management

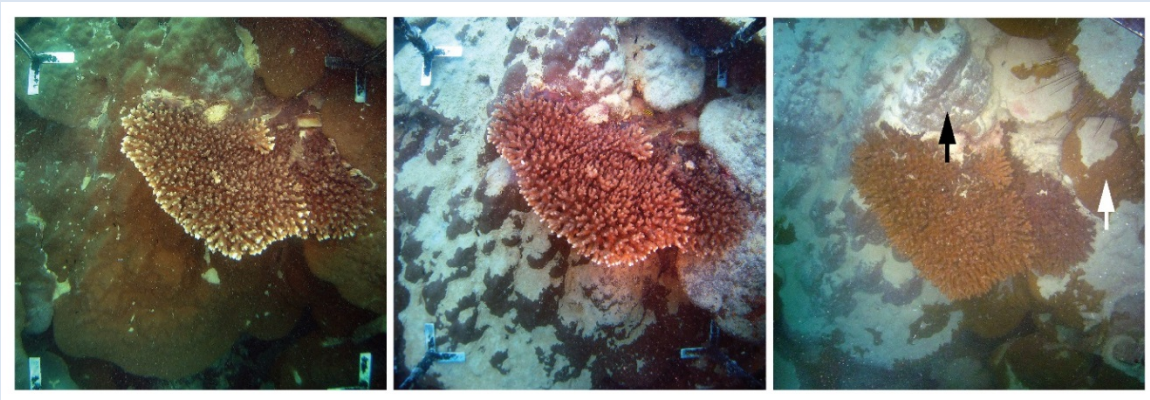
Impact Prediction and Management

The general principle behind using the weight of evidence (WoE) approach for scientific assessments of environmental risk, is the use of all available information from available sources, including laboratory and field studies, physiological and ecological endpoints, and *in situ* and *ex situ* observations – and judging how well they collectively tell a consistent story. These laboratory based studies delivered a coherent narrative, which when considered with the field based studies (Projects 4.2 and 4.9) have allowed the development of guidelines and approaches for guideline development for environmental impact assessment and management of dredging projects near corals reefs. Guideline development and derivation is discussed in detail in Project 4.9.

The conclusions from the laboratory investigations are that light attenuation and sediment deposition are the two dominant cause-effect pathways, although SSCs most likely play an interactive role. Light reduction and sediment deposition affects different coral species and morphologies in different ways and over different time frames. This has implications for pre- and post-development surveys and for impact prediction, which is considered first below.

Text Box 3 Cause-effect pathways

The images below show a branching (tabulate *Acropora* spp.) overlying a massive *Porites* spp. colony during a dredging project in Western Australia. The corals were located ~1.4 Km from the excavation activities and images taken 77, 206 and 343 days after dredging started.



4 August 2010 (day 77) 11 December 2010 (day 206) 27 April 2011 (day 343)

The massive growth morphology has clearly become smothered in sediment, whilst the more sieve-like branching morphology is comparatively unaffected by deposition and it is light availability that is probably the main pressure affecting the coral. Note that in the image on the right hand side, the white arrow indicates clean, sediment-free coral tissue and the black arrow indicates sediment-free coral tissue that has developed a thin semi-transparent mucous sheet. Mucous sheet formation and sloughing in the *Porites* spp. is thought to be a mechanism whereby they can remove sediment when deposition rates get too high (Bessell-Browne et al. (2017b)).

Predictions of the effects of dredging activities have historically focussed on suspended sediment concentrations. SSCs are modelled during the pre-dredging environmental impact assessment (EIA) stage using dredging production rates feeding into coupled sediment transport and fate models. SSCs are typically monitored during dredging, albeit using nephelometers which measure turbidity and provide proxy estimates of SSCs (nephelometrically-derived SSCs). Water quality monitoring used to decide whether to alter (or stop) dredging activities are also usually based on derived-SSC thresholds. This dependence on SSCs is perhaps because it is the output of the models and perhaps because of a historical legacy as SSCs were the focus during early dredging

projects in the inshore GBR >15 years ago (Koskela et al. 2002, Orpin et al. 2004). The focus on SSCs is intuitive because it is associated with the sediment itself, but **consideration should be given to incorporating benthic light availability for impact prediction when dredging around coral reefs and using light-based thresholds for dredge management frameworks. Numerical modelling of sediment generation and transport should be undertaken in such a way as to enable the outputs to be easily transformed into light at the seabed so that DLIs can be calculated and expressed as running means over user-defined periods (e.g. 14 days).**

High turbidity levels can profoundly affect underwater light levels, with sites close to dredging frequently experiencing low light (twilight or caliginous) periods which could last for weeks (Fisher et al. 2015, Jones et al. 2015). **Guideline values for benthic light should include a time component that is related to the physiological responses and time courses of any effects.** Projects 4.6.2 and 4.6.3 showed corals can undergo photoadaptation to low light by increasing pigment concentrations (chlorophyll and peridinin) in a matter of days. There is some discrepancy in the literature as to whether exposure to low light also results in an increase in the density of the coral's symbiotic algae, but where it does, the time course is also over a period of several days to weeks. **These responses are reasonably quick, and for monitoring programs developing light thresholds based over similar periods (i.e. a running mean 14 d threshold (see Fisher et al. (2017)) seems appropriate.**

In terms of extreme light attenuation, resulting in benthic light availability of <~0.04 mol quanta d^{-1}, which has been recorded for several days in a row close to dredging activities, the time course is quite rapid. Projects 4.6.1 and 4.6.2 showed that extreme low light (and darkness) can cause corals to bleach through loss of algal symbionts in over a timeframe of 7–10 d. **Consideration could also be given to a guideline value based on the number of consecutive days in darkness (or 'functionally' in darkness, such as a DLI of <~0.04 mol quanta d^{-1}) which would provide a more acute guideline to more extreme conditions. Evidence from the laboratory based studies suggests that corals can begin to bleach after 7–10 d in near darkness.**

The experimental results suggest that although there may be differences in the low light tolerance between shallow water coral species, no impacts are expected if the DLI is >4 mol quanta m^{-2}. In experiments where there was no sediment deposition on the corals, *A. millepora*, *P. damicornis, Porites* spp. and *Montipora* spp. collected from clear water reefs can survive 1.1 mol quanta m^{-2} d^{-1} for 28 d in clean (0 mg L^{-1}) seawater, but at 30 and 100 mg L^{-1} there was some partial mortality (Projects 4.6.1 and 4.6.2). *A. millepora*, *T. mesenterina* and *Porites* spp. could survive a combination of 2.2 mol quanta m^{-2} d^{-1} and 10 mg L^{-1} for 28 d whilst *P. damicornis* was slightly affected at this combination (Projects 4.6.3). **Overall, the most sensitive species appeared to be the branching species *P. damicornis* > *A. millepora* followed by the massive corals *Porites* spp. The foliose coral *T. reniformis* was the most tolerant species, which is consistent with its reputation as a turbid water specialist (Veron 2000). So in the absence of sediment accumulation, if SSCs remain below 10 mg L^{-1} and if daily light levels are maintained at >2.2 DLI it is expected that there may be some sub-lethal effects on corals but no mortality**.

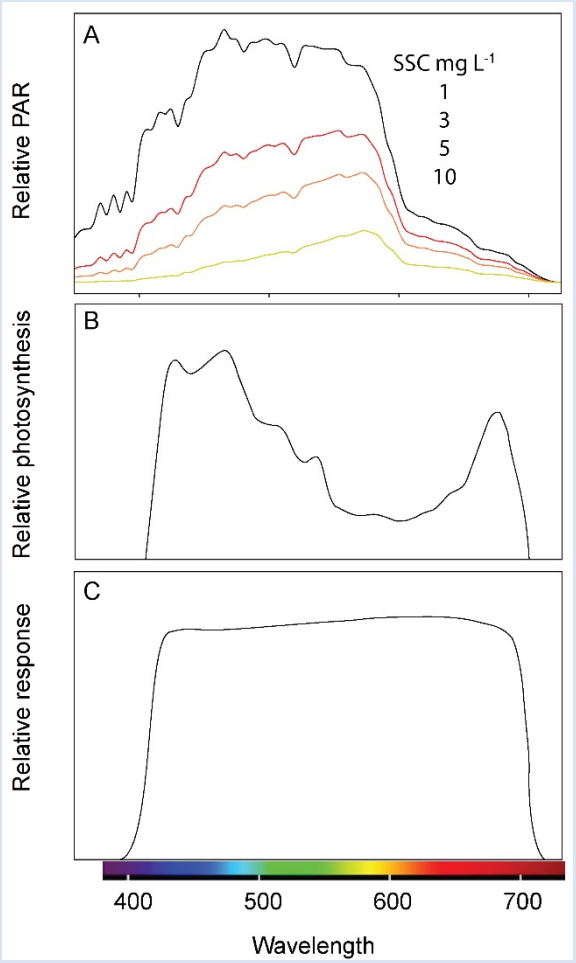
Corals are known to use lipids as a biochemical pool of energy they can draw upon when needed. All species lost lipids at the highest turbidity levels and *T. reniformis,* which was most tolerant, had ~2× higher initial lipid concentrations than the other species. **Somatic energy reserves of lipids are likely to act as buffers for corals during extended periods of low light and corals are likely to regain the reserves during clement conditions. If stores are not regained, recurrent bouts of low light may reduce reserves to the point where the corals are much more susceptible to low light than when in a 'healthy' state.**

Assessments of the relative energy stores of corals within the receiving environment may be used as a bioindicator and provide insight into the current capacity of a coral population to endure further periods of low light conditions. **However, this is not recommended as the extraction and analysis processes are far too time-consuming for routine monitoring and incorporation into management frameworks where decisions are needed within hours or days**. Further understanding how lipid storage levels relate to turbidity tolerance, and especially how quickly different coral species can regain their lipids once depleted, is recommended for future studies (see below), and likely to provide further insights into the tolerance levels of coral to episodic periods of low light. **The emphasis here is that the laboratory based studies show that corals do have a clear capacity to**

photoadapt to low light, to temporarily endure low light periods (and periods of darkness) because of energy reserves, and can temporarily tolerate energy debts. More information is needed to properly understand natural trends in lipid concentrations and their relationship with susceptibility to dredging related pressures.

Text Box 4. Photosynthetically Active Radiation (PAR) and Photosynthetically Useable Radiation (PUR)

Sediment plumes not only change the quantity of benthic light available for photoautotrophs but also the quality of light. Underneath sediment plumes there is a reduction in blue and red wavelengths and a clear shift to yellow-green light. The top figure below shows simulated down-welling irradiance spectra at 5 m depth (for a clear sky at tropical noon) with varying SSCs from 1–10 mg L^{-1} based on empirical data collected during a dredging project (Jones et al. 2016). Yellow green light is outside of the major absorption peak for photo pigments of the symbiotic algae of corals, and a photosynthetic action spectrum of photosynthesis of algal symbionts from an *Acropora* spp. coral is shown in the middle figure opposite, indicating that relative photosynthetic rates are poor in this area of the spectrum. Changes in the spectral quality of light under dredging plumes has been highlighted in the Dredging Science Node (see Theme 3 and Jones et al. (2016)), and in recent investigations of dredging in Gladstone (Queensland, Australia, see Chartrand et al. (2012)). Importantly, the types of light sensors commonly used in monitoring programmes integrate across the entire PAR wavelengths (see bottom image opposite) and, by not accounting for any spectral changes, are potentially misleading with respect to the amount of photosynthetically useable radiation (PUR) photoautotrophs actually receive under a plume.



During natural sediment resuspension events similar changes in spectral quality of light should also occur, so determining light thresholds based on background, baseline light profiles do not need to take spectral changes into account. Where it does matter is in interpreting the results of laboratory-based studies where light intensity is varied but light quality is not. Such experiments could underestimate the amount of PAR that is needed.

This is a comparatively new area of research and it is now possible to examine the effects of spectral changes in laboratory based studies given recent advances in lighting technology (see Jones et al. (2016)). In the interim period, and since standalone field deployable multispectral radiometers are now commercially available, their use should be considered for future dredging projects. It is possible to calculate both PAR as well as PUR based on action spectra of the symbiotic dinoflagellates. Light loggers are typically smaller than nephelometers and can be more easily deployed and retrieved and less effort is needed for maintenance and calibration. Using underwater acoustic modems or cables and telemetering from surface buoys using mobile telecommunication technology, would allow near real time data transfer.

The types of sediments released into the water column by dredging activities can range from biologically-derived carbonate sediments to terrestrially derived purely siliciclastic sediments, although in the majority of cases would most likely be composed of a range of combinations of the two. Different sediments have

different colours, sizes, and shapes that affect the light absorption and scattering. This is a known issue for estimating of SSC by proxy (i.e. by nephelometry), which can be very dependent on particle composition and potentially result in misleading assessments of SSCs. Different types of resuspended sediment will also affect the underwater light spectra in different ways. **The problems associated with different sediment types and accurate pressure field characterization with nephelometers can effectively be circumvented by (a) transitioning to light based monitoring, (b) using multi- or hyper-spectral radiometers, and (c) calculating PUR as opposed to PAR. This would allow accurate pressure field characterization, regardless of sediment type and particle size distribution and light and scattering properties (including changes in quality and quantity) in the water column**.

Whilst sediment deposition (see below) is a key pressure parameter for some coral morphologies, other morphologies (branching, tabulate) are much less affected by deposition. For these morphologies it is likely the reduction in light quantity (and quality) that accompanies the high SSC levels that caused the deposition events is of more significance.

Impact Prediction - Sediment deposition

As discussed in the review of the existing literature on the effects of sediments on corals **sediment deposition and sediment smothering of coral is arguably the most significant cause-effect pathway, resulting in mortality of some types of corals during dredging programs (Jones et al. 2016).** Once the self-cleaning (sediment rejection) ability of corals is exceeded then smothering can result, ultimately leading to focal and multifocal lesion formation (pathological discontinuities of tissue) and tissue mortality.

Susceptibility to sediment deposition is very dependent on coral morphology, and is affected by water flow (Project 4.6.4). Sediments accumulated on foliose and massive species to a much greater extent than on branching species. Under higher flow rates sediment smothering was much less on live corals than dead (enamel-covered) skeletons, suggesting an interaction between flow and active sediment rejection i.e. that elevated flow rates assisted the corals in their active sediment shedding (predominantly muco-ciliary transport).

In the non-branching morphologies the movement (shedding) or sediments was invariably down inclines, but sediments frequently became trapped in hollows (dips, depressions and concave areas) of the colony (i.e. 'local minima'). Although there were some areas where sediments tended to accumulate on the branching species, usually at junctions of the branches, this was much less common than the other morphologies.

Smothering corals in organically enriched sediment will cause mortality within days (Weber et al. 2012), which was much faster than with low organic content sediment used in these studies where smothering for 16 d induced bleaching but did not cause mortality. **The organic content of recently deposited sediment (that has been released to the water column by dredging activities) is presently unknown, but from a management perspective, any evidence of sediment accumulation on corals should be considered undesirable.**

Previous studies have drawn a distinction between the sediment shifting ability of corals and different sized sediment particles (i.e. sands versus silts). However, sand sized sediments are unlikely to be part of far field plumes that travel considerable distances from dredging activities. In this study, more environmentally relevant sediment particle sizes were used, and there was no significant difference in the sediment rejection ability of the corals between fine silt and coarse silt at deposition rates of <20 mg cm^{-2} d^{-1}. There were some differences at exceptionally high (235 mg cm^{-2} d^{-1}) deposition rate, where coarse silt was removed on average 3× more efficiently than fine silt.

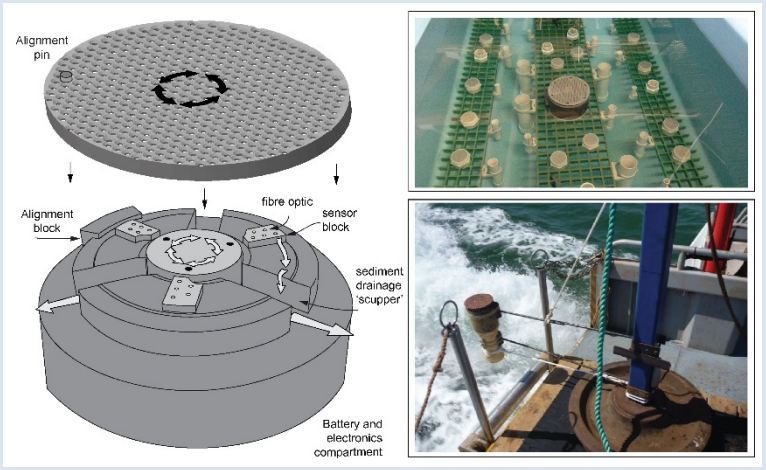
The corals also cleared siliciclastic, terrestrially derived sediments from their surfaces faster than more carbonate based (biologically-derived) sediments. Given the existing uncertainties associated with measuring sediment deposition rates and assessing the likely sediment deposition rates *in situ* during dredging (see Text Box 5), the results between different sediment types and sizes are difficult to evaluate. **There are no management recommendations as yet for guideline values based on mineral composition of the sediments being dredged.**

When sediment deposition rates exceed the rate of the corals' ability to self-clean, sediments will remain on the surface, and sediments will begin to accumulate over successive days. This successive accumulation onto previously sediment-covered surfaces is likely to be producing the images in Text Box 3– as opposed to a single deposition event. Light will be progressively attenuated under the sediment layer resulting in bleaching and eventual mortality. Mortality will be quicker under organically enriched sediments where microbially-mediated anoxia and changes in pH can result in localised necrosis in a few days.

Sediment smothering is therefore a key pressure parameter associated with turbidity generation, resulting in boundary-related effects and decreased solute (such as oxygen) and metabolite exchange and decreased filtering/feeding. Once smothered, the only way the area of the corals can recover is if sediments are removed by a storm before lesions are formed.

Text Box 5. Sediment deposition

Whilst sediment deposition is one of the key pressure parameters for corals, the problem is that there is a lack of suitable instrumentation to measure relevant sediment deposition over appropriate scales (e.g. mg cm^{-2} d^{-1}). These measurements are very important for understanding the pressures and risks associated with dredging activities and especially zones of high and moderate impact, and for contextualizing past laboratory and field based studies of sediment deposition and benthic community responses. The problem has been addressed within Theme 4 in terms of the re-design, calibration, laboratory testing, and field deployment of an *in situ* optical backscatter (OBS) sediment deposition sensor capable of measuring sediment deposition rates over intervals of a few hours (see opposite and Whinney et al. (2017)). This capability enables the quantification of *in-situ* sediment deposition rates, in ecologically relevant units, that provide direct measures of the actual pressures experienced by corals during a dredging program.



Increases in SSCs and reductions in benthic light levels associated with natural events such as storms are of a similar magnitude (*intensity*) to conditions that occur in dredging projects – although the *duration* and *frequency* is much higher during dredging (Jones et al. 2015). For sediment deposition we have argued that the *intensity* of the disturbance might be much higher than occurs naturally (Jones et al. 2016) as evidenced by *in-situ* observations of sediment smothering. Project 4.6.4 showed that the ability of corals to clear sediments diminished with increasing deposition events, nevertheless key guideline values for sediment deposition during dredging should be associated with more short term, acute levels, and avoiding rates of deposition where sediment smothering can occur (i.e. above coral clearance capabilities).

There are many variables involved in determining when and where sediment deposition will occur, including SSCs, sediment particle size, sediment type and density, flocculation and water column hydrodynamics including wave orbital velocities and currents. **The lack of suitable instrumentation to measure sediment deposition over appropriate scales (see Text Box 4) means there are no data sets that can be reliably used to calibrate/validate sediment deposition modules in numerical models. Furthermore, the absence of reliable information makes it difficult to design and test realistic exposure levels in laboratory experiments.** This can be best achieved in future project from *in situ* surveys of sediment accumulation on corals coupled to measurements using

customised sediment deposition sensing technology (see Whinney et al. (2017)). **In the interim period, the results from this study show that most coral species and morphologies tested were capable under slight flow (<3 cm s^{-1}) of removing all sediment up to 20 mg cm^{-2} d^{-1} leaving only slight residual deposits typically less than a few percentage of the surface area. The circular massive morphology (*Goniastrea retiformis*) could do the same up to 40 mg cm^{-2} d^{-1}. The branching species *A. millepora* managed to clear a sedimentation rate (under static conditions) of up to 235 mg cm^{-2} d^{-1}, an order of magnitude higher than the other morphologies.**

There were clear differences in the susceptibility among taxa in terms of their capacity to cope with periods of reduced light, as well as acute sedimentation events. **This suggests that impact prediction and management thresholds may need to be targeted to the particular coral communities, paying particular attention to growth morphology (see further below). Furthermore, as both light and deposition based mortality pathways operate on different parts of the coral communities, it is important to consider thresholds capturing both exposure pathways in impact prediction and risk assessments. This issue is discussed further in Project 4.9.**

Coral bleaching

Coral bleaching events caused by marine heatwaves have been increasing in frequency in the last 25 years. Warm-water bleaching events have coincided with many long-term dredging projects in WA[2,3,4,5] and elsewhere in Australia (Jones 2008), and the world (Miller et al. 2016).

Corals that were first experimentally bleached by elevated seawater temperatures, were far less capable of removing sediments from their surfaces, and sediment accumulated 3 to 4-fold more than on normally-pigmented corals (Project 4.6.5). The pattern was similar across 3 growth forms (branching, massive, and foliose), from 3 common and widely distributed coral species. This is significant, as sediment deposition leading to sediment smothering is likely to be one of the key cause-effect pathways determining where coral mortality will occur.

The probability of a marine heatwave (and subsequent coral bleaching event) occurring during the baseline and operational phases of extended capital dredging projects has reached a point where it is recommended that consideration be given as to how to manage the project should one occur.

For example, dredging and dredge material placement environmental management plans could include **a pre-agreed list of pragmatic, practical solutions to minimize risk from dredging if a warm water bleaching event occurs.**

From a management perspective an important consideration would be how to define when a bleaching event has occurred, and equally, when it is over. Depending on the severity and intensity of the bleaching event there could be a series of different management options and degrees of action. One way to do this is based on what percentage of colonies in a population are exhibiting what percentage of bleaching. Based on the expert opinion and best-guess estimates of a group of coral experts, the green area in the analysis in Figure 3 below shows what they consider is the normal background levels of bleaching i.e. level 0. The yellow, orange and red areas represent different levels of bleaching intensity, and associated with them were different management options. These include informing internal advisory groups and external expert panels (Level 1 and Level 2), through to immediate action (Level 3). These 'decision curves' were originally developed during a capital dredging project in Cleveland Bay, Queensland (see Benson et al. 1994), and in this context bleaching was considered a sublethal response to dredging related pressures (Oliver 1995), as opposed to the effects of elevated water temperatures which is being considered here. Nevertheless, the approach could be used to identify the start and finish of an event and to contextualize the severity of an event and to link a sequence of tiered management intervention options.

[2] Pluto LNG Development, Burruwp Peninsula: WA Environmental Protection Authority Bulletin 1259, Ministerial Statement No. 757
[3] Cape Lambert B project: WA Environmental Protection Authority Bulletin 1357, Ministerial Statement 840
[4] Gorgon Gas Development Barrow Island Nature Reserve: WA Environmental Protection Authority Bulletin 1221 Ministerial Statement No. 800
[5] Wheatstone Development - Gas Processing, Export Facilities and Infrastructure: WA Environmental Protection Authority Bulletin 1404 Ministerial Statement No. 873

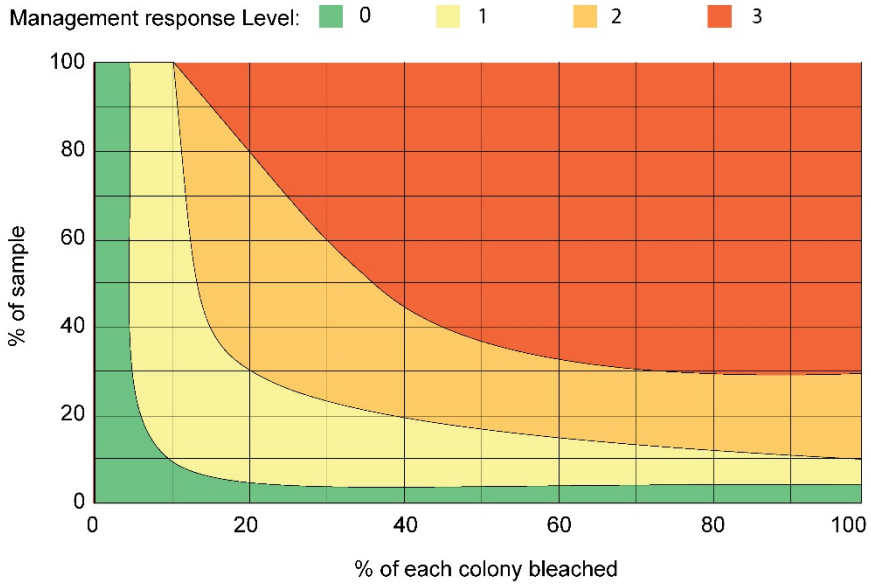


Figure 3. A 'decision curve' analysis for management action based on the percentage of colonies in a sample which exhibit varying levels of bleaching (reproduced from (Oliver 1995)) that could be applied to dredging management.

A set of pre-agreed management responses and risk reduction activities could be established for each of the 4 management response levels. The responses could be tiered and range from 'business-as-usual' at level zero, through to triggering further investigations, alerting regulators and technical panels and/or modifying dredging activities. Modifying dredging could involve, for example: changing dredge types and sizes, reducing production rates, reducing or stopping overflow, relocating away from reefs where possible, using more distant dredge material placement sites, and in extreme cases potentially ceasing all turbidity generating activities.

The anomalous La Niña during the summer of 2010-2011 induced mass bleaching of corals along central and southern WA corals. Location, depth and cumulative heat stress measured in Degree Heating Days [maxDHD[6]] accounted for a large amount of overall variability in the observed bleaching response (Moore et al. 2012). *In situ* seawater temperature should be monitored during all future dredging projects to supplement broader scale analyses of cumulative heat stress from satellites to determine the likelihood of bleaching events occurring. For such analyses, information is readily available from the National Oceanographic and Atmospheric Administration (NOAA) Coral Reef Watch Program experimental daily global 5km (0.05°) satellite coral bleaching heat stress monitoring product suite.

Predevelopment surveys

From an operational perspective, using light-based thresholds requires a sufficient understanding of natural temporal and spatial variability in light climates. The influence of ebb and flow, and spring and neap tides, and seasonal weather patterns (wet/dry and winter/summer) are particularly important as these will help describe the baseline state. The influence of severe events (e.g. storms and cyclones) are important to understand as it provides the maximum level of severity and duration of (extreme) natural events. Understanding the recent antecedent conditions also helps understand/interpret the structure and cover of the existing coral communities. Understanding inter-annual variability in weather patterns and cyclone frequency is also useful for scenario testing. Knowledge of the influence of large scale weather patterns (e.g. ENSO and Madden–Julian oscillations) can also be useful. **If dredging activities have already caused a reduction in light at monitoring sites then**

[6] Degree Heating Days (maxDHD) are calculated as the sum of positive deviations over the climatological monthly means accumulated over the 3 month operational period of the product from the beginning of December to the end February during the Austral summer.

forecasting conditions in the next few days to weeks associated with tides and weather patterns might be informative for deciding what type of dredging could occur, or whether a change to dredging practices should occur. Appropriate techniques for characterizing sites based on light availability have been described in Fisher et al. (2015), Jones et al. (2015). Cyclical periodicity has already been identified in baseline (pre-dredging) water quality data on a semi-diurnal basis associated with tides, a diurnal basis associated with daily sea breezes, and on a fortnightly basis associated with spring-neap tidal cycles.

The *in situ* images in Text Box 3 typify the findings of the *ex-situ* laboratory-based investigations of the effects of elevated suspended sediment concentrations on corals. The images show that morphology plays a very significant role in determining the primary cause-effect pathway (light attenuation versus sediment deposition etc). Erftemeijer et al. (2012) emphasized that the effects of sediment on only 10% of all known reef-building corals has been investigated, and as such there is still a rather poor understanding of the relationship between sediment stress and the response of most corals. However, all the primary morphologies i.e. laminar [plate-like], encrusting, columnar, free-living, foliaceous [foliose], massive and branching have been examined and it is morphology level rather than species level differences that are most important.

In addition to species- or genus-level description of coral distributions, pre-development surveys should consider the dominant morphologies present at different distances from dredging and where possible using standardized descriptions (see https://coraltraits.org/species). Such surveys should also recognize that some species of corals exhibit quite high levels of morphological plasticity with their geometry changing with depth, tending to flatten out to reduce self-shading hence maximise light harvesting.

Since for the most part corals can clear their surfaces of sediments under natural resuspension events, quantifying evidence of sediment accumulation on coral surfaces *in situ* as percentage cover per colony could be a very useful indicator. Assessing sediment accumulation would be useful for rapid surveys of coral health in gradients from the near-field to the zone of Influence to confirm model predictions. Similarly, mucus sheet production in massive *Porites* spp. colonies (see Text Box 3) has been shown to be closely associated with sediment load and is also an effective sub-lethal bioindicator of sediment exposure (Bessell-Browne et al. 2017b). *Porites* spp. (*P. lutea* and *P. lobata*) are common throughout the Indo-Pacific, and are found from offshore clear water reefs to coastal, turbid regions. Sediment cover and mucus production can be rapidly assessed at potential impact sites and references sites from diver-based observations and is amenable to diver-less techniques from photographs or video collected by ROV. **If these approaches are followed then baseline (pre-dredging) surveys should be conducted to define the range of background levels of sediment cover and mucus production (including after storms or natural resuspension events), and determine both the percentage of colonies covered and the percentage of their surface area covered by sediment**.

Since sediment clearance ability is significantly affected by bleaching, such surveys could also be especially useful in informing management decisions if dredging continues when corals are in a bleached state. The focus of these studies should be on encrusting and foliose and massive (dome shaped) colonies that have indents and local depressions on the surface (e.g. *Porites* spp.).

Branching Pocilloporid species which are typically small with usually brooding reproduction, fast growth rates, generalist symbionts and a high population turnover, are considered 'weedy' species as opposed to the slow-growing, massive corals (Knowlton 2001, Darling et al. 2012, McClanahan 2014). The *P. damicornis* species

complex, including *P. damicornis, P. acuta, P. aliciae, P. verrucosa, P. meandrina, P. eydouxi, P.cf brevicornis. P. bairdi* (Schmidt-Roach et al. 2014) is widely distributed, and given the sensitivity of *P. damicornis* and *P. acuta* to light reduction used in this study (Project 4.6.2 and 4.6.3) may be useful genus-level indicator species for light attenuation.

Residual knowledge gaps

More research is needed on the implications of changes in the spectral quality of light under dredging plumes (see Text Box 4) and the physiological responses of corals (and other photoautotrophs) to those changes. Collecting light data using multispectral radiometers in future dredging projects would increase the knowledge base and allow investigations of differences in submarine light fields between low light caused by cloud cover and low light from sediment plumes, and plumes of different sediment types. This is amenable to examination by both lab and field based studies.

A better understanding is needed of the time course of recovery of lipid concentrations in corals following periods of low light. Even under natural, non-dredging conditions some corals may temporarily undergo energy deficits and use lipids as energy stores, buffering them from low light periods. The rate at which corals can replenish their energy reserves during clement weather is not known, but would be informative for the EIA of longer term, capital dredging projects that could extend over several years.

As noted above, the organic content of sediments that settle on the corals can determine the ultimate fate of the underlying, smothered tissues. It is comparatively easy to determine organic content of the surface sediments, but there is no reason to assume the organic content and sediment composition will be representative of what corals experience *in situ* from a plume. Surficial sediments released by the drag or cutter head (or propeller wash) will undergo winnowing processes in the water column as they settle back out of suspension. Similarly, sediments that have undergone the high intensity mechanical disturbances associated with excavation pumping to hoppers and/or barges, and then after overflow or placement and winnowing processes in the water column are likely to be very different from surficial sediments. This is especially significant for capital dredging projects where much deeper sediment layers are mobilized.

Further research is needed to understand natural and dredging-related sediment deposition rates and this can be best achieved from *in situ* surveys of sediment accumulation on corals coupled to measurements using customised sediment deposition sensing technology (see Whinney et al. (2017)).

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Impacts of turbidity on corals: The relative importance of light limitation and suspended sediments

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ABSTRACT

As part of an investigation of the effects of water quality from dredging/natural resuspension on reefs, the effects of suspended sediment concentrations (SSCs) (0, 30, 100 mg L^{-1}) and light (~0, 1.1, 8.6 mol photons m^{-2} d^{-1}) were examined alone and in combination, on the corals *Acropora millepora*, *Montipora capricornis* and *Porites* spp. over an extended (28 d) period. No effects were observed at any sediment concentrations when applied alone. All corals in the lowest light treatments lost chlorophyll *a* and discoloured (bleached) after a week. Coral mortality only occurred in the two lowest light treatments and was higher when simultaneously exposed to elevated SSCs. Compared to water quality data collected during large dredging programs and natural resuspension events (and in the absence of sediment deposition as a cause-effect pathway) these data suggest the light reduction associated with turbidity poses a proportionally greater risk than effects of elevated SSCs alone.

1. Introduction

Dredging is an essential activity for port operations and its requirement is projected to increase in the future associated with the current trend towards larger ships with deeper draft requirements (Ports Australia, 2014). Dredging releases sediment into the water column, creating turbid plumes which can migrate away from the initial activity and onto nearby sensitive habitats (Foster et al., 2010). The suspended sediments can reduce light, clog filtering and feeding apparatus, and settle onto benthic organisms, and therefore pose an environmental hazard (Bak, 1978; Brown et al., 1990; Dodge and Vaisnys, 1977; Erftemeijer et al., 2012; Foster et al., 2010; Jones et al., 2016; Rogers, 1990). To effectively manage this hazard, it is critical to identify and understand the specific cause-effect pathways for dredging-relating pressures on key biota, especially for ecologically important, habitat forming groups such as corals. Partitioning the various impacts of dredging, such as light attenuation, shifts in light wavelength, increased suspended sediment concentrations (SSCs), and sediment deposition is important to enable more targeted and effective generation of concentration-response relationships (reviewed by Jones et al. (2016)). Water quality thresholds developed following this process will have increased environmental relevance, and once established will improve the ability of dredging proponents to predict the impact of dredging (at the environmental impact assessment stage) and to minimise the impact of dredging using adaptive management (Holling, 1978).

Most shallow water tropical corals are sessile colonies of filter-feeding polyps that live in a mutualistic symbiosis with dinoflagellates of the genus *Symbiodinium* (Stat et al., 2008; Trench, 1979). They can obtain energy heterotrophically, and capture up to meso/macro sized zooplankton by nematocyst discharges and tentacle grabbing (reviewed by Houlbrèque and Ferrier-Pagès (2009)). Corals can also ingest and assimilate particles in suspension (Anthony, 1999a; Anthony, 1999b; Anthony and Fabricius, 2000; Goreau et al., 1971), or that have settled on their surfaces (Mills et al., 2004; Mills and Sebens, 2004). Corals can also obtain energy autotrophically, and the endosymbiotic algae provide the coral host with photosynthate that can represent up to 90% of its daily energy requirements (Falkowski et al., 1984; Muscatine, 1990; Muscatine et al., 1981). Some corals have flexibility in their feeding strategies and can maintain a positive energy balance by shifting from photoautrophy to heterotrophy with increasing depth (Palardy et al., 2006), following bleaching (Bessell-Browne et al., 2014; Grottoli et al., 2006), and in turbid environments (Anthony and

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Fabricius, 2000). Despite this plasticity, the dual nutritional mode leaves corals vulnerable to pressures, such as dredging, that can affect both the heterotrophic and autotrophic modes of nutrition.

One of the key proximal stressors associated with dredging is an increase in SSCs (reviewed by Rogers (1990) and Jones et al. (2016)). Suspended sediments typically have small particle sizes (silt and clay sized) and remain in suspension for extended periods with limited water turbulence (Masselink et al., 2014). Several studies have shown that corals may benefit from ingestion of organic matter associated with sediments at low concentrations (Anthony, 2006; Anthony et al., 2007; Mills and Sebens, 1997; Mills et al., 2004); however, higher SSCs can cause coral polyps to contract and feeding to cease (Anthony, 2000; Mills and Sebens, 1997).

Another key proximal stressor associated with dredging is decreased light availability from increased turbidity (reviewed by Jones et al. (2016)). The amount of light attenuation that occurs in a plume depends on depth, as well as the sediment concentration and its scattering and absorption properties including colour, composition, and particle size (Storlazzi et al., 2015). Recent modelling studies of benthic light availability experienced during dredging plumes, showed that incident down-welling irradiance of ~725 μmol photons m^{-2} s^{-1} at 5 m depth in 1 mg L^{-1} SSC is reduced to <5 μmol photons m^{-2} s^{-1} in a 30 mg L^{-1} SSC plume (Jones et al., 2016). Most hermatypic scleractinian corals have high photosynthetically active radiation (PAR, 400–700 nm) requirements due to their association with symbiotic dinoflagellates (Achituv and Dubinsky, 1990; Falkowski et al., 1984; Gattuso et al., 2006; Muir et al., 2015). Prolonged light attenuation will lead to decreased photosynthesis, a negative energy balance and reduced growth (Falkowski et al., 1990; Richmond, 1993). In extreme cases it can even result in dissociation of the coral-algal symbiosis (bleaching) (Brown, 1997; DeSalvo et al., 2012; Glynn, 1996; Kevin and Hudson, 1979; Yonge and Nicholls, 1931).

The close association between suspended particles and light attenuation creates difficulties for assigning a coral's response to one or both of these pressures following turbidity events such as plumes from dredging, river discharge, or natural resuspension. Water quality monitoring programs associated with dredging projects have typically focused on measuring turbidity using nephelometric turbidity units (NTUs) as a proxy measure of pressure fields (Foster et al., 2010; Hanley, 2011; Sofonia and Unsworth, 2010). This approach has recently been questioned by Sofonia and Unsworth (2010), who suggested a refocus on PAR rather than NTU, as it is more relevant biologically and inclusive of other site conditions. In this study, we examined the potential impacts of sediments on corals by experimentally exposing three common morphologies to elevated SSCs and light reduction alone, and in combination (3 light × 3 SSC regimes). Sediments were kept in suspension in these studies, reducing or eliminating a suite of other cause-effect pathways associated with sediment smothering such as anoxia. The purpose of the study was to provide insights into the cause-effect pathways of turbidity for each of these species, determine viable indicators of stress, and guide the development of future experiments to determine appropriate concentration-response relationships for management purposes.

2. Materials and methods

The study was conducted with *Acropora millepora* (Ehrenberg 1834), *Porites* spp. and *Montipora capricornis* (Veron 1985), representing branching, massive, and foliaceous morphologies respectively. All these species are common throughout the Indo-Pacific, including the east and west coasts of tropical Australia. For *A. millepora* and *M. capricornis*, 8 colonies were collected by hand, while 8 colonies of *Porites* spp. were cored with a pneumatic drill. All coral species were collected between 3 and 10 m from the lagoon of Davies Reef, a mid-shelf reef centrally located in the Great Barrier Reef (GBRMPA permits G12/35236.1 and G13/35758.1). Due to difficulty identifying *Porites* spp. colonies to species in the field as they have small and variable corallites (Veron, 2000) a mixture of species (*P. lutea* and *P. lobata*) were used for the experiment. Colonies that were free of biofouling and diseases were fragmented (~15 cm^2) into replicates. Fragments were then glued onto aragonite coral plugs and held in 200 L flow-through holding tanks in the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS), in Townsville, Australia for 6 weeks to recover from the collection and preparation procedures. During the holding period, corals were exposed to a 12-h light:dark (L:D) cycle made up of a 2 h period of gradually increasing light in the morning (06:00–8:00 h), 8 h of constant illumination at 200 μmol photons m^{-2} s^{-1}, and then a 2 h period of gradually decreasing light in the afternoon (16:00–18:00 h). Over the course of the day the corals experienced a daily light integral (DLI) of 7.2 mol photons m^{-2}.

Experiments were conducted in clear PVC tanks (115 L capacity) with an inverted pyramid at the base to reduce sediment deposition on any horizontal surfaces. Water was circulated by a magnetic drive, centrifugal pump that collected water from the top of the tank and forced flow up from the centre point of the inverted pyramid at the base, also reducing sediment deposition (see Fig. 1. A for a schematic representation of the experimental system). A second pump VorTech ™ MP10 (EcoTech Marine, PA, US) was placed in the tank at the same height as the corals to aid in circulation. Experiments were conducted with 100 L of ultra-filtered (to 0.4 μm) seawater pumped into each tank at a rate of 400 mL min^{-1} to ensure 6 complete turnovers of water each day. Water temperature and salinity was maintained at 27 ± 0.5 °C and 33‰ respectively. Turbidity within each experimental tank was monitored using nephelometers (Turbimax CUS31, Endress and Hauser) and nephelometric turbidity units (NTUs) were converted to mg L^{-1} by applying sediment specific algorithms (see below). To replace sediment lost from the tanks during water exchanges, new sediment was periodically introduced from a concentrated stock suspension housed in a separate 500 L tank. The dosing of the tanks was controlled using a programmable logic controller (custom control logic on Siemens S7-1500 PLC) that opened and closed pivoting solenoid valves connected to the stock suspension tank via a high velocity loop powered by an air diaphragm pump. Light was provided by two AI Hydra FiftyTwo™ HD LED lights (Aquaria Illumination, IA, US) suspended above each tank, which generated even illumination with an equal mix of white, blue, and red light. To ensure there was no sediment deposition on coral tissue, *A. millepora* fragments consisted of a single, upright, straight branch, while *Porites* spp. and *M. capricornis* fragments were positioned vertically. Light intensity was measured at the depth of the corals using an underwater spherical quantum sensor (Li-COR LI-193).

All sediment used in the study was biogenic calcium carbonate sediment collected from Davies Reef (Great Barrier Reef Marine Park Authority permit: G13/35758.1). Sediment was first screened to 2 mm and then ground with a rod mill grinder until the mean grain size was ~30 μm (range: 0.5–140 μm), measured using laser diffraction techniques (Mastersizer 2000, Malvern instruments Ltd., UK). Total organic content of the sediment was 0.25%.

Experiments were conducted using 9 treatments, made up of 3 SSCs levels (0, 30, 100 mg L^{-1}) and 3 light levels (darkness, 1.1, 8.6 mol photons m^{-2} d^{-1}). For the darkness treatments, the tanks were wrapped in black plastic (to reduce light contamination), but the corals nevertheless experienced very low level light exposure (albeit for a few minutes), during weekly photographing (see below); thus, the treatment is referred to as a DLI of ~0 mol photons m^{-2}. For the remaining two light treatments the corals were exposed to a 12-h L:D cycle composed of a 6 h period of gradually increasing light in the morning (06:00–12:00 h), reaching 50 or 400 μmol photons m^{-2} s^{-1} at local noon, and then a 6 h period of gradually decreasing light in the afternoon (12:00–18:00 h). Over the course of the day the corals experienced a daily light integral (DLIs) of 1.1 or 8.6 mol photons m^{-2} respectively. A total of 8 coral fragments from each of the 3 species

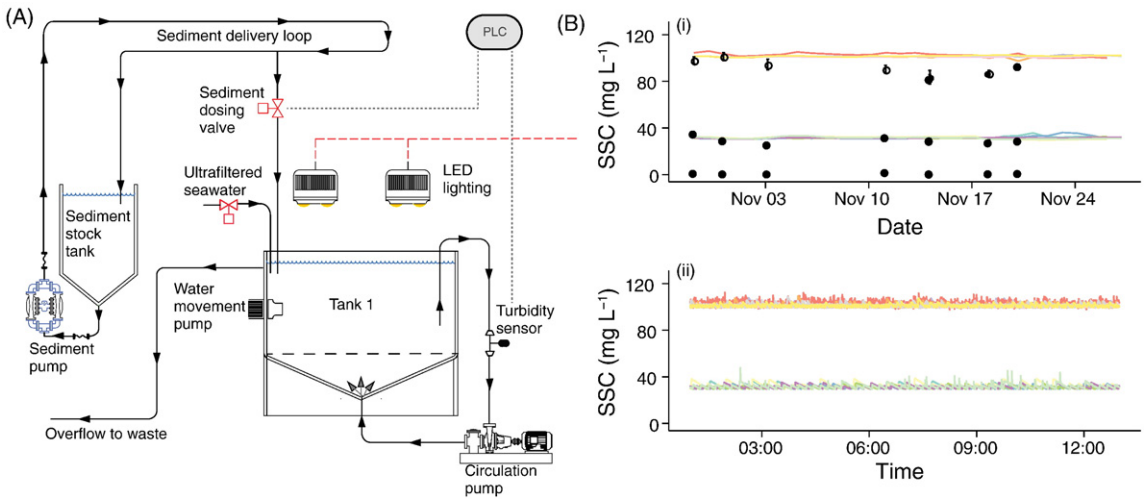

Fig. 1. (A) Schematic representation of the experimental dosing system showing one of the 18 holding tanks, the sediment delivery (stock) tanks, and the position of the recirculation pump, water movement pump and in-line turbidity sensor. Delivery of sediment from the stock tanks was controlled by the PLC system from input from the turbidity sensor. (B) Suspended sediment concentration (SSC) conditions in each tank showing (i) averaged daily SSC for the 28 d exposure period (lines) and gravimetric analyses (points, mean ± SE). Note probe values were adjusted from the 17th of November due to sensor drift; (ii) raw data from the first 12 h of a representative day (8th of November) showing a saw tooth pattern of sediment delivery.

were placed in each of 2 replicate tanks for each of the nine SSC × light combinations.

SSCs in each tank were determined gravimetrically from 500 mL water samples filtered through pre-weighed 47 mm diameter polycarbonate filters (0.4 μm nominal pore size), dried at 60 °C for ≥24 h, and weighed to 0.0001 g. SSCs were examined at weekly intervals to check the NTU to SSC conversion factors used by the PLC to dose the system, and NTUs were logged at 10 s intervals via the PLC.

Coral fragments were photographed each week using a high resolution digital camera. The camera settings and the surrounding light environment were kept the same during the photographing over the duration of the experiment. Changes in the colour of coral tissue was assessed weekly from photographs as a non-destructive indicator of bleaching throughout the experiment. The photographs were analysed for colour with the image processing software program ImageJ (Schneider et al., 2012), using the histogram function on a selection of representative live tissue, taking the arithmetic mean of pixel values (range 0–255) on a black and white scale. At the end of the experiment, these were standardised to the maximum and minimum values for each species, and converted to a range between 0 and 1. During the photographing process, any partial mortality of the corals was noted and quantified from the photographs using ImageJ.

Chlorophyll fluorescence of the endosymbiotic dinoflagellate algae within tissue of each coral fragment was measured using a mini-PAM fluorometer (Walz, Germany). Measurements were obtained using a 6 mm fibre-optic probe positioned perpendicular to the coral fragment and 3 mm away (controlled by a rubber spacer). Initial fluorescence (F_0) was determined by applying a weak pulse-modulated red light (650 nm, ~0.15 μmol photons m^{-2} s^{-1}). Maximum fluorescence (F_m) was then measured following a saturating pulse of white light. Maximum quantum yield (F_v/F_m) is the proportion of light used for photosynthesis by chlorophyll when all reaction centres are open (Genty et al., 1989) and is determined by the following equation:

$$\frac{F_v}{F_m} = (F_m - F_0)/F_m$$

Coral fragments were dark-adapted for 2 h prior to measuring the yield. Fluorescence data was collected before the experiment began, and after 7, 14, 21 and 28 d. Measurements were only taken over live tissue, and 1–4 measurements were taken and averaged per fragment, depending on live tissue available.

At the end of the experiment, each fragment was snap frozen in liquid nitrogen and then stored at −80 °C. For tissue biomass and pigment analysis, fragments were crushed and then subsampled and material for tissue biomass freeze-dried. Chlorophyll *a* (hereafter Chl *a*) concentrations were extracted twice from coral fragments using 95% ethanol and quantified spectroscopically using the equations of Ritchie (2008) and Lichtenthaler (1987). Endolithic algae were not visible in the samples and assumed not to contribute any significant amount of Chl *a* to the samples. Ash free dry weights of tissue biomass were determined by weighing each sample before and after combustion at 400 °C for 24 h.

Chlorophyll concentrations were standardised to ash-free dry weight of the organic fraction of the coral fragment (host tissue and algal symbionts). This normalisation is often preferred as the polyp structure and penetration of tissue into the skeleton differs between species, making tissue biomass a more robust normalisation than surface area (Edmunds and Gates, 2002).

2.1. Data analysis

All data were analysed with R software (version 3.2.3, R Core Team (2015)). The relative influences of environmental factors on coral health parameters were assessed using a full subsets model selection approach (Burnham and Anderson, 2002), where models were compared with Deviance Information Criterion (DIC) and R^2. The models with the lowest DIC were chosen as the best fit and if another model was within 2 DIC, that with fewer parameters was selected.

For health parameters assessed through time (partial mortality, F_v/F_m and colour index) a logit function was used with generalised linear mixed models to determine the impacts of health parameters for each species. Each health dataset was explored using the protocol described by Zuur et al. (2010). For modelling of relationships, tank and coral fragment identity were included as random factors. A Gaussian generalised linear mixed model was used, with time included as a 3rd order polynomial with variance modelled as a function of the included factor variables to account for heterogeneity of variance among treatments. Models were fitted in JAGS via the R2jags package (Plummer, 2003). Variable importance was calculated based on differenced in R^2 values between models with different fixed factors (SSC, DLI, time and species).

The same models as above were used to explore the health parameters measured at the end of the experiment (partial mortality, colour index, chlorophyll fluorescence and Chl *a*). Mortality, colour index and F_v/F_m fits were based on a logit transformation, while Chl *a* was fitted

following a cube root transformation. The correlation between colour index and Chl *a* concentrations for the end time point (28 d) was assessed using a basic linear regression to determine whether the colour index parameter was representative of fragment pigmentation.

3. Results

Water quality conditions remained stable throughout the duration of the experiment for each of the 3 SSC treatment levels (Fig. 1, B). There was a period when SSC readings from the probes began to drift due to slight changes in sediment particle size and a conversion factor was added to algorithms to account for this on the 17th of November (Fig. 1, B i). Throughout each day there was inevitable fine scale variation in concentrations, with the dosing of sediment creating a saw tooth pattern of delivery (Fig. 1, B ii).

Light level (DLI), species, sediment (SSC), and time were all driving factors for mortality, with all three being included in the best model according to DIC (Table 1, SEM Table S1). For both quantum yield (F_v/F_m) and colour index, the model with the best fit included light (DLI), time and species, with little to no effect of sediment (SSC) (Table 1, SEM Tables S2 and S3).

The relative explanatory value of each of the factors included in the experiment (DLI, SSC, species and time) varied for each health parameter (Fig. 2). Maximum quantum yield (F_v/F_m) was most influenced by light levels, followed by time, species and then SSCs (Fig. 2). Colour index was similar to quantum yield with the most influential factors being DLI and time, followed by species and SSCs, which had limited influence (Fig. 2). Partial mortality had different drivers, with time having the largest influence, followed equally by DLI, species and SSCs (Fig. 2).

No full colony mortality was observed as part of this experiment; however, up to 65% partial mortality (11 ± 4%, $n = 24$, mean ± SE) was observed in the zero light treatment (DLI of ~0 mol photons m^{-2}) for individual fragments of *A. millepora*, 39% (9 ± 2%, $n = 24$, mean ± SE) for *M. capricornis*, and 44% (2 ± 1%, $n = 24$, mean ± SE) for *Porites* spp. (Fig. 3). In the 1.1 mol photons m^{-2} d^{-1} DLI treatment, the maximum partial mortality in individual fragments was 69% (6 ± 3%, $n = 24$, mean ± SE) for *A. millepora*, 29% (5 ± 2% $n = 24$, mean ± SE) for *M. capricornis*, and 78% (7 ± 4%, mean ± SE, $n = 24$) for *Porites* spp. (Fig. 3). Mortality was variable across the SSCs for both low light treatments (Fig. 3). *A. millepora* and *M. capricornis* only exhibited mortality in the highest SSC treatment at low light (1.1 mol photons m^{-2} d^{-1}), and increasing mortality with higher sediment concentrations in the dark treatment (~0 mol photons m^{-2} d^{-1}). There was no partial mortality for any of the species in the 8.6 mol photons m^{-2} d^{-1} treatment, regardless of SSC (Fig. 3).

The colour of coral tissue changed throughout the duration of the experiment with all three species initially darkening over the first week of the exposure (Fig. 4). Lightening of the tissues (bleaching) was observed in the dark (~0 DLI) treatment, with fragments from all species bleaching extensively by 28 d (Fig. 4). In *A. millepora* exposed to 1.1 DLI there was no difference in colour from the 8.6 DLI treatment (Fig. 4). *M. capricornis* fragments in the 1.1 DLI treatment had reduced colour compared to those fragments in the 8.6 DLI treatment, with both decreasing over time from 14 days, with those in the 1.1 DLI treatment pale by the end of the experiment (Fig. 4). *Porites* spp. showed similar differentiation between DLI treatments as *M. capricornis*, with gradual reduction in colour through time after 7 days of exposure to the 0 and 1.1 DLI treatments (Fig. 4). Those *Porites* spp. fragments in the 1.1 DLI treatment were pale at the end of the experiment, while those in the ~0 DLI treatment were bone white (Fig. 4).

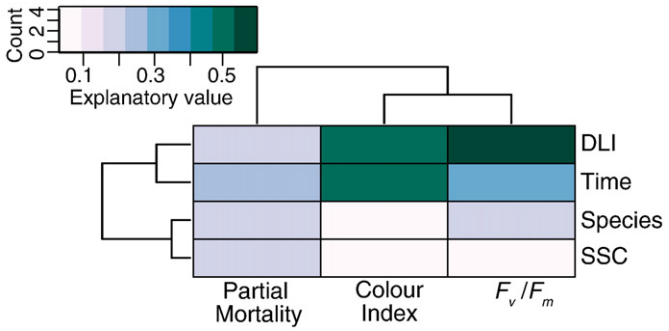

Fig. 2. Explanatory value of each of the 4 fixed factors included in the models, including DLI (mol photon m^{-2} d^{-1}), Time (d), Species and SSC (mg L^{-1}), with darker colours indicating increased importance of that variable. Explanatory value was calculated simply as the additional R^2 obtained when a variable was included in a complete interaction model, compared to a model excluding just that variable.

The colour index score in the ~0 DLI treatment was 0.07 ± 0.01 for *A. millepora*, 0.19 ± 0.02 for *M. capricornis*, and 0.13 ± 0.01 for *Porites* spp. (Fig. 4). Colour index was higher in the low light treatment (1.1 DLI) with a colour index score 0.68 ± 0.01 for *A. millepora*, 0.47 ± 0.01 for *M. capricornis*, and 0.35 ± 0.03 for *Porites* spp., and higher again in the control 8.6 DLI light treatment, with 0.71 ± 0.01 for *A. millepora*, 0.63 ± 0.01 for *M. capricornis*, and 0.65 ± 0.02 for *Porites* spp. observed (all mean ± SE, $n = 24$) (Fig. 4). There was no influence of SSC treatment on colour index across any of the light treatments (Table 1, Fig. 4). The ~0 mol photons m^{-2} d^{-1} treatment caused a decline in maximum quantum yields over time, with a F_v/F_m of 0.14 ± 0.0 recorded for *A. millepora*, 0.5 ± 0.0 for *M. capricornis*, and 0.5 ± 0.0 for *Porites* spp. (all mean ± SE, $n = 24$) (Fig. 4). F_v/F_m in the corals in the 1.1 and 8.6 mol photons m^{-2} d^{-1} did not change through the experiment (Fig. 4).

After the 28 d chronic exposure period, partial mortality was driven by an interaction between all three parameters (DLI × Species × SSC) (Table 2, SEM Table S4), with mortality higher in *A. millepora* and *M. capricornis*, compared to *Porites* spp., and only in the lower light treatments (~0 and 1.1 DLI) and with elevated sediment levels (30 and 100 mg L^{-1}) (Fig. 5). Colour index, maximum quantum yields (F_v/F_m) and Chl *a* were all best described by the model including species and light treatment (DLI × Species) (Table 2, SEM Tables S5, S6, S7). For all three species, colour index was lowest in the ~0 DLI treatment,

Table 1
Top model fits for each health parameter measured through time (partial mortality, colour index and F_v/F_m), including the model, number of parameters (n), deviance information criterion (DIC), δ DIC, model weights and R^2 values.

Parameter	Model	n	DIC	δ DIC	DIC weight	R^2
Mortality	DLI × Species × SSC + Time	59	−6459.06	0	0.97	0.11
	DLI × Species × SSC	56	−6450.93	8.1	0.02	0.11
	DLI × Time × Species × SSC	137	−6450.56	8.5	0.01	0.39
Colour index	DLI × Time × Species	47	1037.63	0	0.83	0.87
	DLI × Time × Species + SSC	51	1040.81	3.2	0.17	0.87
	DLI + Time × Species × SSC	137	1063.98	26.4	0	0.89
F_v/F_m	DLI × Time × Species	47	−503.28	0	0.70	0.74
	DLI × Time × Species + SSC	51	−501.55	1.7	0.30	0.74
	DLI × Time × Species × SSC	137	−434.22	69.1	0	0.77

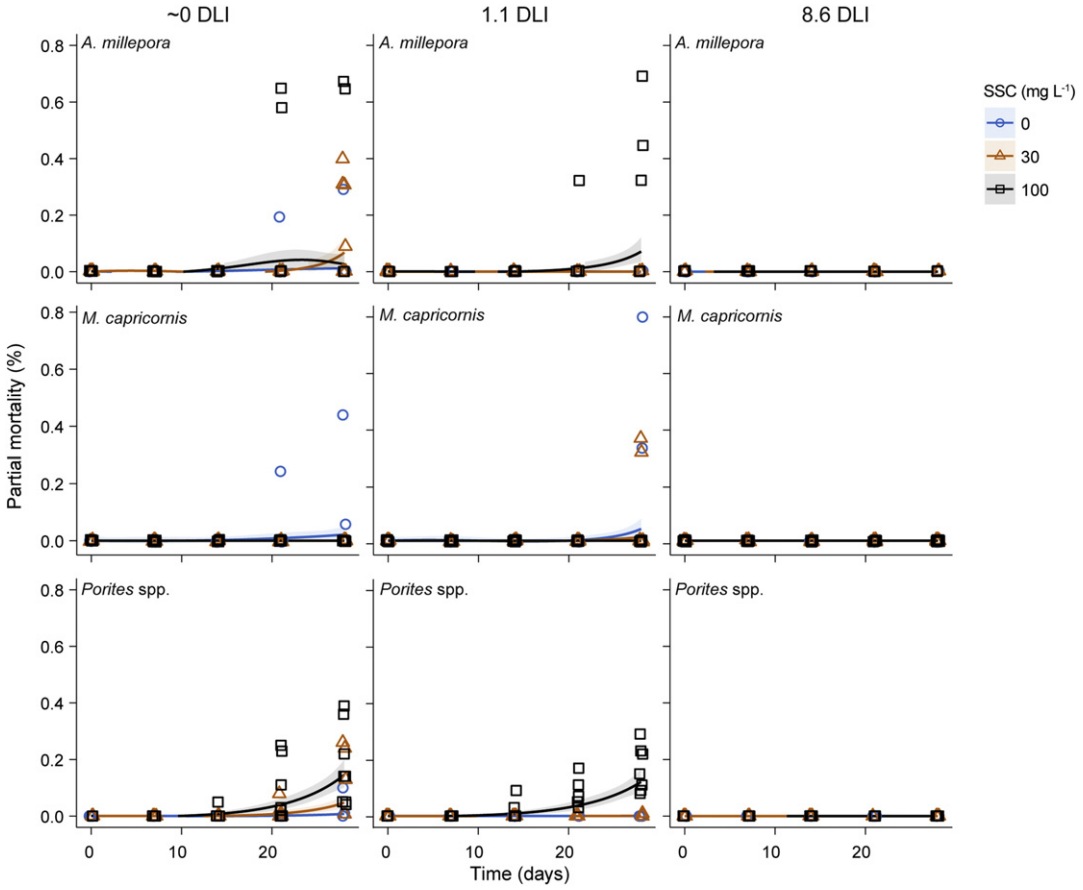

Fig. 3. Partial mortality (%) of each coral fragment of *A. millepora*, *M. capricornis* and *Porites* spp. across 3 light levels (~0, 1.1, 8.6 mol photons m^{-2} d^{-1}) and 3 sediment treatments (0, 30,100 mg L^{-1}). Raw data are presented with modelled relationship and 95% credible intervals.

before increasing in the 1.1 and 8.6 DLI treatments (Fig. 5). Colour index in the 1.1 DLI treatment varied between species, with *A. millepora* having a similar colour to the 8.6 DLI treatment, while *M. capricornis* had reduced colour compared to *A. millepora*, and *Porites* spp. had a lower colour index again (Fig. 5). Maximum quantum yields (F_v/F_m) were considerably lower in the ~0 DLI treatment than the 1.1 and 8.6 DLI

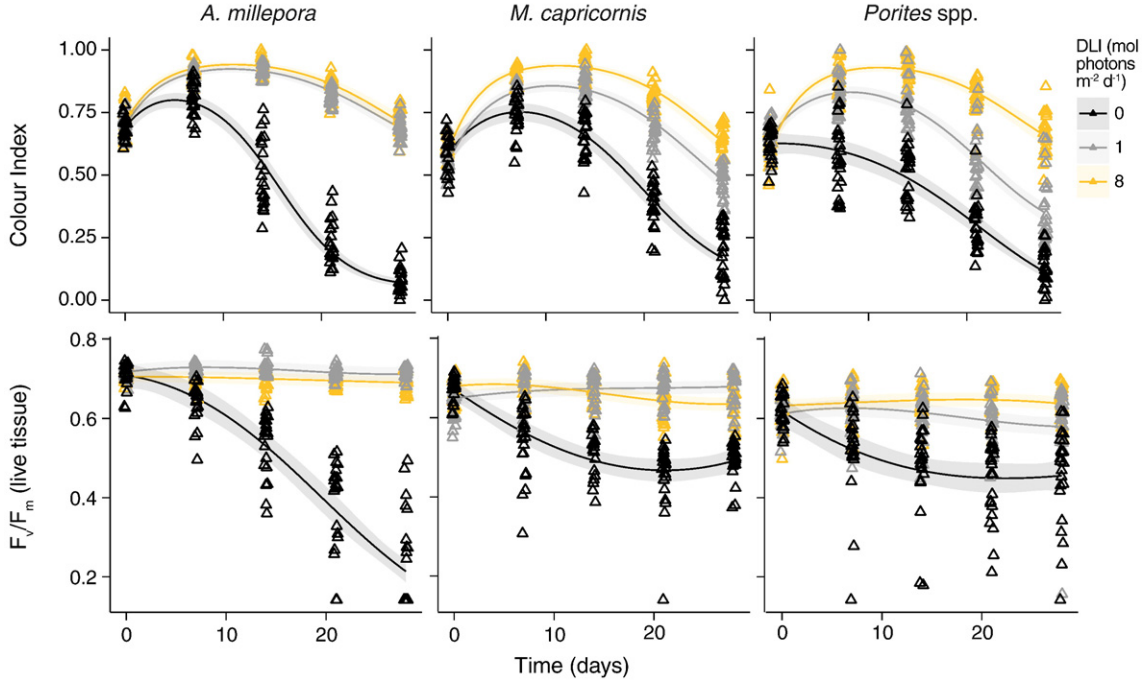

Fig. 4. Colour index and maximum quantum yield (F_v/F_m) of for *A. millepora*, *M. capricornis*, and *Porites* spp., for 3 light levels (~0, 1.1, and 8.6 mol photons m^{-2} d^{-1}) across all sediment concentrations. Raw data is presented with modelled relationship and 95% credible intervals.

Table 2
Top model fits for each health parameter, including partial mortality, colour index, maximum quantum yield (F_v/F_m) and Chl *a*, after 28 days of exposure to treatment conditions, including the model, number of parameters (*n*), deviance information criterion (DIC), δ DIC, model weights and R^2 values.

Parameter	Model	*n*	DIC	δ DIC	DIC weight	R^2
Mortality	DLI × Species × SSC	29	526.3	0	0.99	0.40
	DLI + SSC × Species	13	536.5	10.27	0.01	0.25
	Species + DLI × SSC	13	549.7	23.45	0.00	0.18
Colour index	DLI × Species	11	362.5	0	0.55	0.85
	DLI × Species + SSC	13	363.1	0.59	0.41	0.86
	DLI × Species × SSC	29	367.4	4.92	0.05	0.88
F_v/F_m	DLI × Species	11	138.0	0	0.60	0.78
	DLI × Species + SSC	13	139.0	1.01	0.36	0.78
	DLI × Species × SSC	29	143.8	5.86	0.03	0.81
Chl *a*	DLI × Species*	11	249.2	0	0.41	0.86
	DLI × Species + SSC	13	248.5	-0.71	0.58	0.86
	DLI × Species × SSC	29	256.3	7.14	0.01	0.88

* If models were within 2 DIC of each other, that with fewer parameters was chosen as the best model.

treatments for *A. millepora*, while smaller differences were observed between the other two species (Fig. 5). Maximum quantum yields were similar between the 8.6 and 1.1 DLI treatments with *A. millepora* having higher yields than *M. capricornis*, which had higher yields than *Porites* spp. (Fig. 5). Chl *a* was highest in the 8.6 DLI treatment for all species, followed by the 1.1 and ~0 DLI treatments (Fig. 5). Again, *A. millepora* had a large difference between the 0 and 1.1 and 8.6 DLI treatments for Chl *a*, similar to the patterns observed with colour index and maximum quantum yields, while smaller differences were observed between *M. capricornis* and *Porites* spp. (Fig. 5).

Comparing Chl *a* concentrations with colour index data after 28 d of exposure to treatment conditions revealed links between these two parameters (Fig. 6). They suggest that colour index is a suitable proxy representative of Chl *a* concentrations for *A. millepora* and *M. capricornis*, while *Porites* spp. showed increased changes in colour index with minimal changes in Chl *a*, demonstrating that although colour index is not an exact representation of pigmentation for this genera it is representative of changes in pigmentation, with this potentially due to standardisation to dry weight rather than surface area.

4. Discussion

In this study, several species of corals with varying morphologies were exposed to different SSCs (0, 30, 100 mg L^{-1}) and light levels (~0, 1.1, 8.6 mol photons m^{-2} d^{-1}) alone, and in combination, over an extended (28 d) period. Harris et al. (2014) emphasize the critical importance of defining and testing realistic and environmentally relevant exposure scenarios, and to comprehensively justify those exposure conditions. The SSC and light combinations selected were based on water quality information collected during three recent large-scale capital dredging projects on the reefs of northern Western Australia (Fisher et al., 2015; Jones et al., 2016; Jones et al., 2015). In particular, monitoring data from the Barrow Island project (8 Mm^3, capital dredging project in a clear-water, offshore environment) was used, as this project had the most comprehensive record of spatial and temporal changes in water quality. Interpretations of the response of the corals to the treatments outlined below need to be mindful of the fact that there was no deposition of sediment on the corals that led to smothering during experimental manipulations, which can introduce another suite of impacts on coral health, including anoxia and tissue necrosis (Weber et al., 2012; Weber et al., 2006).

All corals survived the high SSCs (100 mg L^{-1}) over the 28 d period, when light levels remained sufficient (in this case 8.6 mol photons m^{-2} d^{-1}, see further below). For contextual purposes, the 95th percentile of SSCs over an equivalent (30 d) running mean period during the Barrow Island dredging project was 21 mg L^{-1} (range: 11–29 mg L^{-1}) for 7 sites located <1 km from the dredging (using an NTU:SSC conversion factor of 1.45), with this data attained through concentration, duration, frequency analysis (Jones et al., 2015). The 100 mg L^{-1} experimental SSC treatment was, therefore, ~5 fold higher than observed during the dredging operations, and >30 fold higher than during the pre-dredging (baseline) period of 2.9 mg L^{-1}. SSCs exceeding 100 mg L^{-1} are possible during dredging programs, but over much shorter periods i.e. hours

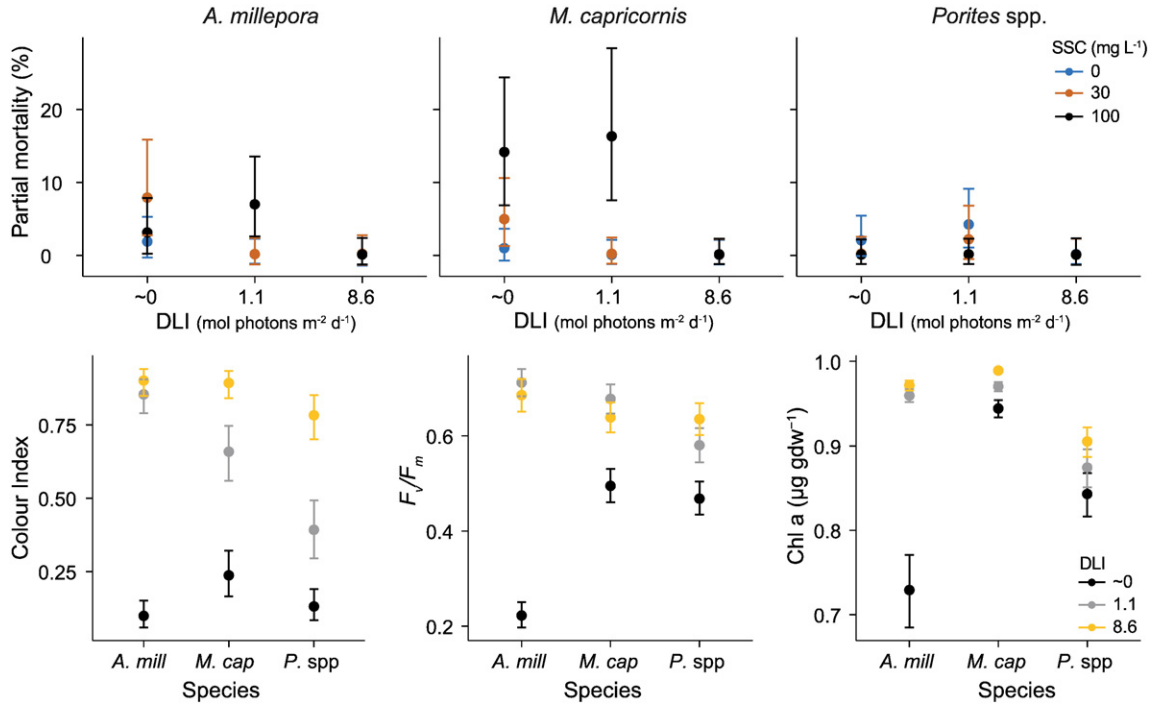

Fig. 5. Changes in partial mortality, colour index, maximum quantum yield (F_v/F_m) and Chl *a* of coral tissue of *A. millepora*, *M. capricornis* and *Porites* spp. after 28 d of exposure across the 3 light levels (0, 1.1, 8.6 mol photons m^{-2} d^{-1}) and 3 sediment treatments (0, 30,100 mg L^{-1}). Modelled data is presented with 95% credible intervals.

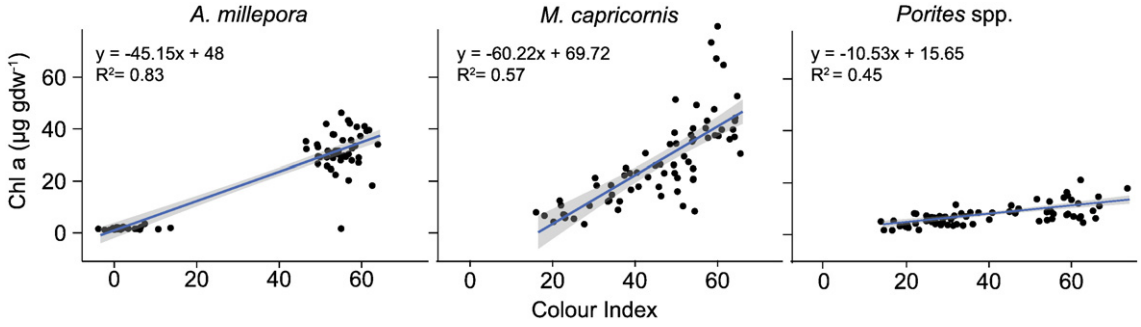

Fig. 6. Relationship between Chl *a* concentrations (µg gdw^{-1}) and colour changes, depicted as colour index, measured from photographs for *A. millepora*, *M. capricornis*, and *Porites* spp.

(Fisher et al., 2015), and much less than the 28 d exposure period used in this study.

The 100 mg L^{-1} treatment (for 28 d) also exceeds any likely natural scenario corals may experience, even in highly turbid systems. For example, in the turbid reef zone of the central Great Barrier Reef (GBR), SSCs near reefs can often exceed 50 mg L^{-1} during natural wind-wave events (Cooper et al., 2008; Larcombe et al., 2001; Larcombe et al., 1995) but only occasionally exceed >100 mg L^{-1}, and only then for short periods of time i.e. hours (Browne et al., 2013; Orpin et al., 2004). Long term series of both turbidity and light data are not common, but in the 18 month time series at Magnetic Island (also in the turbid central inshore GBR), Cooper et al. (2008) recorded a mean turbidity of 13 NTU (20–30 mg L^{-1}) and average DLI of 0.7 ± 0.5 mol photons m^{-2} d^{-1} over a 10 d of very high winds associated with a storm (Orpin and Ridd, 2012). Peak NTU values during the period of sustained winds was 65 NTU (or ≥100 mg L^{-1}) but this only lasted for a few hours (Orpin and Ridd, 2012).

These comparisons highlight the importance of the exposure duration as well as intensity (concentration) when comparing experimental and field-based exposures (Jones et al., 2015). Maintaining constant experimental SSCs represents the simplest scenario to explore the effect pathways and physiological responses of corals, and was therefore the approach taken here. Further work is required to determine the impacts of more natural, fluctuating patterns in SSCs and if possible guideline development should consider a wider range of exposure scenarios.

Under such high SSCs (100 mg L^{-1}) corals would be continually encountering and clearing the fine silt and clay-sized sediment particles that become entangled in the surface mucus (Riegl and Branch, 1995; Stafford-Smith and Ormond, 1992). The epidermal muco-ciliary system used by corals to manipulate and ingest or reject sediment (see Stafford-Smith and Ormond (1992)) bears a metabolic cost, although recent evidence suggests cilia movement itself constitutes a negligible fraction (<0.1%) of the coral's energy budget (Shapiro et al., 2014). SSCs above 30 mg L^{-1} can cause corals (*Pocillopora damicornis* and *A. millepora*) to contract their polyps (Anthony, 2000; Anthony and Fabricius, 2000). The expansion and contraction patterns of polyps can affect the intensity of light that the symbiotic dinoflagellates are exposed to in hard corals (Crossland and Barnes, 1977) and soft corals (Fabricius and Klumpp, 1995). Contraction of polys also reduces solute exchange with the surrounding water (Levy et al., 2006). No contraction of polyps was observed in any of the species used in this study in response to 100 mg L^{-1} treatment. A previous study exposed vertical *A. millepora* branches to similar sediment types at 100 mg L^{-1} for 3 months without substantial light limitation (2 mol photons m^{-2} d^{-1}) reported no mortality associated with exposure to suspended sediments (Flores et al., 2012), supporting the results of this study. Based on the experimental data described here, partial mortality of corals caused by exposure to elevated SSCs alone (i.e. in the absence of associated light attenuation) seems unlikely.

Exposure of the corals to extended periods of darkness (~0 mol photons m^{-2}) resulted in a decrease in maximum quantum yield (dark-adapted F_v/F_m) and all 3 species began discolouring (paling) after 7 d. The discolouration continued until the end of the experiment, leaving some of the species fully bleached (i.e. bone-white). Bleaching of corals held in darkness was first reported by Yonge and Nicholls (1931) who noted discolouration and extrusion of symbiotic algae of a range of reef flat corals over 18 d (*Fungia scrutaria*), 22 d (*Psammocora gonagra*) and 19 d (*Galaxea fascicualris*). Darkness-induced bleaching of corals has been reported to occur in the temperate (low-light adapted) coral *Pleasiastrea versipora* after 45 d (Kevin and Hudson, 1979). In this study the bleaching occurred over a much shorter time period, and the results are more consistent with the recent studies with *Acropora palmata* and *Montastraea faveloata*, where bleaching was observed after 4 and 5 d respectively when held in complete darkness (DeSalvo et al., 2012).

Complete loss of all light has been recorded during natural turbidity events (Anthony et al., 2004; Cooper et al., 2008; Jones, 2008) and also during dredging projects associated with elevated SSCs (Fisher et al., 2015). For example, during the Barrow Island dredging project, 1 of the 7 water quality monitoring sites located close (<1 km) to the dredging experienced 2 consecutive days of darkness (defined as a DLI of <0.04 mol photons m^{-2}) during the pre-dredging, baseline phase. During the dredging phase, each of the 7 impact sites experienced between 1 and 6 consecutive days in darkness caused by turbid sediment plumes. Based on the experimental data described here, bleaching, dissociation of the coral-symbiosis and mortality from exposure to extended periods of darkness alone, seems possible.

Although complete days in darkness was common at sites close to dredging, a much more common occurrence was portions of the day (i.e. several hours) in darkness, and generally extended periods of low light (Jones et al., 2015). For the 7 water quality monitoring sites located close (<1 km) to the dredging, the P_5 of DLIs over a 30 d running mean period was 1.9 mol photons m^{-2} (range: 1.2–2.8 mol photons m^{-2}) during the pre-dredging periods, as compared to 0.6 mol photons m^{-2} (0.4–1.2 mol photons m^{-2}) during the dredging phase. The corals exposed to the 1.1 mol photons m^{-2} d^{-1} treatment for 30 d began to discolour after 14 d, although the colour loss was not as extreme as in the ~0 mol photons m^{-2} d^{-1} treatment. Based on the experimental data described here, sub-lethal bleaching or tissue discolouration of corals caused by extended low light periods from dredge plumes also seems possible.

The colour changes observed in these studies, including bleaching to near bone-whiteness, were caused by a loss of chlorophyll *a* as opposed to reversible tissue retraction (Brown et al., 1994). The areal concentration of symbiotic dinoflagellates was not quantified, in favour of the use of non-destructive colour indexing techniques for assessing colour changes with time throughout the experiment (see for example (Anthony et al., 2008; Edmunds et al., 2003; Siebeck et al., 2006)). The colour changes were largely preceded by a decrease in the maximum quantum yield of the symbionts *in hospite* during the experiments. Decreases in quantum yield preceding dissociation of the symbiosis have regularly been observed in corals in response to heat stress (Jones et al., 1998), high-light (Jones and Hoegh-Guldberg, 2001), and exposure to chemicals such as cyanide (Jones and Hoegh-Guldberg, 1999), and

herbicides (Jones and Kerswell, 2003). Given how pale (i.e. bone-white) some of the corals were, it seems likely that the colour changes observed were as a result of dissociation of the coral-algal symbiosis as opposed to degradation of algal pigments *in hospite* (Douglas, 2003).

One interesting observation was the initial darkening of all the corals in the first week of the experiment which occurred across all treatments. During the pre-experimental holding period, the corals were held under a DLI of 7.2 mol photons m^{-2} d^{-1} as opposed to 1.1 or 8.6 mol photons m^{-2} d^{-1} in the 28 d experimental treatments. In the lower light treatment, and the darkness treatment, the darkening of the colour could be a photo-adaptation and associated with changes in photosynthetic and accessory pigment concentrations (Anthony and Hoegh-Guldberg, 2003; Falkowski and Dubinsky, 1981; Falkowski et al., 1984). This time-frame is consistent with the 5–10 d time-course of photoadaptation of corals during a high light to low light transition described by Anthony and Hoegh-Guldberg (2003). Darkening of corals in the SSC treatments could also have been due to slight reductions in light caused by clay/silt sediments sticking to the corals' mucus layer reducing light availability to the underlying endosymbionts. However, the corals exposed to the 8.6 mol photons m^{-2} d^{-1} treatment in 0 mg L^{-1} SSC also initially darkened. The same types of LED lights were used in both the holding tanks before the experiment and the experimental tanks, but the light profile was slightly different (see Material and methods). Another possible explanation is that reflection of light from the container wall and floor was slightly different between the holding tanks and experimental tanks.

In this study, very high (up to 100 mg L^{-1}) SSCs had no direct effect of the quantum yield of the algal symbionts *in hospite*. In contrast, several other studies have described pronounced changes in quantum yield following sediment exposure and the results discussed in terms of 'photo-physiological' stress (Philipp and Fabricius, 2003; Piniak, 2007; Weber et al., 2012; Weber et al., 2006). The main difference is that these earlier studies have measured quantum yields in areas of corals where sediments have previously smothered the surfaces to depths of >3 mm thickness (Philipp and Fabricius, 2003; Piniak, 2007; Weber et al., 2012; Weber et al., 2006). Weber et al. (2012) describe the rapid sequence of events whereby sediment smothering causes tissue mortality, involving reduced O_2 and pH, resulting in anoxia and host tissue degradation, followed by hydrogen sulphide formation and bacterial decomposition of the dead tissue. Inferences of 'photo-physiological' stress and direct effects of sediment on photochemical efficiency of photosystem II is perhaps inappropriate if the measurements are made of algal symbionts trapped in a situation of decaying coral tissue.

An interaction between reduced light levels and elevated SSCs was evident with partial mortality of coral fragments of each species. This interaction saw increased partial mortality in those fragments in the ~0 and 1.1 mol photons m^{-2} d^{-1} treatments when also exposed to elevated SSCs (30 and 100 mg L^{-1}). These results suggest a SSCs alone do not result in mortality, but when combined with periods of reduced light, pressures on coral health are increased. Therefore, during dredging projects periods of reduced light and increased SSCs, which are generally interlinked, should be monitored to ensure excessive stress to corals does not result.

For environmental impact assessments associated with dredging operations, combining thresholds with water quality predictions (models) are critical for forecasting the possible spatial extent of any damage to habitats (see EPA (2016)). Thresholds are equally important for adaptive operational monitoring during dredging as triggers of response actions (such as stopping dredging or moving the dredge(s) to a different location). The analyses described here are perhaps too coarse to develop minimum light requirements, and these need to be examined over a range of low light levels, including DLIs between 1 and 2 mol photons m^{-2} and for a range of coral species. Coral bleaching and the associated colour changes are useful sub-lethal bio-indicators of a light limitation response. We caveat these conclusions with the observation that the levels of light reduction needed to induce these responses in corals only really occur in close proximity to dredging operations, at distances where sediment deposition and smothering are also likely to be a key-cause effect pathway. Future work should focus on identifying which of these pressures is most influential to different coral taxa to develop realistic thresholds that can be applied to managing dredging activities in the vicinity of coral reefs.

The results presented here indicate that when light levels are experimentally manipulated (to avoid limitation), corals are highly resilient to a combination of intensity (100 mg L^{-1}) and duration (28 d) that is many times higher than would occur even very close (<1 km) to large scale (capital) dredging projects or during natural resuspension events (based on recent water quality analyses (Fisher et al., 2015; Jones et al., 2016; Jones et al., 2015)). However, corals held in darkness, or in extended low light (twilight) conditions showed various degrees of bleaching and/or partial mortality at combinations (of light reduction and duration) that are quite plausible close (<1 km) to dredging operations. Combining light reduction and elevated SSCs resulted in interactive effects and increased mortality in low-light exposed corals.

We caveat these conclusions with the observation that the levels of light reduction needed to induce these responses in corals only occur in close proximity to dredging operations, at distances where sediment deposition and smothering are also likely to be a key-cause effect pathway. Future work should focus on identifying which of these pressures is most influential to different coral taxa to develop realistic thresholds that can be applied to managing dredging activities in the vicinity of coral reefs. Measurements of benthic light availability are essential for water quality monitoring during dredging projects. The challenge is to derive light thresholds that take into account the level of light reduction and the duration, as well as the period (frequency) between low light events where corals may be able to replenish energy reserves.

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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.2017.01.050.

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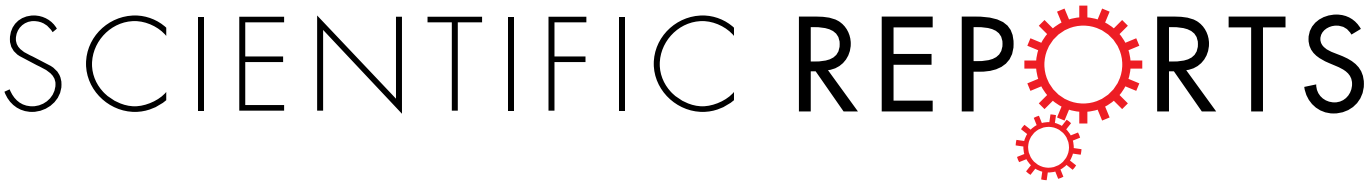

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Impacts of light limitation on corals and crustose coralline algae

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Turbidity associated with elevated suspended sediment concentrations can significantly reduce underwater light availability. Understanding the consequences for sensitive organisms such as corals and crustose coralline algae (CCA), requires an understanding of tolerance levels and the time course of effects. Adult colonies of *Acropora millepora* and *Pocillopora acuta*, juvenile *P. acuta*, and the CCA *Porolithon onkodes* were exposed to six light treatments of ~0, 0.02, 0.1, 0.4, 1.1 and 4.3 mol photons m^{-2} d^{-1}, and their physiological responses were monitored over 30 d. Exposure to very low light (<0.1 mol photons m^{-2} d^{-1}) caused tissue discoloration (bleaching) in the corals, and discolouration (and partial mortality) of the CCA, yielding 30 d EI_{10} thresholds (irradiance which results in a 10% change in colour) of 1.2–1.9 mol photons m^{-2} d^{-1}. Recent monitoring studies during dredging campaigns on a shallow tropical reef, have shown that underwater light levels very close (~500 m away) from a working dredge routinely fall below this value over 30 d periods, but rarely during the pre-dredging baseline phase. Light reduction alone, therefore, constitutes a clear risk to coral reefs from dredging, although at such close proximity other cause-effect pathways, such as sediment deposition and smothering, are likely to also co-occur.

A key to the ecological and evolutionary success of scleractinian corals is the formation of a mutualistic symbiosis with endosymbiotic dinoflagellate microalgae (*Symbiodinium* spp.)[1,2]. Carbohydrates produced by oxygenic photosynthesis of the algal symbionts and translocated to the coral host provide much of the energy required for maintenance, growth and reproduction[3–5]. This exchange has enabled the symbiosis to survive and coral reefs to proliferate in oligotrophic environments, however, the light dependency has also placed constraints on phototropic corals, limiting their distribution to comparatively low latitudes (~32° north and south of the equator), and shallow depths (~10% of surface light or 50 m)[6–9].

Benthic light availability is largely determined by surface irradiance (insolation), and primarily influenced by cloud cover, water depth, and transmittance through the water, i.e. water cloudiness or turbidity[10]. Turbidity is mainly affected by suspended sediments[11], and light attenuation is affected by sediment concentration as well as sediment particle size, shape and colour[12]. Sediments can enter the water column from terrestrial runoff, river plumes, flood water[13–15], and by natural re-suspension events from currents and wind-driven waves[16,17]. On a more local scale, sediments can also be released into the water column by dredging and dredging related activities (such as spoil disposal)[18].

The effects of turbidity on benthic light availability have been quantified for natural resuspension events[10], flood plumes[19,20], and most recently dredging projects[21]. For dredging, shallow (5–10 m depth) habitats close to dredging activities were found to routinely experience complete darkness, sometimes for up to several days in a row[21,22]. However, a more common feature was extended periods of extreme low light levels (i.e. caliginous or twilight periods)[22,23]. For example, the daily photosynthetically active radiation (PAR) close to a large dredging operation averaged <10 µmol photons m^{-2} s^{-1} over a 30 d period, which equated to a daily light integral (DLI) of ~1 mol photons m^{-2} d^{-1} [22,23]. This is far below the light requirements for many shallow-water, tropical coral species[6], thus light reduction, in addition to other possible effects of suspended sediments and sediment deposition, constitutes a hazard to shallow benthic communities such as corals[21,24–26].

Some corals can nevertheless thrive in highly turbid regions where irradiance is frequently attenuated by elevated suspended sediment concentrations (SSCs); however, these corals have adapted over extended (ecological) time frames to low-light conditions and are generally limited to shallow depths (<4 m)[16,27–30]. Coral communities

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living in turbid, nearshore areas may also comprise different species compared to offshore, clear-water reefs, and their tolerance may be due to both community composition and physiological adaptations[31,32]. On shorter time scales of days to weeks, corals can tolerate episodic periods of low light (<1 mol photons m^{-2} d^{-1}) through a range of behavioural and physiological responses. These include photoadaptation of the symbionts and changes in the sub-saturation point for photosynthesis[33], and in some species switching from phototrophic to heterotrophic feeding[34,35]. Corals can also temporarily rely on energy reserves[36], rapidly replenishing reserves when conditions become more favourable[37].

Only a few studies have examined the effects of exposure to very low light (<0.1 mol photons m^{-2} d^{-1}) on corals, and these have mostly been associated with investigating the role of the symbiotic dinoflagellates in the symbiosis. For example, Yonge and Nicholls[38] showed that extrusion of *Symbiodinium*, and subsequent discolouration (bleaching), occurred in response to darkness for a variety of tropical reef flat corals over 18 d (*Lobactis scutaria*), 22 d (*Psammocora contigua*) and 19 d (*Galaxea fascicularis*). Franzisket[39] exposed four species of hermatypic corals (*Pocillopora elegans*, *Porites compressa*, *Montipora verrucosa* and *Fungia scularia*) to darkness for 60 d. All colonies bleached within 10–20 d and there was no growth observed over the exposure period[39]. *Pocillopora elegans* died after 30 d while the remaining species survived over the exposure period[39]. Kevin and Hudson[40] showed the temperate coral, *Plesiastrea urvillei*, lost algal symbionts after ~40 d in darkness. Hoegh-Guldberg and Smith[41] observed bleaching of *Stylophora pistillata* in the dark after 10 d, while Titlyanov, *et al.*[42] observed bleaching of *S. pistillata* after 4 d. In a study investigating the mechanism of bleaching, DeSalvo, *et al.*[43] reported colonies of *Acropora palmata* and *Montastraea faveolata* becoming pale and eventually bleaching after 3–5 d in darkness.

A temporary reduction in benthic light is a well-known hazard of dredging-related activities[24]. We recently demonstrated that light attenuation represents a greater threat to coral health than any physical effects of suspended sediment particles[44]. The study investigated the impacts of three light levels (~0, 1.1 and 8.3 mol photons m^{-2} d^{-1}), and three suspended sediment concentrations (0, 30 and 100 mg L^{-1}), on three common coral species, including *Acropora millepora*, *Porites* spp. and *Montipora capricornis*; and found bleaching of corals in low light treatments (~0 and 1.1 mol photons m^{-2} d^{-1}) and no mortality associated with 100 mg L^{-1} of suspended sediments when light levels remained high (8.3 mol photons m^{-2} d^{-1}). This result demonstrated the importance of light reduction on coral health and the need to identify low light thresholds to improve the management of future sediment generating activities undertaken in the vicinity of coral reefs[44]. The risk to nearby coral reef communities could be better predicted and managed if there was a clearer understanding of the associated physiological effects, along with the time-frame of any effects, and tolerance limits of key benthic organisms.

To that end, we investigated here the thresholds for light reduction on adult colonies of *A. millepora* and *Pocillopora acuta*, juvenile (7 month old) colonies of *P. acuta*, and on the crustose coralline alga (CCA) *Porolithon onkodes*. Like corals, CCA are essential structural components of coral reef ecosystems[45–47], and provide chemical cues for settlement of many benthic invertebrate larvae, including corals[48–50]. However, their response to extended periods of low light (<1 mol photons m^{-2} d^{-1}) has not been investigated. The aim of the study is to understand the response thresholds, and time-course of the response, of high light adapted adult and juvenile corals, and CCA, to extended periods of low light relevant to conditions generated by offshore dredging[22,23]. To contextualise the results of the laboratory based study, results are discussed with respect to temporal and spatial changes in benthic light availability recently described for a large scale capital dredging project[22,23].

Results

Fragments of 2 coral species (*A. millepora*, and *P. acuta*), along with juvenile *P. acuta* (7 months old) and a species of crustose coralline alga (*P. onkodes*) were exposed to 6 light treatments (~0, 0.02, 0.1, 0.4, 1.1 and 4.3 mol photons m^{-2} d^{-1}). Non-destructive techniques were used to monitor coral health throughout the exposure period, including image analysis of coral colour and photochemical efficiency (F_v/F_m) of algal symbionts. At the end of the exposure period photosynthetic incubations were conducted to determine the photosynthetic capacity of the corals. Irradiance-response relationships were then determined to identify thresholds of low light conditions to guide the management of future dredging and other sediment generating activities.

Health parameters assessed through time. Coral colonies in the lower light treatments gradually lost colour though time, with paling observed after 10 d in all groups when exposed to <0.1 mol photons m^{-2} d^{-1}. By 20 d corals exposed to <0.1 mol photons m^{-2} d^{-1} were bone white, while those exposed to 0.4 mol photons m^{-2} d^{-1} were very pale. This colour loss was uniform across each fragment. At the end of the exposure period there was a clear gradation in colour from fully pigmented in the 4.3 mol photons m^{-2} d^{-1} treatment, to bone white in the ~ 0 mol photons m^{-2} d^{-1} treatment (Fig. 1). CCA were dark red at the start of the exposure period and through time this colour intensified in fragments exposed to 0.4 and 1.1 mol photons m^{-2} d^{-1}. Those CCA fragments exposed to ≤0.1 mol photons m^{-2} d^{-1} discoloured rapidly and had sections of pale tissue and sections of bone white skeleton where cells had been lost.

Light treatment (DLI), time of exposure (Time) and species (Species) all strongly influenced the measured coral health parameters (partial mortally, colour index (a proxy for bleaching), and maximum quantum yield (F_v/F_m)) (Table 1). There was strong evidence (AICc weights all near 1, Table 1) that a full three way interaction between these predictors was the best model to describe the changes observed.

Partial mortality was observed in juvenile and adult *P. acuta* as well as in *P. onkodes* during the light limitation exposures, while *A. millepora* showed no signs of tissue loss regardless of light intensity, even after 30 d of exposure (Fig. 2). *P. acuta* adults suffered from more partial mortality than juveniles, and tissue loss was apparent in the ~0 and 0.1 mol photons m^{-2} d^{-1} treatments after 10 d (Fig. 2). The mortality observed in juvenile

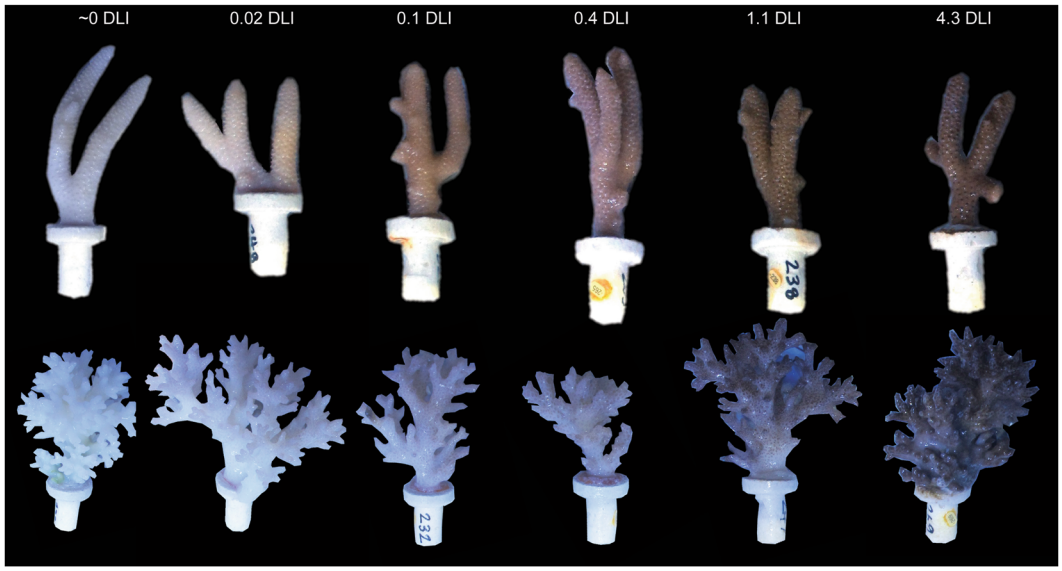

Figure 1. Photographs of representative *A. millepora* and *P. acuta* fragments after 30 d of exposure to the six daily light integral (DLI) irradiance treatments of ~0, 0.02, 0.1, 0.4, 1.1 and 4.3 mol photons m^{-2} d^{-1}.

Parameter	Model	*n*	AICc	δ AICc	AICc weight	R^2
Partial mortality	DLI × Time × Species	51	1965.7	0	1	0.34
Colour index	DLI × Time × Species	51	1973.8	0	0.97	0.56
F_v/F_m	DLI × Time × Species	51	2087.7	0	1	0.72

Table 1. Top generalised linear mixed effect model fits for each health parameter measured through time (partial mortality, colour index and F_v/F_m), including number of parameters (*n*), Akaike information criterion (AICc), δ AICc, model weights and R^2 values. See Supplementary Information Tables S1–S3 for the complete full subsets output.

P. acuta was inconsistent across treatments, with highest morality occurring for the second highest treatment (1.1 mol photons m^{-2} d^{-1}), suggesting this mortality may not be associated with low light conditions of the experimental treatments (Fig. 2). *P. onkodes* exhibited the highest level of partial mortality, with the majority apparent after 25 d in the ~0–0.4 mol photons m^{-2} d^{-1} treatments, while no mortality was observed at 4.3 mol photons m^{-2} d^{-1} (Fig. 2).

The tissue colour index of corals declined in the light treatments ≤0.4 mol photons m^{-2} d^{-1} and this response became more pronounced over time, especially in the darkness treatment (~0 mol photons m^{-2} d^{-1}) (Fig. 2). There was also a subtle increase in pigmentation in the two highest light treatments (≥1.1 mol photons m^{-2} d^{-1}) (Fig. 2). The colour index of *P. onkodes* varied throughout the experiment, with pigmentation lowest after 30 d in the dark treatment (~0 DLI) (Fig. 2).

A gradual decline in F_v/F_m was observed for *A. millepora* colonies in each of the light treatments from the first 10 d, with the most pronounced decreases observed in the light treatments ≤0.1 mol photons m^{-2} d^{-1} (Fig. 2). F_v/F_m also declined in adult *P. acuta* colonies exposed to 0.4 mol photons m^{-2} d^{-1}. The F_v/F_m of those corals in the darkest exposures (≤0.02 mol photons m^{-2} d^{-1}) were 0, as few *Symbiodinium* spp. remained in these treatments after 20 d. The F_v/F_m of *P. acuta* juveniles also declined over the 30 d in the ≤0.1 mol photons m^{-2} d^{-1} treatments (Fig. 2). *P. onkodes* had reduced F_v/F_m after five d of exposure to treatment conditions, while F_v/F_m were lowest in the ~0 DLI treatment and remained stable in all other treatments (Fig. 2).

Photosynthetic Incubations. Photosynthetic incubations at the end of the exposure period at the saturating irradiance of 419 µE m^{-2} s^{-1} (determined from photosynthesis irradiance curves), revealed limited to no photosynthetic capacity in adult coral colonies exposed to a DLI of ≤0.4 mol photons m^{-2} d^{-1} (Fig. 3, Supplementary Fig. S1). Fragments that were exposed to <1.1 mol photons m^{-2} d^{-1} for the duration of the experiment displayed no increase in oxygen production or photosynthetic capacity (Fig. 3).

Irradiance-response relationships. Patterns of mortality were not observed in *A. millepora* or *P. acuta* juveniles, however, increased mortality with decreased light exposure after 30 d were apparent in *P. acuta* and *P. onkodes* (Supplementary Fig. S2). Patterns of decreasing colour index with reduced light exposure were clear, and were similar across all species, with *A. millepora* and *P. acuta* juveniles exhibiting the lowest colour index values (Fig. 4). Similar trends were observed for F_v/F_m in *A. millepora* (Fig. 4). The patterns observed after 20 d, particularly for F_v/F_m were more well defined than after 30 d, and relationships after 10 d showed less clear patterns again

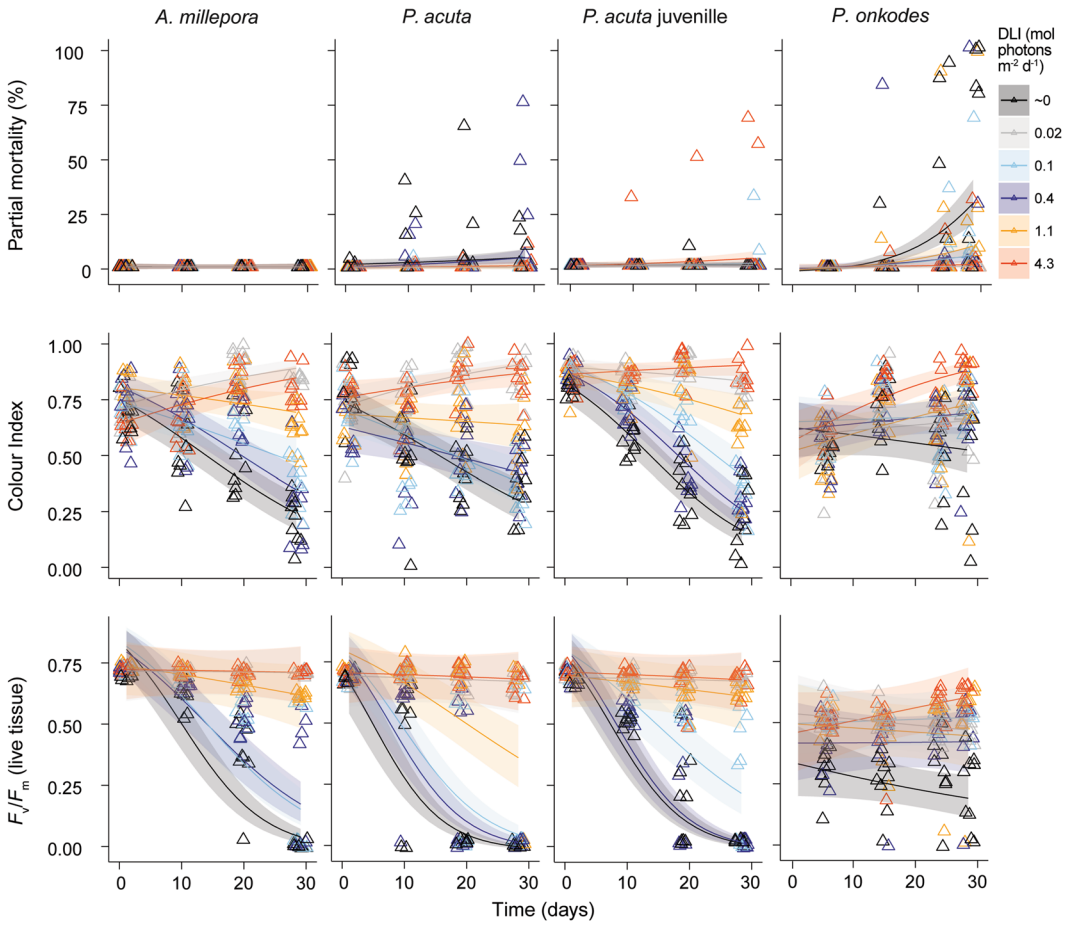

Figure 2. Partial mortality, colour index and maximum quantum yield (F_v/F_m) of the corals *A. millepora*, *P. acuta* adults, *P. acuta* juveniles and the crustose coralline alga *P. onkodes*, for the 6 light treatments of ~0, 0.02, 0.1, 0.4, 1.1 and 4.3 DLI (mol photons m^{-2} d^{-1}), as indicated by the colours. Raw data are presented (triangles), along with curves showing best-model fitted relationships (lines) and corresponding 95% credible intervals (ribbons).

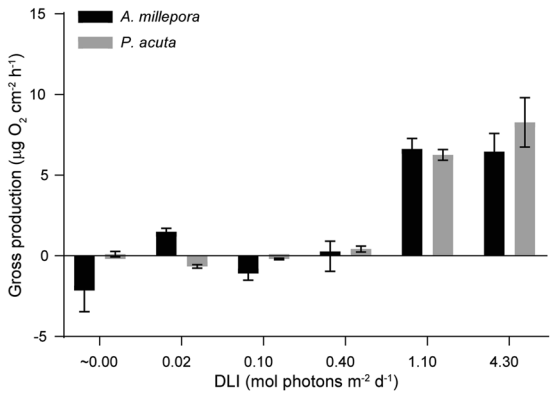

Figure 3. Gross photosynthesis (negative values indicate respiration) at saturating irradiance (419 µmol photons m^{-2} s^{-1}), determined from photosynthesis irradiance (P–I) curves for both *A. millepora* (black) and adult *P. acuta* (grey) colonies across the 6 light treatments (~0, 0.02, 0.1, 0.4, 1.1 and 4.3 mol photons m^{-2} d^{-1}). Data presented are mean ± SE, $n = 3$.

(Supplementary Fig. S3). Trends in Chl *a* content increased with increasing light exposures, reaching a maximum around 1.1 mol photons m^{-2} d^{-1} (Fig. 4), and correlations were observed between colour index and Chl *a* for all

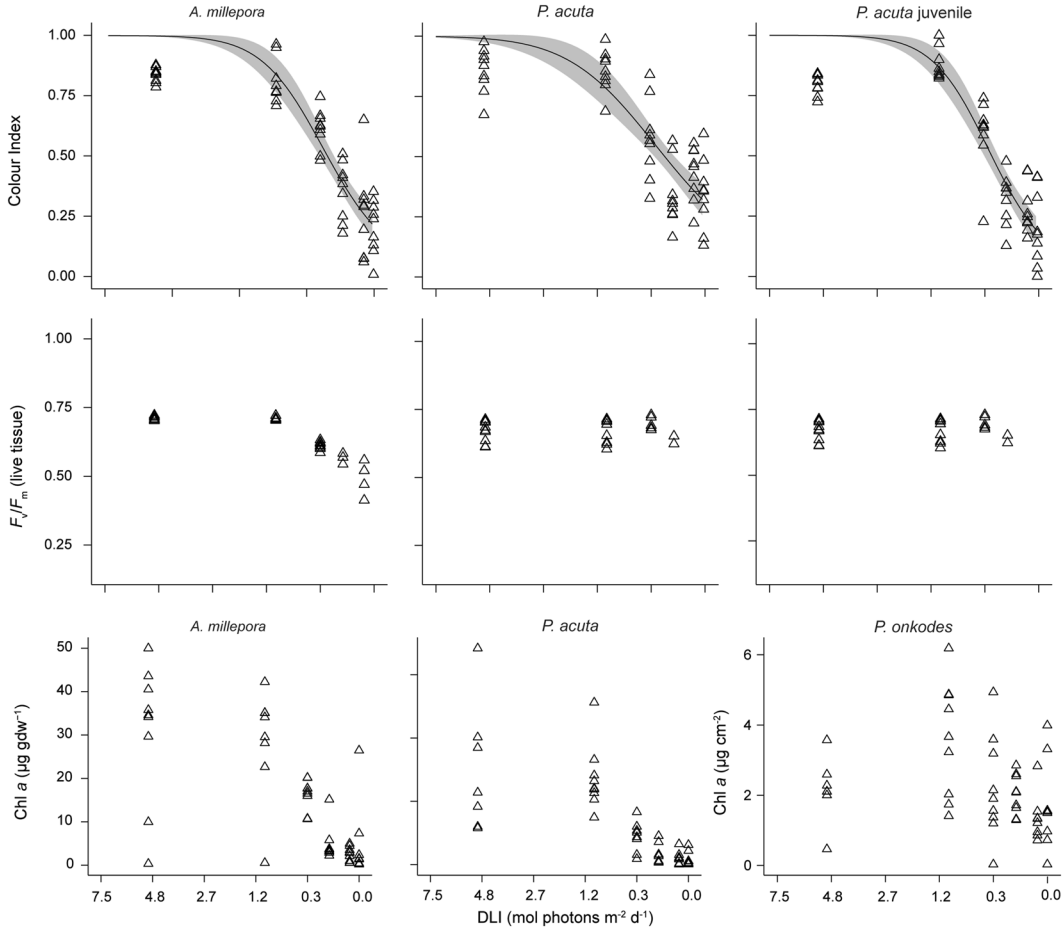

Figure 4. Irradiance-response relationships for colour index and maximum quantum yield (F_v/F_m), and Chl *a* concentrations of corals *A. millepora*, *P. acuta* adults, *P. acuta* juveniles and the crustose coralline alga *P. onkodes*, after 30 d of exposure to 6 light treatments of 0, 0.02, 0.1, 0.4, 1.1 and 4.3 mol photons m^{-2} d^{-1} (note inverse DLI values on x-axis). Raw data are presented (triangles), with modelled relationships (lines) and 95% confidence intervals (ribbons). See Supplementary Information Figs S2 and S3 for relationships after 10 and 20 d.

coral species at 30 d (Supplementary Fig. S4). No clear trends in any of the sub-lethal health parameters were detected for the CCA *P. onkodes*.

The effect threshold for irradiance EI_{10} was defined as irradiance which elicited a 10% effect on mortality, colour, F_v/F_m or Chl *a* content. A higher EI_{10} (or EI_{50}) indicates a more sensitive response (the effect was reached with less light attenuation). After 10 d exposure, the sub-lethal impacts associated with even the lowest light treatment represented less than a 10% change, meaning that an EI_{10} threshold could not be calculated (i.e. even complete loss of light did not cause a 10% decline in colour index or F_v/F_m). After 20 d, the threshold irradiances for colour index in the corals (also a proxy for 10% bleaching) ranged from EI_{10} 0.39–1.4 mol photons m^{-2} d^{-1} (Table 2). After 30 d, the EI_{10}s for colour index increased to 1.2–1.9 mol photons m^{-2} d^{-1} indicating the bleaching thresholds had been reached with less attenuation. The EI_{50} values (a proxy for 50% coral bleaching) occurred under conditions of greater light attenuation and ranged from 0.16–0.23 mol photons m^{-2} d^{-1} after 30 d (Table 2).

Thresholds of low light relative to dredge related water quality conditions. During the 336 d pre-dredging baseline phase at Barrow Island, mean daily turbidity levels at a site 0.8 km from the excavation activities was typically very low (0–10 NTU), and the DLI ranged between 1 and 8 mol photons m^{-2} d^{-1} (Fig. 5). The 30 d running mean DLI only dropped below the average EI_{10} bleaching threshold for all species (Table 2) for a short period in June of 2008 (see arrow Fig. 5). During the 530 d dredging phase turbidity was much higher (0–50 NTU), and daily irradiance correspondingly lower, associated with plumes of resuspended sediment moving over the monitoring site (Fig. 5). Days with very low light levels (i.e. <0.1 mol photons m^{-2} d^{-1}) were more common, and the 30 d running mean DLI was very low towards the end of the dredging period, when elevated NTUs combined with low winter insolation levels (Fig. 5). Cyclones during the baseline and dredging phases had noticeable short term effect on light availability, but did not result in light reduction below the EI_{10} threshold value on a 30 d running mean scale (Fig. 5).

Quantiles of the 30 d running mean periods indicate that during the pre-dredging phase, the EI_{10} threshold is exceeded approximately 10% of the time for *P. acuta* adults (~34 d) and approximately 2% of the time in *A. millepora* and *P. acuta* juveniles (~8 d) (Fig. 5). During the dredging, these quantile values are higher, with *P. acuta*

Health variable	Species	Day 20		Day 30	
		EI_{10}	EI_{50}	EI_{10}	EI_{50}
Proportional mortality	*A. millepora*	NE	NE	NE	NE
	P. acuta	NE	NE	1.50 (0.69,2.63)	NE
	P. acuta juv	NE	NE	NE	NE
	P. onkodes	NE	NE	8.99 (2.56,19.33)	1.44 (0.23,3.65)
Colour Index	*A. millepora*	0.86 (0.35,1.6)	0.04 (0.00,0.17)	1.4 (1.0, 1.9)	0.23 (0.17,0.30)
	P. acuta	1.4 (0.69,2.3)	NE	1.9 (1.1, 2.8)	0.16 (0.09,0.24)
	P. acuta juv	0.39 (0.25,0.56)	0.02 (0.01,0.04)	1.2 (0.83, 1.6)	0.22 (0.16,0.28)
F_v/F_m	*A. millepora*	NE	NE	1.4 (0.77,2.30)	0.36 (0.22,0.53)
	P. acuta	1.2 (0.44,2.30)	0.26 (0.13,0.44)	NE	NE
	P. acuta juv	NE	NE	NE	NE

Table 2. Nonlinear regression (four-parameter logistic function) results of proportional mortality, colour index and maximum quantum yield (F_v/F_m) for *A. millepora*, *P. acuta* adults and *P. acuta* juveniles after 10, 20 and 30 d of exposure to treatment conditions. Both the 10% and 50% effect irradiances (EI_{10} and EI_{50}) are presented as mol photons m^{-2} d^{-1} with 95% confidence intervals. A higher EI_{10} (or EI_{50}) indicates a more sensitive response (the effect was reached with less light attenuation). No EI_{10} and EI_{50} effects were observed at day 10 for any species, and the irradiance thresholds for Chl *a* reductions could not be determined using non-linear regressions. NE indicates no effect for the given level of change (10% or 50%).

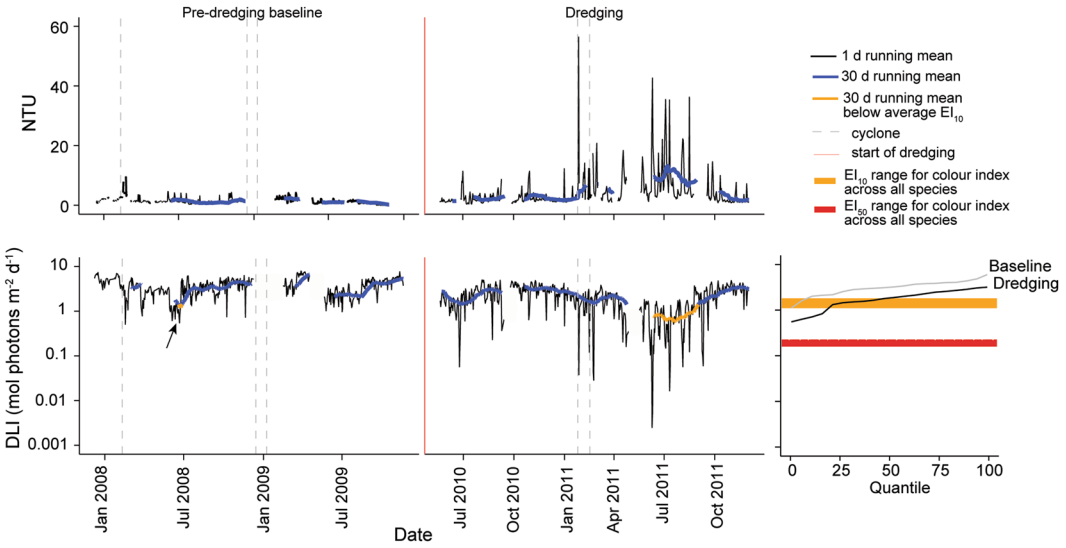

Figure 5. Water quality conditions before and during a large-scale, capital dredging project on the coral reefs surrounding Barrow Island (north-west Australia) where ~7.6 M m^3 of sediment was removed over a 530 d period (for further details see Jones, *et al.*[23] and Fisher, *et al.*[22]). Turbidity (NTU) and benthic PAR levels (DLI, mol photons m^{-2} d^{-1}) are shown for the extended pre-dredging baseline and dredging phase at one site, located 0.8 km from the primary excavation site at 6.2 m depth. Horizontal coloured ribbons on the right hand quantile plot show the range of calculated DLI thresholds for each of the 3 species and life stages (see Table 2) investigated, including *A. millepora*, *P. acuta* and *P. acuta* juveniles for both 10 and 50% impacts on colour index (EI_{10} = orange and EI_{50} = red). Data presented are the daily mean NTU and DLI (black), with 30 d running means (blue solid line). Periods when the 30 d running mean DLI drops below the experimentally calculated threshold values (Table 2) are indicated by the appropriate threshold colour. Quantiles of 30 d running mean DLI are also presented across the pre-dredge (grey) and dredging (black) phases.

adults exceeding the EI_{10} approximately 50% of the time (~265 d), while for *A. millepora* and *P. acuta* juveniles this threshold is exceeded approximately 25% of the time (~132 d) (Fig. 5). Light levels over 30 d were not low enough to reach the EI_{50} values for these species (Fig. 5, Table 2).

Discussion

Exposure to extended periods of low irradiance and darkness had considerable impacts on the health of high light adapted coral and CCA. Corals (both adult and juvenile) became bleached, losing colour and Chl *a* content. At the end of the exposure period corals in the very low light treatments (<1 mol photons m^{-2} d^{-1}) were heavily bleached (bone-white) signifying loss of algal symbionts. Tissue loss (partial mortality) was observed in adult *P. acuta* after prolonged periods of near darkness (<0.4 mol photons m^{-2} d^{-1}). The CCA *P. onkodes*, was also

sensitive to light-limitation showing discoloration and partial mortality. The 30 d EI_{10} thresholds for bleaching in the corals (mean irradiance which results in a 10% change in colour) was 1.2–1.9 mol photons m^{-2} d^{-1}. Underwater light levels measured during a dredging project on a shallow (~6 m), tropical, clear water reef (see Fisher, *et al.*[22] and Jones, *et al.*[23]), were found to routinely fall below this value in close proximity (~800 m away) from a working dredge. Light levels rarely fell below the threshold during the pre-dredging baseline phase. This study demonstrates that light reduction alone constitutes a clear risk to clear-water coral reefs from dredging, although at such close proximity other cause-effect pathways, such as sediment deposition and smothering, are likely to also occur.

The gradual loss of colour and eventual bleaching of corals exposed to low light (<1 mol photons m^{-2} d^{-1}) are consistent with studies which exposed corals to complete darkness. In this study corals began noticeably paling after 4–5 days and were heavily bleached after 10 days, similar to the observations of impacts caused by complete darkness reported by Hoegh-Guldberg and Smith[41], Franzisket[39], Yonge and Nicholls[38] and Titlyanov, *et al.*[42], for a range of reef flat species, but slower than observed by DeSalvo, *et al.*[43], who observed heavy bleaching of *Acropora palmata* and *Montastraea faveolata* after 3 and 5 d in darkness respectively. While these studies provide important thresholds determining the time required to bleach in complete darkness, our study provides critical light thresholds for bleaching that can be applied to manage dredging that causes near-darkness for weeks[22,23].

Low light thresholds for adult and juvenile corals varied. Juvenile *P. acuta* were slightly more resilient than the adults, however, as the difference was small (30 d EI_{10} for colour loss of 1.2 versus 1.9 mol photons m^{-2} d^{-1} respectively), the thresholds developed for adult corals would be applicable to 7 month old recruits. *P. acuta* colonies were far more sensitive to low light (<1 mol photons m^{-2} d^{-1}) conditions in terms of partial colony mortality than *A. millepora*, where no mortality occurred. The relative sensitivity contradicts what might be expected when considering the life history traits of these two species, with *A. millepora* considered a competitive species, while *P. acuta* is an early colonising, weedy species and, therefore, anticipated to be more resilient to stressors[51].

Several microsensor studies have shown that when placed in darkness, coral tissue rapidly (within minutes) enters a hypoxic and then near anaerobic state[52–55]. This is due to high metabolic activity of the symbiotic dinoflagellates and polyp tissue, limiting the diffusive supply of O_2 from the surrounding water through the diffusion boundary layer. Although corals routinely enter hypoxia at night time, tissue oxygen concentrations also rapidly increase on exposure to light in the early morning[53]. How corals tolerate hypoxia is unknown, although symbiotic anemones have been found to survive through fermentation processes involving glycolysis[56–58]. Such fermentation processes have been observed in corals when exposed to hypoxia from sediment smothering[59]. These processes produce ATP at approximately 6-fold lower yields than aerobic respiration[60], offering a short term, temporary energy source, but not over extended periods in low light (<1 mol photons m^{-2} d^{-1}).

A characteristic of the patterns of low-light induced bleaching was the uniform, even, tissue discolouration (Fig. 1), as opposed to the often variegated and sunlight orientated patterns of discolouration that can occur during warm-water bleaching events[61]. This suggests a different mechanism of bleaching, but the cue that initiates the dissociation is not clear. In *A. millepora*, and *P. actua* adults and juveniles, the quantum efficiency F_v/F_m of the *Symbiodinium* spp. decreased following long periods in darkness and the very low-light treatments (<0.4 mol photons m^{-2} d^{-1}). This could be due to unstacking and structural changes of the thylakoid membrane, leading to reduced electron transport[43,62]. A reduction in the translocation of photosynthate from the algal symbionts to the host has been suggested as a potential cue for warm bleaching[63,64]. Alternatively, if the hypoxia of the coral tissues in very low light is related to the metabolic activity of the symbionts in the coral tissues, then elimination of the source of the problem, the algal symbionts (i.e. bleaching), seems a relatively simple explanation and survival strategy. Irrespective of the underlying mechanism, towards the end of the exposure period the loss of algal symbionts at daily light integrals lower than <1.1 mol photons m^{-2} d^{-1} resulted in photosynthesis:respiration ratios of less than one, demonstrating little photosynthetic capacity. As the colonies were not fed during the exposure period, they were most likely drawing on energy reserves to meet their metabolic requirements[3,65].

It is possible to contextualise the results from these laboratory-based studies using information from a recent detailed analyses of spatial and temporal patterns of benthic light availability measured before and during a large scale, capital dredging project on a clear-water reef (at Barrow Island, ~50 km offshore of the Pilbara coast of north-west Western Australia[22,23]). Extended periods of low light naturally occurred during the pre-dredging period in the (austral) winter time, associated with shorter days, lower solar declination and probably increased cloud cover, but the E_{10} thresholds for discolouration were rarely reached. However, during the dredging phase, there were marked reductions in benthic light availability, and a site 800 m from the dredging routinely experienced periods of daytime darkness, darkness over the whole day (defined as <0.04 mol photons m^{-2} d^{-1}), and darkness for 1 to 6 consecutive days[22]. These periods, again, occurred during the winter time when turbid plumes combined with seasonal light minima. Although the hazard associated with dredging turbidity and light reduction have been known since the 1970s[24], these results better describe the risk and the spatial context associated with the elevated turbidity. Under prolonged periods of light reduction, some corals could survive by switching from phototrophic to heterotrophic feeding to maintain a positive energy balance[3,34,35,65], or temporarily draw on energy reserves[36], replenishing them when light conditions become more favourable[37].

CCA was more sensitive to the impacts of low irradiance than both adult and juvenile corals, and suffered from higher levels of partial mortality. However, patterns of colour loss and decreases in maximum quantum yields (F_v/F_m) with light limitation were not as clearly defined as those in corals, with reductions apparent almost immediately followed by stability over time. While some CCA species are well adapted to low light levels in the mesophotic zone[66], the results presented here suggest that high light adapted species, such as *P. onkodes*, are not able to readily adapt to periodic low light exposure. Loss of CCA has implications for reef health, as it is one of the most important and widespread reef-builders in the marine photic zone worldwide and provides important cues for the settlement of coral larvae[45,48–50]. Changes in CCA abundance can therefore influence the structure and function of coral reef ecosystems[45]. Reduced prevalence of CCA associated with low light conditions during

dredging may result in declines in coral recruitment, potentially exacerbating issues associated with increased deposited sediments interfering with coral settlement[67]. Clearly more work is needed to understand the potential changes associated with dredging for key non-coral biota, such as CCA, and the persistence and recovery time associated with CCA decline resulting from exposure to low light conditions.

The thresholds for effects of light limitation on corals and CCA identified here are likely to be conservative as they did not take into account potential shifts in available spectra that may occur under dredging plumes. Light attenuation through a plume of suspended sediments will be characterised by a shift in spectra towards yellow and green wavelengths, that are less useful for photosynthesis[21]. It is possible that the impacts on coral and CCA health by light attenuation caused by sediment plumes would be more severe than reported in the current study, where shifts in spectra to less useful wavelengths were not applied. Furthermore, light attenuation is only one of several potential stressor pathways related to sediment plumes caused by dredging[21,25,26]. Although suspended particles are not likely to significantly exacerbate the impacts of shading in turbid waters[44], elevated SSCs needed to significantly attenuate light in shallow water (<10 m) tropical reef environments will most likely also result in appreciable levels of sediment deposition, which in turn can smother corals resulting in tissue necrosis[21,59,68,69]. In addition, periods of high light attenuation from dredging are likely to be dispersed with periods of less attenuation[23], which may alleviate some of the negative impacts of long exposures to poor water quality and/or long dredging campaigns. The compounding effects of decreased light quality and quantity, elevated SSCs, and deposited sediment as well as the periodic nature of these stressors clearly require further investigation.

In summary, these results provide light limitation thresholds for high light adapted, shallow water corals and CCA; as well as insights into both direct and indirect pathways associated with the effects of dredging on the physiology of corals and the ecology of coral reefs. Exposure to a DLI of ~1.5 mol photons m^{-2} d^{-1} for a period of 30 d caused a 10% decline in the health of corals and partial mortality in some species (i.e. *P. acuta*), and exposure to less than ~0.2 mol photons m^{-2} d^{-1} resulted in a 50% decline. The principle physiological response was dissociation of the coral-algal symbiosis, a well-known sub-lethal stress response of corals[70]. Indirect ecological effects include reducing the health of CCA which provide important cues for the settlement of coral larvae[49]. Water quality programs designed to reduce impacts on reefs during dredging campaigns should recognise the potential for the effects of elevated turbidity to combine with annual light minima to reduce light levels below identified required minima for corals and CCA. The effects of other dredging related water quality pressures, such as sediment deposition also need to be considered. The light attenuation scenarios presented here (high light adapted corals and CCA exposed to low light conditions) represents one of several scenarios, and more work is needed to clarify the sensitivity of a wider range of reef-building corals and CCA to low light periods experienced during dredging and natural re-suspension events so turbidity-generating activities, such as dredging, can be managed to effectively protect these ecologically important taxa.

Methods

Experiments were conducted using adults of two hard coral species *Acropora millepora* (Ehrenberg 1834) and *Pocillopora acuta* (Lamarck 1816), juvenile (7 month old) *P. acuta* colonies and the crustose coralline algae (CCA) *Porolithon onkodes* (Penrose & Woelkerling 1992). Eight colonies and subsequent genotypes of *A millepora*, *P acuta* and *P. onkodes* that were free of biofouling and disease were collected from 3–10 m in lagoonal area of Davies Reef and Broadhurst Reef (both mid-shelf reefs centrally located in the Great Barrier Reef (GBRMPA permits G12/35236.1 and G13/35758.1) and transferred to the Australian Institute of Marine Science (AIMS) National Sea Simulator (SeaSim) at Cape Cleveland near Townsville Queensland. Corals and CCA were fragmented into replicates with a surface area of ~10 cm^2 *A. millepora* and *P. acuta* and ~3 cm^2 *P. onkodes*, and fragments were glued onto aragonite coral plugs. The fragments were then held in 200 L flow-through holding tanks in the SeaSim for 6 weeks to recover from the collection and preparation procedures. During the holding period, corals and CCA were exposed to a 12-h light:dark (L:D) cycle comprising of a 2 h period of gradually increasing light in the morning (06:00–8:00 h), 8 h of constant illumination at 200 µmol photons m^{-2} s^{-1}, and a 2 h period of gradually decreasing light in the afternoon (16:00–18:00 h). Our previous study indicated no effect of irradiance on the bleaching of *A. millepora* between 1 and 8 mol photons m^{-2} d^{-1} daily light integral (DLI, or total summed PAR) over 28 h[44] and corals and CCA in the present system experienced an intermediate DLI of 7.2 mol photons m^{-2} d^{-1}, consistent with the typical range at the site of collection (4 – 8 mol photons m^{-2} d^{-1}).

P. acuta juveniles were reared from parent colonies collected at Davies Reef. Colonies that were free of biofouling and diseases were kept in the SeaSim and larvae were collected monthly over the summer. These larvae were left to settle on small aragonite plugs using chips of CCA to induce settlement[49]. Recruits were then left to develop over 7 months before being transferred to the same holding tanks as adult fragments for the 6 week healing and light acclimatisation period.

All experiments were conducted over a 30 d period in clear PVC tanks holding 49 L of filtered seawater. In this experiment we did not feed the corals in order to mimic the impacts of an offshore dredging scenario where heterotrophic feeding is less important, and where the carbonate sediments from dredging contain very low levels of organic carbon[21] and are not a useful source of energy. Our previous study exposing corals to both low light and carbonate sediments demonstrated that only low light affected coral health[44]. In tank circulation was maintained with a TUNZ pump (EcoTech Marine, PA, US). Seawater was fed into each tank at 800 mL min^{-1} (resulting in ~6 complete water turnovers d^{-1}). Water temperature was maintained at 26 ± 0.5 °C, and salinity at 33 ± 0.5‰ throughout the experiment. Above each tank two Sol White LED lights (Aquaria Illumination, IA, US) were suspended to ensure even illumination throughout the tank.

For the dark treatments, the tanks were covered in black corrugated plastic sheets (to reduce light contamination) and for the remaining five light treatments the corals were exposed to a 12-h L:D cycle composed of a 6 h period of gradually increasing light in the morning (06:00–12:00 h), and a 6 h period of gradually decreasing light in the afternoon (12:00–18:00 h). Light levels were measured at the depth of the corals using an underwater

spherical quantum sensor (Li-COR LI-193). Over the course of the day the corals experienced DLIs of 0, 0.02, 0.1, 0.4, 1.1 or 4.3 mol photons m^{-2}. For the 5 light treatments, their maximum intensity was 1, 5, 20, 50 and 200 µmol photons m^{-2} s^{-1} respectively. Corals held in darkness did experience very low level light exposure (albeit for a few minutes) during weekly photographing (see below), and thus the treatment is hereafter referred to as a DLI of ~0 mol photons m^{-2}. Three tank replicates were used for each treatment and three replicates of each species per tank were used for general health assessments, with different genotypes randomly allocated amongst tanks. Light levels throughout the exposure period were measured as 0.00 ± 0.00, 3.68 ± 0.83, 7.25 ± 0.67, 12.11 ± 0.66, 45.44 ± 0.60 and 167.50 ± 1.35 µmol photons m^{-2} s^{-1} (all mean ± standard error) in the 0, 0.02, 0.1, 0.4, 1.1 and 4.3 mol photons m^{-2} d^{-1} treatments respectively (Supplementary Fig. S4). These light regimes were selected based on analyses of benthic light levels measured during a large-scale, capital dredging project on the coral reefs surrounding Barrow Island (north-west Australia) where ~7.6 Mm^3 of sediment was removed over a 530 d period (for further details see Jones, *et al.*[23] and Fisher, *et al.*[22]).

All species were photographed every 10 d using a high resolution digital camera and the camera settings and the surrounding light environment kept the same during the photographing process over the duration of the experiment. Changes in colour were assessed weekly from the photographs. Images were analysed with the image processing software program ImageJ[71], using the histogram function on a selection of representative live tissue, taking the arithmetic mean of pixel values (range 0–255) on a black and white scale. At the end of the experiment, these were standardised to the maximum and minimum values for each species, and converted to a range between 0 and 1. During the photographing process, any partial mortality of the corals was noted and quantified from the photographs using ImageJ. We previously demonstrate a good correlation between colour index and Chl *a* concentration[44].

Chlorophyll fluorescence of the endosymbiotic dinoflagellate algae within tissue of each coral fragment was measured using a mini-PAM fluorometer (Walz, Germany). Measurements were obtained using a 6 mm fibre-optic probe positioned perpendicular to the coral fragment and 3 mm away (controlled by a rubber spacer). Initial fluorescence (F_0) was determined by applying a weak pulse-modulated red light (650 nm, ~0.15 µmol photons m^{-2} s^{-1}). Maximum fluorescence (F_m) was then measured following a saturating pulse of light. Maximum quantum yield (F_v/F_m) is the proportion of light used for photosynthesis by chlorophyll when all reaction centres are open[72] and is determined by the following equation:

$$\frac{F_v}{F_m} = (F_m - F_0)/F_m$$

Coral fragments were dark-adapted for 30 min prior to measuring the yield. Fluorescence data were collected before the experiment began, and after 10, 20 and 30 d. Measurements were only taken over live tissue, and 1–4 measurements were taken and averaged per fragment, depending on live tissue available.

Oxygen respirometry was conducted using a system of 8 sealed, clear, perspex chambers with a magnetic stir bar that were submerged in a jacket of running water to buffer temperature fluctuations (maintained between 25.5 and 26.5 °C). Of the 8 chambers, 6 contained coral fragments, while the other two were seawater blanks (to correct for seawater production/respiration). Each chamber was fitted with an oxygen spot (OXSP5, Pyroscience, Germany) and connected to a fibre-optic oxygen meter (Firesting O_2, Pyroscience, Germany), which had been calibrated to 100 and 0% O_2. Above the chambers two Sol White LED lights (Aquaria Illumination, IA, US) were suspended to ensure even illumination. The chambers were exposed to 8 discrete light intensities (0, 10, 30, 75, 150, 300, 480 µmol photons m^{-2} s^{-1}) for between 15 and 30 minutes each. Surface area and volume of each coral skeleton were determined using wax dipping and volume displacement for standardisation.

All data were analysed with R software (version 3.2.3, R Core Team[73]). The relative influences of environmental factors on coral health parameters were assessed using a full subsets model selection approach[74], where models were compared with Akaike Information Criterion with corrections for sample size (AICc) and R^2. The models with the lowest AICc (within 2) and the fewest parameters was chosen as the 'best' model. For modelling of relationships, tank and coral fragment identity were included as random factors. For health parameters assessed through time (partial mortality, F_v/F_m and colour index) a logit transformation was used with generalised linear mixed models to determine the impacts of health parameters for each species. Each health dataset was explored using the protocol described by Zuur, *et al.*[75]. For modelling of relationships, species, time and DLI were included as fixed factors. Gaussian generalised linear mixed models were fit with the package lme4[76]. Full subsets comparison was completed using dredge in the MuMIn package[77]. The final model was re-fit using MCMC to allow calculation of error terms using the R2jags package[78]. Chl *a* concentrations were modelled with a Tweedie distribution using the cplm package[79].

Pressure-response relationships were examined after 10, 20 and 30 d across the six light levels for each species and health parameter. These relationships were not modelled for partial mortality as effect irradiance calculations (i.e. EI_{10}, EI_{50}) would be meaningless without reaching full fragment mortality, instead we modelled the probability of observing any mortality using a binomial distribution. The remaining health parameter (colour index, maximum quantum yield and Chl *a*) relationships were fitted with drc package[80]. Models were fitted as 4-parameter logistic regressions where the data showed a clear trend in responses across light treatments, with 10 and 50% impact levels subsequently determined. 10 and 50% impact levels were calculated in comparison to the controls (4.3 mol photons m^{-1} d^{-1} exposure at day 0).

Hyperbolic tangent functions were fitted to incubation gross production data for both *A. millepora* and adult *P. acuta* fragments.

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Author Contributions

P.B.-B., A.N., R.F., P.C. and R.J. conceived the study. P.B.-B. ran the experiment and completed the lab work. P.B.-B. and R.F. conducted the analysis. P.B.-B. and R.J. drafted the manuscript. All authors reviewed and approved the manuscript.

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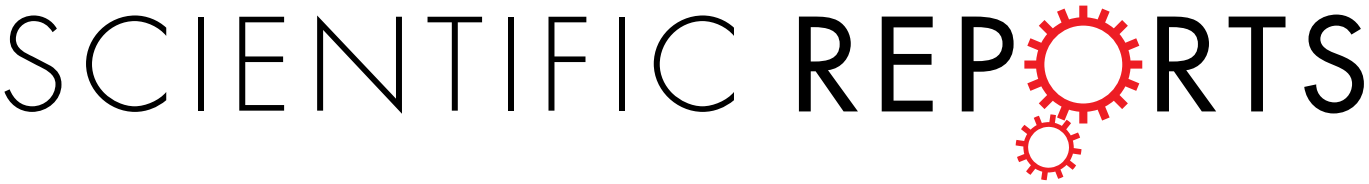

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Cumulative impacts: thermally bleached corals have reduced capacity to clear deposited sediment

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The interaction between local, anthropogenic stressors, and larger scale regional/global stressors, is often used to explain the current poor condition of many corals reefs. This form of cumulative pressure is clearly manifested by situations where dredging projects happen to coincide with marine heatwaves that have caused coral bleaching. A key pressure associated with dredging is elevated sedimentation. In this study, 3 coral species (*Acropora millepora*, *Porites* spp. and *Turbinaria reniformis*), representing three common morphologies (branching, massive and foliose respectively), were experimentally induced to bleach by exposure to a temperature of 31 °C for 21 d. The corals were then subjected to a range of sedimentation rates (0, 11, 22 and 40 mg cm^{-2} d^{-1}), and their sediment-rejection ability quantified after 1 and 7 successive sediment deposition events. Bleached corals were less capable of removing sediments from their surfaces, and sediment accumulated 3 to 4-fold more than on normally-pigmented corals. Repeated deposition resulted in a ~3-fold increase in the amount of sediment remaining on the corals, regardless of bleaching status. These results suggest that adaptive management practices need to be developed to reduce the impacts of future dredging projects that follow or coincide with elevated sea surface temperatures and coral bleaching events.

A well cited model for the current poor condition of many corals reefs is the interaction between local anthropogenic factors (e.g. coastal development, poor water shed management, pollution and overfishing), and larger scale regional and global factors (e.g. rising seawater temperatures and ocean acidification)[1–7]. This combination (and possible interaction) of local and global stressors represents one of the largest uncertainties for predicting environmental change[5,8]. Conserving reefs in the face of predicted increases in seawater temperatures associated with climate change[3,9–11], and the pernicious threat of coral bleaching[12,13], is a significant challenge faced by regulatory agencies. Cumulative impacts and interactions of local and global stressors or drivers (see Côté, *et al.*[14]), can manifest themselves in many ways, and are epitomised by situations where dredging projects coincide with 'natural' warm-water coral bleaching events[15].

Coral bleaching, or the dissociation of the coral-algal symbiosis, is a well-known stress response of corals[16–18], and is frequently observed in response to periods of elevated water temperatures[3,16,19,20]. Bleaching events can occur at multiple scales from local events (e.g. Jones[18] and Jones[21]), to regional (mass bleaching) events[22,23], and even global bleaching events[3,24,25]. Bleaching events can occur rapidly (within days) from only short term acute periods of temporarily elevated water temperatures[21], as well as in response to more chronic periods of warm water[26]. The loss of the symbionts is often associated with high levels of partial and whole colony mortality, and at the ecological level recovery of reefs impacted by severe bleaching occurs over decadal time frames[27]. Bleaching events differ considerably in severity and duration, and the sub-lethal response along with inter and intraspecific variability in bleaching of corals is commonly observed[28,29]. While bleaching can lead to whole colony mortality, under some conditions heavily bleached (bone-white) colonies can regain their algal symbionts, and return to a normal pigmentation with no associated mortality[21].

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At a physiological level, recovery of algal symbionts can take many months to upwards of a year[26, 30–35]. This time frame is much longer than predicted from models based on the number of dividing *Symbiodinium* and duration of the division phase[34]. The extended time period needed to re-establish the symbiosis may be related to sorting processes within the tissues, i.e. the movement of newly divided algal cells into empty gastro-dermal cells[34]; however, it may also be due to tissue damage incurred during the bleaching process itself. In addition, heterotrophic food sources facilitate tissue repair following bleaching along with energy reserves, and limitations in either of these will also slow recovery[36–40]. Histopathological examinations of bleached corals sometimes show loss of architecture, various degrees of atrophy and necrosis, and disruption of the gastro-dermal layer[41–43]. Bleached corals have also been found to possess significantly depleted numbers of epidermal mucous secreting cells (mucocytes), compared to normally-pigmented corals[44, 45]. Corals exposed to elevated water temperatures also exhibit a six-fold higher release rate of undischarged cnidae, indicative of host cell necrosis or detachment[46] during the bleaching process[47].

Irrespective of the mechanism of recovery, bleached corals are in a compromised state, with decreased tissue thickness[48–50], and in some cases low energy reserves[26, 51]. The reduced ability to acquire energy phototrophically can in some species be compensated for by increased heterotrophic feeding[36, 52]. However, most studies confer that bleached corals are in a weakened state and susceptible to range of different stressors, such as algal colonisation[53], disease[54], and periods of poor water quality[15].

Concepts of multiple stressors acting synergistically, and of interactions between local anthropogenic factors and larger global factors, was highlighted recently with the Miami Harbor Phase III Federal Channel Expansion Project, which was conducted during a regional mass coral bleaching event[55, 56]. Similar situations have occurred in the inshore, central Great Barrier Reef[21, 57], and a series of dredging projects off the west coast of Australia in recent years[58]. The projects in Western Australia were large scale, capital dredging projects, which involved the removal of ~50 Mm^3 of sediments from coral reef environments. These projects included the 2010–2011 Barrow Island project[59], the 2007–2010 Pluto project[60], and the 2013–2015 Wheatstone project[61]. These dredging campaigns each happened to coincide with a series of local and mass coral bleaching events[62–65].

Dredging and dredging-related activities release sediments into the water column either from mechanical disturbance of the seabed, controlled overflow from hopper barges, or sediment disposal at offshore placement sites[66, 67]. There are many different cause effect pathways where sediment plumes from dredging activities can affect corals (recently reviewed by Jones, *et al.*[68]). Of these, one of the most significant is elevated sedimentation, as resuspended sediments deposit onto the sea floor, often leading to smothering of corals (see images in Foster, *et al.*[66] and Jones, *et al.*[68]). In this study, we examine the consequences of coral bleaching on the tolerance of corals to poor water quality associated with dredging.

Results

Approach. Fragments of 3 coral species (*Acropora millepora*, *Porites* spp., and *Turbinaria reniformis*) were experimentally induced to bleach by exposure to elevated water temperatures. Sediment-rejection by these bleached corals was then tested against normally-pigmented 'control' corals, in a series of sediment deposition events up to a rate of 40 mg cm^{-2} d^{-1}. Non-destructive techniques were used to monitor coral health throughout the sediment exposure period, including image analysis of coral colour and photochemical efficiency of algal symbionts. Corals were exposed to these sediment deposition events for 7 consecutive days, and at the end of each day any sediment accumulating on the surfaces was cleaned by water motion. The sediment-rejection ability of the corals was quantified after day 1 and then again at day 7 by determining the mass of sediment remaining on each coral.

Effects of bleaching on coral survival, colour and physiology. Bleaching was induced in the corals by slowly raising water temperatures (0.5 °C per day for 8 d) and holding the temperatures at 31 °C for 3 weeks under a daily light integral of 8.6 mol photons m^{-2} d^{-1}. Bleaching (tissue lightening) was observed after ~15—20 d in the 31 °C temperature treatment. No bleaching was observed in any of the corals held at 27 °C. For the branching *A. millepora*, paling occurred first on the upper light exposed surfaces, and towards the end of the exposure the upper surfaces were heavily bleached (bone white), and the lower (shaded) surfaces of the branches were pale in colour. The hemispherical *Porites* spp. also discoloured first on the upper more horizontal surface, with the edges of the colonies still retaining some pigmentation. Bleaching in *T. reniformis* was more uniform across the surface and the corals took on a pale yellow colouration (from animal pigments) as the bleaching progressed. There was no partial or whole-colony mortality resulting from the 31 °C temperature treatment, or in any of the corals held at 27 °C. The maximum quantum yields (F_v/F_m) of the bleached fragments were ~3, 2 and 6-fold lower in *A. millepora*, *Porites* spp., and *T. reniformis* respectively, and bleached corals had ~50% lower colour index scores than the normally-pigmented fragments for all species (Fig. 1).

Effects of pulsed sediment on coral survival, colour, physiology and sediment clearance. The bleached and normally-pigmented corals were exposed to temporarily high suspended sediment concentrations (SSCs), and water motion in the tanks was subsequently stopped to allow the sediments to settle out of suspension and onto the corals. Settlement of sediment in the tanks occurred rapidly, with most sediment dropping out of suspension in the first 1–2 h after the pumps were turned off each day (Fig. 2). The amount of sediment accumulating on the flat, concrete filled PVC cylinders (SedPods) averaged 0.05 ± 0.03, 10.8 ± 3.7, 22.4 ± 2.4 and 39.6 ± 2.3 mg cm^{-2} (mean ± SE, $n = 3$) over the 7 successive deposition events (Fig. 2).

There was no whole colony mortality in response to the sediment exposures and the only partial mortality occurred in a bleached *Porites* spp. fragment (which suffered 26% partial mortality in the 11 mg cm^{-2} d^{-1} treatment), and a bleached fragment of *T. reniformis* (which suffered > 5% mortality in the 22 mg cm^{-2} d^{-1} treatment).

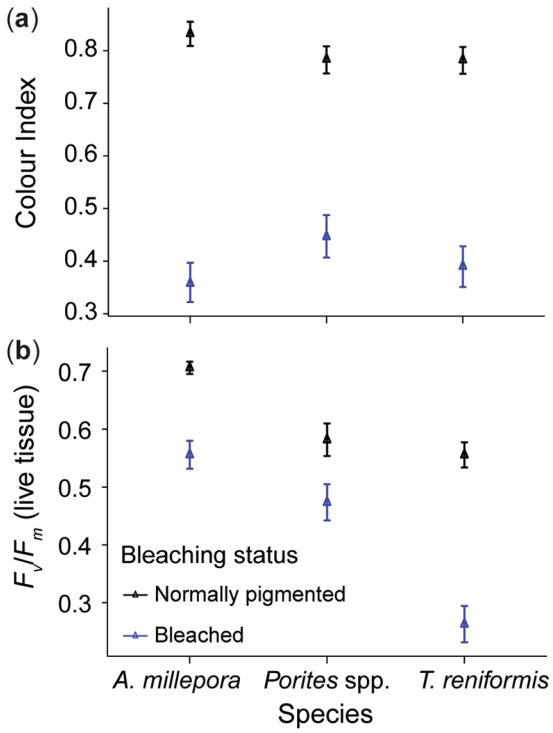

Figure 1. Differences in coral tissue colour and maximum quantum yield of the algal symbionts after the experimental bleaching. (**a**) Colour score index and (**b**) F_v/F_m of bleached and normally-pigmented corals after exposure to 31 °C or 27 °C for 3 weeks and before the sediment deposition experiments. Average data is presented with SE, $n = 48$ fragments per bleaching status for each species.

During the sediment exposures, all species had expanded and partially expanded polyps irrespective of bleaching status. Mucus secretion was commonly observed in *T. reniformis* and *Porites* spp., but less so in *A. millepora*. All corals appeared to corral and collect the sediments into mucus-laden patches with well–defined, discrete, edges. The patches were then slowly moved under muco-ciliary transport to the sides of the colonies and ultimately shed. Occasionally, sediments patches became stuck in local depression or concave features of the surface and remained trapped there. For the *A. millepora* similar trapping of sediment was occasionally observed at the junction point of neighbouring branches.

The colour index of bleached and normally-pigmented corals differed considerably for all three species, while there was limited apparent impact of sediment treatment (Table 1, Fig. 3). The best fit model suggested that colour index was driven by an interaction between bleaching status, species and time, with an additive impact of sediment treatment having a lower model weight than when sediment was included (Table 1, Fig. 3). Chl *a* was best explained by a model including an interaction between bleaching status and species (Table 1, Fig. 3). At the end of the experiment Chl *a* concentrations differed between normally-pigmented and bleached corals, with substantially less Chl *a* present in bleached fragments, with this consistent across all three species, while the smallest difference was apparent in *T. reniformis* (Fig. 3). Similar to colour index, there was no evidence for an impact of sediment deposition treatment on Chl *a* concentrations (Fig. 3), with a model not including sediment having a higher model weight (Table 1). F_v/F_m also differed between normally-pigmented and bleached corals, and this effect was dependent on species, time and sediment (Table 1). While F_v/F_m remained stable across deposition treatments for the normally-pigmented corals, F_v/F_m values were lower in higher sediment treatments in bleached corals of all species (Fig. 3).

Normally-pigmented corals were effective at removing sediment from their surfaces, and at the highest sedimentation level the amount of sediment remaining was $0.6 \pm 0.2\,mg\,cm^{-2}$ (mean ± SD, range 0.3–0.7 $mg\,cm^{-2}$, $n = 36$), or 2.1% of the accumulation rate measured on the SedPods on that day (Supplementary Table S1, Fig. 4). The difference between the sediment mass on the corals and SedPods is due to the self-cleaning ability of the corals. Sediments were washed off the corals each day (during the re-suspension process), and after the last of the 7 consecutive daily deposition events, the amount of sediment remaining on the surfaces of the highest sedimentation level, was much higher, being $2.5 \pm 0.3\,mg\,cm^{-2}$ (mean ± SD, range 2.3–2.8 $mg\,cm^{-2}$, $n = 36$), or 6.4% of the accumulation rate measured on the SedPod on that day (Supplementary Table S1, Fig. 4). Overall, for the normally-pigmented colonies, 3.1-fold more sediment remained on the surface of the corals after the 7th deposition event than after the first.

Bleached corals were less effective at removing sediment from their surfaces, and at the highest sedimentation level, the amount of sediment remaining was $1.8 \pm 1.4\,mg\,cm^{-2}$ (mean ± SD, range 0.5–3.3 $mg\,cm^{-2}$, $n = 36$), or ~6.5% of the accumulation rate measured on the SedPod on that day (Supplementary Table S1, Fig. 4). After the last of the 7 consecutive daily deposition events, the amount of sediment remaining on the surfaces of the highest

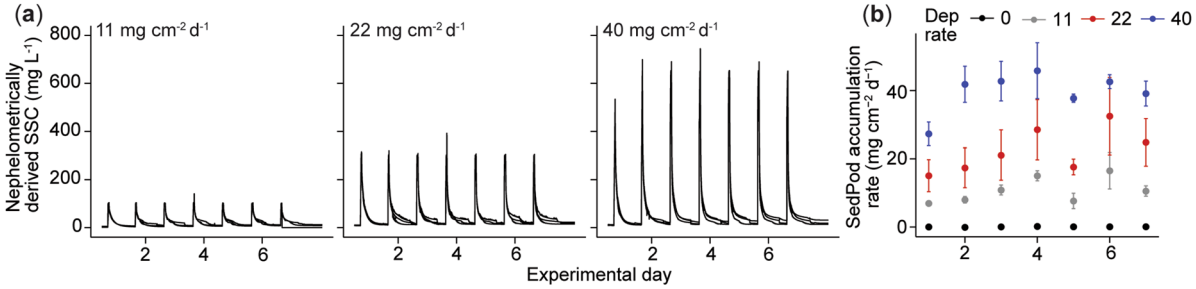

Figure 2. Suspended sediment concentrations (SSCs) and sediment deposition rates in the experimental tanks. (**a**) Nephelometrically-derived suspended sediment concentrations (mg L^{-1}) in each tank for the 7 day exposure period showing resuspension of sediment each afternoon (4:00 pm) followed by a decrease in SSCs as sediment fell out of suspension on the corals and SedPods each night, (**b**) Sedimentation (SedPod accumulation rate, mean ± SE, $n = 3$) after each of the deposition events across the 4 deposition rate treatments of 0, 11, 22 and 40 mg cm^{-2}.

Parameter	Model	*n*	AICc	δ AICc	AICc weight	R^2
Colour index	**ble. × spp. × time**	**15**	**933.6**	**0.0**	**0.33**	**0.83**
	ble. × spp. × time + sed.	16	935.3	1.7	0.14	0.84
	ble. × spp. × time + spp. × time + ble. × time + ble. × spp. + sed.	17	936.0	2.4	0.11	0.84
	spp. × time + ble. × time + ble. × spp.	13	936.0	2.4	0.10	0.83
	ble. × spp. × time + spp. x time + sed. × time + ble. × time + ble. × spp.	17	937.4	3.9	0.05	0.84
	spp. × time + ble. × time + ble. × spp. + sed.	14	937.8	4.2	0.04	0.83
Chl *a*	**ble. × spp.**	**9**	**−650.4**	**0.0**	**0.41**	**0.93**
	ble. × spp. + sed.	8	−649.9	0.5	0.32	0.93
	ble. × spp. + ble. × sed.	10	−646.9	3.0	0.10	0.93
	sed. × spp. + ble. × spp.	11	−645.7	4.2	0.06	0.93
	ble. × sed. × spp.	14	−643.9	6.0	0.02	0.94
	sed. x . spp. + ble. × spp. + ble. × sed.	12	−643.1	6.8	0.02	0.93
F_v/F_m	**ble. × spp. × time + ble. × sed.**	**17**	**798.7**	**0.0**	**0.23**	**0.63**
	ble. × spp. × time + ble. × sed. + spp. × sed.	19	800.0	1.3	0.12	0.64
	ble. × spp. × time + sed. x time + ble. x spp.	18	800.3	1.7	0.10	0.63
	ble. × spp. × time + sed. x time + sed. x spp.	19	801.4	2.7	0.06	0.64
	ble. × spp. × time + ble. × sed. × spp.	20	801.6	3.0	0.06	0.64
	sed. × spp. × time + ble. × spp. × time	21	801.6	3.0	0.05	0.64
Deposited sediment	**ble. × spp. × time + sed. × time + sed. × spp. + sed. × ble.**	**20**	**787.5**	**0.0**	**0.39**	**0.99**
	ble. × spp. × time + ble. × sed. × time	21	789.3	1.9	0.15	0.99
	ble. × spp. × time + ble. × sed. × spp. + sed. × time	22	790.8	3.3	0.07	0.99
	spp. × time + sed. × time + sed. × spp. + ble. × time + ble. x sed.	16	791.0	3.5	0.07	0.99
	spp. × time + sed. × time + sed. × spp. + ble. × time + ble. × spp. + ble. × sed.	18	791.1	3.7	0.06	0.99
	sed. × spp. × time + ble. × spp. × time	22	791.5	4.0	0.05	0.99

Table 1. Top model fits (generalised linear mixed model) for colour index, Chl *a* concentrations, maximum quantum yield (F_v/F_m) and deposited sediment for each of the fixed factors, inducing bleaching status (ble.), species (spp.), time and sediment deposition treatment (sed). Shown are the fitted model, number of parameters (*n*), Akaike information criterion (AICc), δ AICc, model weights, and R^2 values. The model with the fewest parameters within 2 AICc is considered the most parsimonious, and therefore the best model. Selected best models are shown in **bold**.

sedimentation level, was much higher at 9.3 ± 3.9 mg cm^{-2} (mean ± SD, range 4.9–12.3 mg cm^{-2}, $n = 36$), or 24% of the accumulation rate measured on the SedPod on that day (Supplementary Table S1, Fig. 4). Overall 3.7-fold more sediment remained on the surface of the corals after the 7th deposition event than after the first.

The combined effects of the reduced capacity to self-clean with time and lower sediment rejection ability of bleached corals differed between species. For bleached *T. reniformis* and the *Porites* spp. 2.3 to 2.6-fold more sediment remained on the corals after the last deposition event than the first. For bleached *A. millepora*, 15-fold more sediment remained on the corals after the last deposition event than the first (Supplementary Table S1, Fig. 4). The amount of remaining sediment on each fragment (inability to clear sediments), was best described by a complex model involving a three-way interaction between bleaching status, species and time as well as two-way interactions between sediment deposition and species, along with time and bleaching status (Table 1, Fig. 4). Given

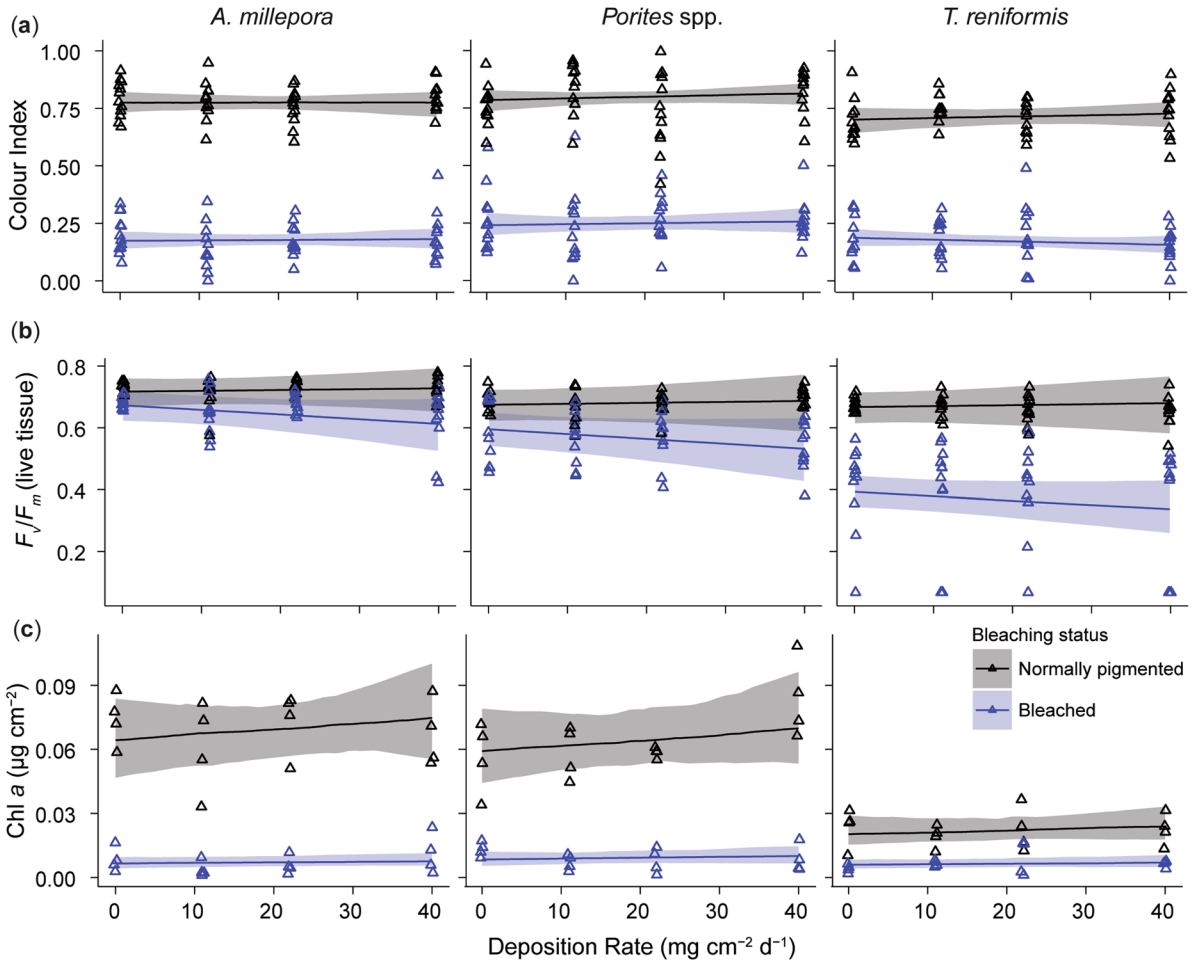

Figure 3. Physiological health parameters of bleached and normally-pigmented corals after 7 consecutive deposition events. (**a**) Colour index, (**b**) Maximum quantum yield (F_v/F_m), and (**c**) Chl *a* concentrations (µg Chl *a* cm^{-2}) of *A. millepora*, *Porites* spp. and *T. reniformis* fragments across 4 deposition rate treatments for both normally pigmented (black) and bleached (blue) fragments after 7 consecutive deposition events. Raw data (triangles) is presented with modelled relationships (lines) and 95% confidence intervals (ribbons).

the high order interactions with deposition, we fitted separate dose response relationships at two times (after 1 deposition and after 7 deposition events), for each species and for both bleached and normally pigmented corals.

Effect concentrations of both 10 and 50% (EC_{10} and EC_{50} respectively) impacts on clearance ability were calculated for bleached colonies of each species after 7 deposition events (Fig. 4). A sediment deposition rate of 40 mg cm^{-2} d^{-1} was not sufficient to reduce the clearance ability of any species while normally pigmented after either 0 or 7 deposition events (Fig. 4). Bleached *A. millepora* demonstrated a 10% reduction of clearance ability at 5 ± 4 mg cm^{-2} d^{-1}, and a 50% reduction at 12 ± 4 mg cm^{-2} d^{-1}, both after 7 deposition events. The 10% impact on clearance in bleached *T. reniformis* after 7 deposition events was 10 ± 3 mg cm^{-2} d^{-1}, while the 50% impact was observed at 13 ± 6 mg cm^{-2} d^{-1}. After 1 deposition event the 10% impact on clearance for *Porites* spp. was 11 ± 4 mg cm^{-2} d^{-1}, while a 50% impact was observed at 16 ± 6 mg cm^{-2} d^{-1}. No effect concentration could be determined for *Porites* spp. after 7 deposition events as the amount of sediment accumulating on the fragments was still increasing at the highest sediment deposition treatment (Fig. 4b).

Based on relative explanatory values of the fixed predictors, species was the most important factor influencing F_v/F_m, followed closely by sediment treatment and time, and then lastly bleaching status, however these were all strong influencers (Fig. 5) Colour index was most influenced by time, followed by species, bleaching status, and finally sediment treatment, which had a limited effect (Fig. 5). Chl *a* concentrations were most influenced equally by bleaching status and species (although time was not included in these models because this was only measured at the end of exposure), followed by sediment deposition rate (Fig. 5). Lastly, the amount of deposited sediment remaining on coral fragments was most strongly driven by bleaching status (Fig. 5).

Discussion

The data from this study provides clear evidence that thermally bleached corals have considerably reduced capacity to clear sediments from their surfaces compared to normally-pigmented corals. The pattern was similar across three growth forms (branching, massive, and foliose), from three common and widely distributed coral species. Sedimentation is considered one of the most widespread, human-induced perturbations on reefs[69], and a key

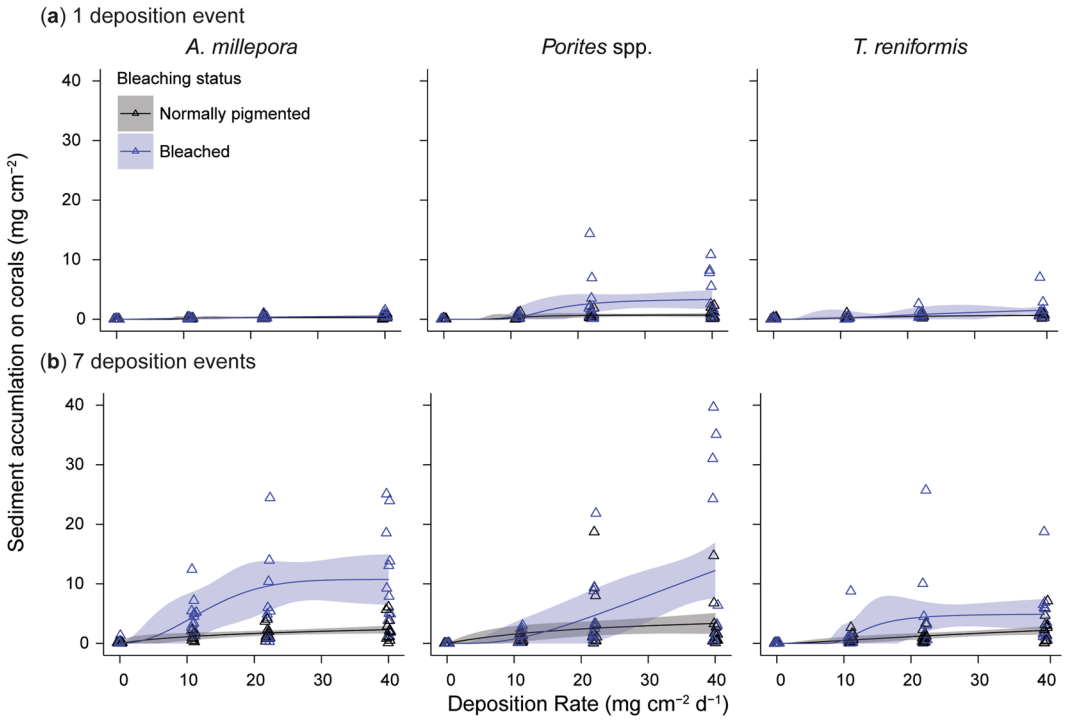

Figure 4. Sediment accumulation on bleached and normally-pigmented corals. The amount of sediment (mg cm^{-2}) accumulated on each fragment of *A. millepora*, *Porites* spp. and *T. reniformis* across 4 deposition rate treatments for both normally-pigmented (black) corals and bleached (blue) fragments after: (**a**) 1 deposition event, and (**b**) a further 6 deposition events. Raw data is presented (triangles) with modelled values (lines) and 95% credible intervals (ribbons).

causal pathway associated with mortality of corals close to dredging activities[68,70–72]. This interaction between coral bleaching and sedimentation pressures clearly represents a consideration for resource managers in the regulation of more manageable local, anthropogenic stressors in the face of much wider-scale, and essentially uncontrollable issues[15], associated with periods of elevated water temperature resulting from a changing climate.

Before the sediment exposure experiment, corals were artificially bleached by heat stress. The time-course and patterns of bleaching are consistent with the current understanding of the bleaching phenomenon based on both field and laboratory experiments[73]. Bleaching was induced by slowly raising water temperatures to 31 °C and exposing the corals for 3 weeks under a daily light integral of 8.6 mol photons m^{-2} d^{-1}. For the mid-shelf reefs of the GBR, at around 18°S, where the corals were collected, the maximum average daily temperatures typically range from 28–30 °C[73]. The 31 °C temperature only marginally exceeds the normal range, although the combination with time (21 d exposure) greatly exceeds temperatures that the corals have previously encountered, and is equivalent to ~4 degree heating weeks (DHW). Such a DHW exposure is generally anticipated to result in significant coral bleaching and this exposure resulted in the dissociation of the symbiosis in all species[74]. Maximum potential quantum yields (dark-adapted F_v/F_m) of the algal symbionts were significantly reduced by the temperature/light combination, and corals preferentially bleached first on their upper, light exposed surfaces. These results and observations are consistent with a photoinhibition model of coral bleaching[3,44,75–80].

Corals have a range of mechanisms to clean their surface of sediments primarily involving muco-ciliary transport, hydrostatic inflation and tentacle movement[72,81–85]. These energy intensive 'active' processes work in combination with 'passive' forces associated with gravity and flow to keep the upper sunlight exposed surfaces sediment-free in all but extreme cases of deposition. If sediments cannot be removed from the surface at a rate equivalent to the deposition, sediment can then build up and smother coral tissue, reducing feeding, solute (gas) exchange, and light transmission to the algal symbionts[86]. If covered with several millimetres of organic rich sediment mortality can occur quickly, in a matter of days[87].

For the most part the corals were able remove all sediments up to the highest deposition rate tested of 40 mg cm^{-2} d^{-1}. For contextual purposes deposition rates of up to 50 mg cm^{-2} d^{-1} have recently been measured during a high wind and wave event on a inshore turbid reef system of the central Great Barrier Reef[88]. These maximum deposition rates occurred during a natural resuspension event and a period of extreme turbidity, where wind-speeds exceeded the 95th percentile for the local area, and SSCs exceeded 100 mg L^{-1}[88]. Under less extreme conditions and when SSCs ranged from a more typical < 1–28 mg L^{-1}, deposition rates in the naturally turbid reef system averaged only 8 ± 5 mg cm^{-2} d^{-1}[88]. This suggests that the high sediment deposition rates investigated here are likely to be associated with either very extreme natural turbidity events or in close proximity to dredging activities.

The corals in this study cleaned their surfaces of sediments using muco-ciliary transport, which is commonly regarded as the primary mechanism whereby corals can move fine silts and clays from their surfaces. The fluidic

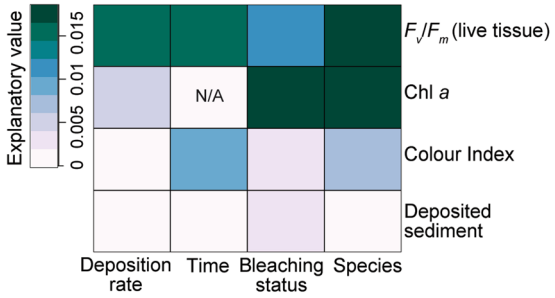

Figure 5. Explanatory value of each of the fixed factors included in the models, including deposition rate treatment (mg cm^{-2}), Time (d), Species and bleaching status (normally pigmented or bleached), with darker colours indicating increased importance of that variable. Explanatory value was calculated simply as the additional R^2 obtained when a variable was included in a complete interaction model, compared to a model excluding just that variable. This in effect represents the unique variance explained by each predictor, rather than the overall R^2 explained by individual best models, as presented in Table 1.

mucus is produced from epithelial secretory cells, mucocytes[89,90], and because of its adhesive characteristics can agglutinate settled sediment. Mucus-entangled sediment[81] was manipulated by co-ordinated ciliary movement (metachronal waves), and the movement of sediment invariably occurred down the face of sub-horizontal, inclined planes until reaching the colony edge where is was subsequently shed. The normally-pigmented corals were highly efficient at removing sediments, and in the highest sedimentation rate the amount of sediment remaining on the tissues was only ~2% of the amount that settled on the inert, flat surface of the SedPods. This difference is due to the self-cleaning, sediment rejection ability of the corals, which actively removed sediment from the colony surface. For both the bleached and normally pigmented corals there was a broadly similar (3.1 and 3.7-fold respectively) increase in the amount of sediment remaining on the tissues after the seventh successive daily deposition than the first, indicating a reduction in self-cleaning capability with time. Where the two types of corals (bleached and normally-pigmented) differed was in the absolute levels of deposited sediment on their tissue, which was typically 3 to 4-fold higher on bleached than the normally-pigmented corals at the highest sedimentation rate (40 mg cm^{-2} d^{-1}). The combined effects of the lower sediment rejection ability of bleached corals and the more general loss of self-cleaning ability with time meant the amount of sediment on the bleached corals after the last deposition event averaged ~24% of the amount that settled on the SedPods. For the most sensitive species, *A. millepora*, this amounted to a 15-fold decrease in the amount of sediment that could be cleared from the surface.

There are numerous plausible mechanisms for these two effects. Histological studies have demonstrated an absence of mucocytes in the epithelium of an experimentally bleached (heat-stressed) coral (*Stylophora pistillata*), and negligible quantities of mucus in the deeper gastro-dermal layer[44]. Similarly, Piggot, *et al.*[45] showed that in field-collected corals, those that have bleached through heat stress have greatly reduced densities of epithelial mucocyte cells, even though the density of mucocytes increases with increasing water temperature. Mucocyte numbers and mucus production was not quantified in this study, but reduced mucocyte density in bleached corals seems plausible. Mucus production comes at an energetic cost to corals[91,92], and numerous studies have qualitatively suggested increased mucus production in sediment-exposed corals[72,93,94] and repeated exposure to sediment deposition events could also exhaust mucus production. Stafford-Smith[94] argued a counterpoint, that it is ciliary transport that becomes exhausted and that cannot be maintained for long period, citing the ability of some corals to produce mucus in response to sediment influx long after sediment rejection slows down. Recent studies have shown that cilia beating is only a negligible fraction of the corals metabolic budget[95]; but possible changes under sediment influx are unknown[68].

Ultimately the energy for mucus production and ciliary transport would come from phototrophic or heterotrophic sources, both of which would be affected by sediment smothering. For phototrophy, both the loss of algal symbionts, and the reduced light availability to remaining algae by a thin layer of sediment would decrease energy availability[92], as light transmission is <1% through a ~2 mm deposit of very fine, silt size sediment[86,87]. Corals were not veneered by sediments in this experiment as they corralled the sediments into discrete patches, but under these patches light availability would be limited, thus impacting upon photosynthesis and potential recovery from the bleached state. Corals rely on heterotrophic food sources and energy stores during recovery from bleaching for at least 11 months[36–38,40]. This suggests that the ability to re-establish the coral-*Symbiodinium* symbiosis depends on the health of the coral host and these alternative energy sources will be vital in the recovery of corals. In addition, some corals have been found to obtain nutritional value from sediment[96], and this may aid in recovery from a bleached state when exposed to elevated sediments, however, this would only occur at low sediment concentrations as SSCs above 30 mg L^{-1} have been found to reduce coral feeding rates[97]. In a natural setting, sediment related stress may be greater than reported here, where sediments have been manually cleared from corals on a daily basis, as while periodic sediment removal may occur naturally during storm events, it seems unlikely this would occur on a daily frequency. Due to this increased accumulation of sediments on coral tissues would likely occur, leading to mucus sheet formation[98] and potentially necrosis[87]. The reduced capacity of bleached corals to removed sediment will mean that such effects will be substantially greater in corals compromised by thermal stress.

In summary, this study has demonstrated that thermally bleached corals have substantially reduced ability to clear deposited sediment, and that this ability is further reduced following consecutive days of sediment deposition. The impacts of this reduction in clearance ability is likely to become exacerbated when combined with increased ocean acidification, another key impact resulting from climate change. The likelihood of a marine heatwave (and subsequent coral bleaching event) coinciding with dredging projects has unfortunately reached a point where explicit consideration needs to be given regarding management practices. Maintenance dredging typically occurs over a few weeks to months, and the timing of the activities can be reasonably predicted and planned in advance[99]. Avoiding dredging when bleaching could occur (i.e. summer maximum temperatures) seems a practical approach. This management practice is similar to concepts associated with 'environmental windows', which involve avoidance of times of the year or particular sites, where key species, ecological communities or critical processes may be particularly vulnerable to pressures from dredging[100,101]. For capital dredging projects which can often occur over extended periods[102], contingency plans in the event of a warm-water bleaching event could be developed before dredging commences. Plans could include defining the scale and intensity of an event and a series of practical and achievable courses of action to ensure minimal impacts and maintain acceptable levels of impact. Appropriate courses of action may include relocation of dredges, altering overflow plans, use of different dredge material placement sites, the use of more conservative water quality thresholds (for managing projects), and possibly cessation of all dredging activities. Several of these approaches were employed on the Great Barrier Reef in a dredging program in 2000–2001[21,57]. From an environmental and management perspective, the significance of sub-lethal bleaching is that the symbiosis is dissociated, and the time for it re-establish may be much longer than the acute physiological effects alone. This serves to amplify the significance of what may be a short-term initial stress, increasing the potential for additional impacts from local, anthropogenic activity (i.e. cumulative impacts).

Materials and Methods

Experiments were conducted with 3 hard coral species, *Acropora millepora* (Ehrenberg 1834), *Porites* spp. and *Turbinaria reniformis* (Bernard 1896), representing branching, massive and foliose morphologies respectively. Due to difficulty identifying *Porites* spp. underwater (they have small and variable corallites[103]) a mixture of two species (*P. lutea* and *P. lobata*) were included. All corals were collected between 3–10 m from the Rib, Trunk and Davies Reef lagoons (mid-shelf reefs centrally located in the central Great Barrier Reef, GBRMPA permits G12/35236.1 and G13/35758.1). For *A. millepora*, 8 colonies were collected by hand, 14 *Porites* spp. colonies were cored with a pneumatic drill, and *T. reniformis* were collected from an extensive thicket ~5 by 10 m where individual colonies were unable to be identified. 10 fragments were collected from each *A. millepora* and *T. reniformis* colony, while 6 were collected from each *Porites* spp. colony. Colonies that were free of biofouling and diseases were fragmented into replicates of ~7 cm^2. Fragments were then glued onto aragonite coral plugs, with genotypes randomly allocated between 6, 200 L flow-through (receiving new water at a rate of 31 L h^{-1} = 3 water turnovers d^{-1}) holding tanks in the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS, Townsville, Australia), for 6 weeks to recover from the collection and preparation procedures (Fig. 6a). Light above each tank was provided by four AI Hydra FiftyTwo™ HD LED lights (Aquaria Illumination, IA, US), which generated even illumination with an equal mix of white, blue, and red light. During the holding period, corals were exposed to a 12 h light:dark (L:D) cycle comprised of a 6 h period of gradually increasing light in the morning (06:00–12:00 h), to a maximum midday instantaneous light level of 400 μmol photons m^{-2} s^{-1} followed by 6 h of gradually decreasing light in the afternoon (12:00–18:00 h). Over the course of the day the corals experienced a daily light integral (DLI, total summed Photosynthetically Active Radiation [PAR, 400–700 nm]) of 8.6 mol photons m^{-2}. Light intensity was measured within tanks at the same depth as the coral fragments using an Underwater Spherical Quantum Sensor (Licor LI-193).

Prior to the start of the sediment clearance experiments, half the coral replicates were induced to bleach by exposing them to elevated water temperatures (Fig. 6b). To induce bleaching water temperatures in four of the six holding tanks was incrementally raised from 27 °C to 31 °C at a rate of 0.5 °C per day for 8 d. Corals were then maintained at 31 °C (or 27 °C) for 3 weeks. Light exposure remained the same as during the holding period. Coral bleaching was observed by the 3rd week of exposure, and was examined throughout the bleaching period by visual assessment, and the use of a colour index (see below). The maximum quantum yield (F_v/F_m) of symbiotic dinoflagellate algae within the live tissue of each coral fragment was also measured using a mini-PAM fluorometer (Walz, Germany) (see below).

Once the corals had been bleached, their ability to clear upward facing surfaces of sediment was compared with normally-pigmented corals, by exposure to a series of sedimentation events of different intensities (Fig. 6c). All experiments were conducted in clear PVC tanks filled with 100 L of 0.4 μm filtered seawater (as not to introduce additional uncontrolled sediment sources) pumped into each tank at 400 mL min^{-1} to ensure 5.8 complete water changes per day, see Bessell-Browne, *et al.*[104] for details of the experimental system. Three replicate tanks were used to enable potential tank-effects to be assessed. Water temperature was maintained at 27 ± 0.5 °C and salinity was 33 ± 0.5‰. Light above each tank was provided by two AI Hydra FiftyTwo™ HD LED lights (Aquaria Illumination, IA, US). Corals were exposed to a daily light integral (DLI) of 8.6 mol photons m^{-2} using the same light regime as the bleaching experiment described previously. Coral genotypes were randomly allocated between the experimental tanks with 4 bleached and 4 normally pigmented corals assigned to each tank.

Corals were placed in the tanks on a fibre reinforced plastic grating (false bottom floor), 25 cm below the water surface. The sediment used for deposition events had a mean grain size of 30 μm, and this was used as it has been found to be the most common grain size suspended and subsequently deposited during dredging campaigns[68]. Deposition events were created in each tank by raising the SSCs to 100, 300 and 650 mg L^{-1} (nephelometrically derived SSCs), and then turning the pumps off and allowing the suspended sediment to settle out of suspension

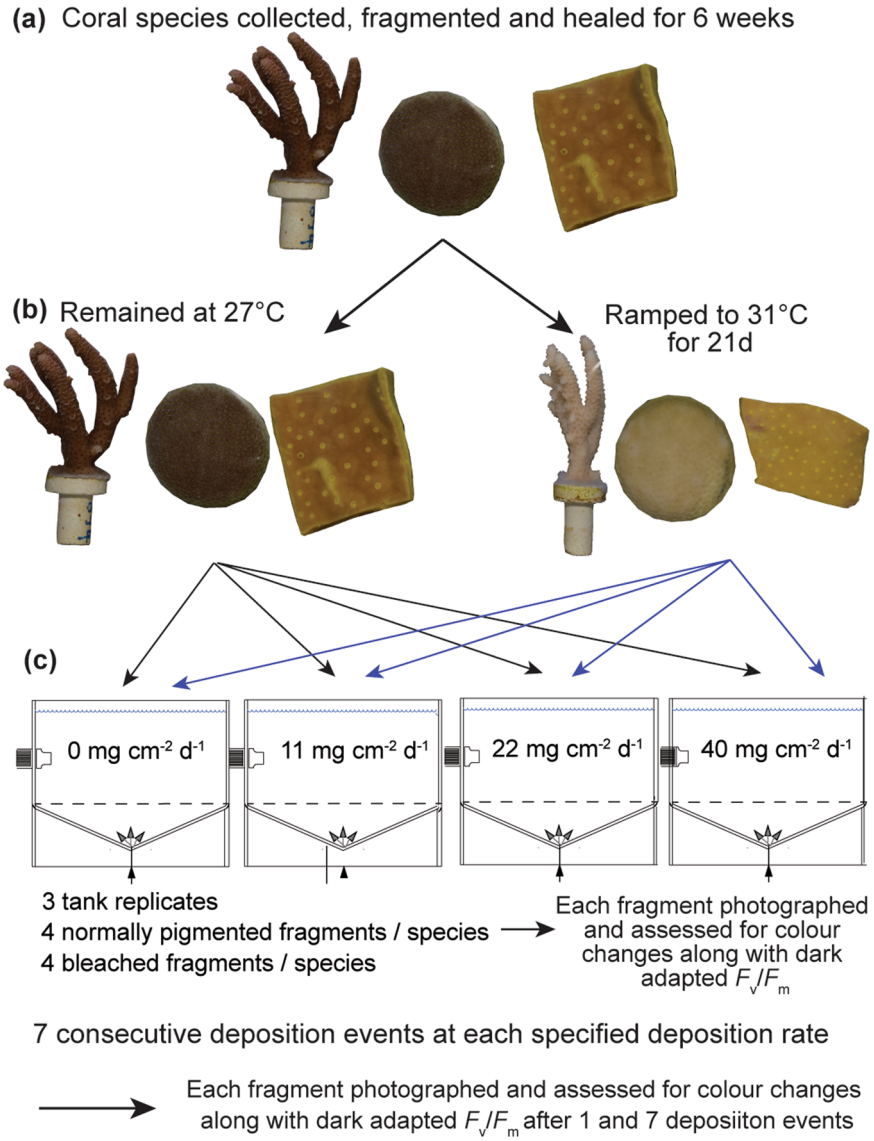

Figure 6. Conceptual diagram of the steps involved in the experiment, including (**a**) the initial healing process, (**b**) bleaching of corals, (**c**) subsequent sediment deposition exposures and health parameters that were assessed at different stages of the experiment.

overnight past the grating holding the corals. At the end of the day (4.00 pm), the pumps were turned on again resuspending all sediment that had settled on the bottom of the tank, grating and the corals. Repeated deposition events were generated over 7 successive days by resuspending the sediments at 4.00 pm each day. Deposition events were thus scheduled to occur at night to avoid attenuation of light by suspended sediments, which is a key dredging related pressure impacting upon coral health[104], and therefore deposition at night reducing the confounding nature of extra causal pathways impacting on health that were not investigated here.

Sediment was delivered to individual tanks by an air diaphragm pump (SandPiper S1F), via a high velocity loop (3 m s^{-1}), from a concentrated (g L^{-1}) stock solution. The desired SSC in each tank was controlled by a programmable logic controller (PLC) coupled to pivoting solenoid valves connected to the stock solution, and based on real time feedback from turbidity sensors (Turbimax CUS31, Endress and Hauser) contained in each of the 12 tanks.

Sediment deposition was measured within each tank using sediment pods (SedPods), which are concrete filled PVC cylinders[105] placed on the grating beside the corals. Each morning SedPods were capped and any accumulated sediment filtered through pre-weighed 0.4 µm, 47 mm diameter polycarbonate filters, incubated at 60 °C for ≥24 h, and weighed to determine sediment mass.

All sediment used was biogenic calcium carbonate collected from Davies Reef (GBRMPA permit: G13/35758.1). Sediment was first screened to 2 mm and then ground with a rod mill grinder until the mean grain size was ~30 µm (range: 0.5–140 µm), measured using laser diffraction techniques (Mastersizer 2000, Malvern instruments Ltd, UK). Total organic content of the sediment was 0.25% (w/w).

For each sediment treatment, there were 3 replicate tanks with 4 normally-pigmented and 4 bleached corals per tanks. Corals were exposed to 7 individual deposition events (one per day). Coral fragments were photographed immediately before the first deposition event and immediately after the last. Changes in the colour of coral tissue was used as a non-destructive indicator of bleaching. The photographs were analysed with Image J[106] using the histogram function on a selection of representative live tissue, taking the arithmetic mean of pixel values (range 0–255) on a black and white scale. These were then standardised by converting to a range between 0 and 1 for each species. During the photographing process, any partial mortality of the corals was noted and then quantified from the photographs using image processing software Image J.

Chlorophyll fluorescence of the endosymbiotic dinoflagellate microalgae within tissue of each coral fragment was measured using a mini-PAM fluorometer (Walz, Germany). Measurements were obtained using a 6 mm fibre-optic probe positioned perpendicular to the coral fragment and 3 mm away (controlled by a rubber spacer). Coral fragments were dark-adapted for 30 min prior to measuring initial fluorescence (F_0), which was determined by applying a weak pulse-modulated red light (650 nm, ~0.15 μmol photons m^{-2} s^{-1}). Maximum fluorescence (F_m) was then measured following a saturating pulse of saturating white light. Maximum quantum yield (F_v/F_m) is the proportion of light used for photosynthesis by chlorophyll when all reaction centres are open[107] and is determined by the following equation:

$$\frac{F_v}{F_m} = (F_m - F_0)/F_m$$

Chlorophyll fluorescence measurements were made at the start of the sedimentation experiments and again at the end. Measurements were only taken over live tissue, with 4 measurements taken and averaged per coral replicate.

The mass of sediment that remained on coral tissue after it was left to settle overnight (~16 h) was quantified after both the first and last deposition event. To do this a plastic bag was placed around each coral and the bag then sealed and shaken to dislodge all sediment that had settled on the surfaces. The suspension was then filtered through pre-weighed 47 mm diameter polycarbonate filters (0.4 μm nominal pore size), dried at 60 °C for ≥24 h, and weighed to 0.0001 g. The mass of collected sediment was then standardised to fragment surface area using the wax dipping technique[108].

At the end of the experiment, one third of the corals were snap frozen in liquid nitrogen and then stored at −80 °C. Fragments were then air blasted to remove tissue and chlorophyll extracted twice from tissue using 95% ethanol, and quantified spectroscopically using the equations of Ritchie[109] and Lichtenthaler[110]. Endolithic algae were not visible in the samples and assumed not to contribute any significant amount of Chlorophyll a (Chl *a*) to the samples. Chl *a* was standardised to the surface area and used as a proxy for coral bleaching.

All data were analysed with R software (version 3.2.3, R Core Team[111]). We used a complete subsets model selection approach[112] to examine the effects of time (1–7 days of repeated exposure), sedimentation level (0, 11, 22 and 40 mg cm^{-2} d^{-1}), species (*A. millepora*, *T. reniformis* and *Porites spp.*), and bleaching status (bleached, normally pigmented) on coral health parameters. This approach involves fitting all possible model combinations (including interactions) and comparing this complete model set using Akaike Information Criterion with corrections for small sample sizes (AICc). The model with the lowest AICc (within 2) and the fewest parameters is considered the most parsimonious, and chosen as the best model. For modelling of relationships, tank and coral fragment identity (to account for repeated measurements through time) were included as random factors in a Generalised Linear Mixed Model (GLMM). A complete subsets information theoretic approach based on GLMM was used over more traditional ANOVA like approaches, as this allows non-independence (associated with repeated measurements through time and tank effects) to be successfully accommodated, as well as flexibility of the statistical distributions used. Colour index and F_v/F_m were logit transformed, as they are both proportions, and then modelled using a Gaussian distribution, with bleaching status, time, sediment deposition treatment and species included as fixed factors. Models were fit using the lmer function from the package lme4[113]. Chl *a* concentrations, and the amount of deposited sediment remaining on coral fragments after the 1st and 7th deposition event, were modelled as GLMMs based on a Tweedie distribution, fit using the cplm package, with fragment number and tank included as random effects[114]. A Tweedie distribution is appropriate for continuously distributed data that can take values of 0 to ∞.

Due to the interaction between time and species on the amount of deposited sediment remaining on coral fragments, pressure-response relationships were subsequently fitted after 1 and 7 deposition events, for both bleached and normally pigmented fragments. These relationships were fitted with the drc package[115].

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Author Contributions

P.B.-B., A.N., R.F., P.C. and R.J. conceived the study. P.B.-B. ran the experiment and completed the lab work. P.B.-B. and R.F. conducted the analysis. P.B.-B. and R.J. drafted the manuscript, all authors reviewed and approved the manuscript.

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Coral morphology and sedimentation

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ABSTRACT

The sediment rejection ability of 8 coral species of 5 families and 3 morphologies were assessed in a series of short term exposure tests over a sedimentation range of 0.5–40 mg cm^{-2} d^{-1} and one longer term exposure test of 235 mg cm^{-2}. Sediment accumulation rates on live corals and dead (enamel-covered) skeletons varied between morphologies, with branching species often more adept at self-cleaning. Flow rates (0–17 cm s^{-1}) significantly affected sediment-shedding ability as did differences in particle sizes, with coarse silt rejected faster than fine silt, but only at very high (235 mg cm^{-2}) deposition rates. Siliciclastic sediment was rejected faster than carbonate sediments and smothering for many days by mms of low organic content carbonate sediment resulted in bleaching, but no mortality. The findings are discussed with respect to turbidity generated in natural and dredging-related resuspension events and in the context for impact prediction for dredging projects.

1. Introduction

Dredging and dredging related activities (such as dredge material disposal in offshore disposal grounds) release sediments into the water column. The increased turbidity (water cloudiness) can negatively impact the local marine environment, especially sensitive marine habitats such as coral reefs, seagrass beds and mixed filter feeder assemblages (Foster et al., 2010; McCook et al., 2015; Jones et al., 2016). The need for dredging is predicted to grow associated with the trends of increasing cruise and container ship sizes and maritime transport (Asariotis et al., 2010; Ports Australia, 2014). An accompanying need is to improve the ability to make scientifically sound predictions of the likely extent, severity, and persistence of environmental impacts associated with dredging (McCook et al., 2015; EPA, 2016). This is predicated upon establishing a relationship between changes in water quality and the health of the underlying communities. Once established, it can be used together with coupled hydrodynamic and sediment transport models to predict the likely spatial extent of any possible effects at the environmental impact assessment stage e.g. Gailani et al. (2016); Nelson et al. (2016), and also used with water quality monitoring during dredging to inform adaptive management.

Elevated sedimentation is one of the key cause-effect pathways that can result in damage to adult and recently settled juvenile corals at sites close to excavation activities (Dodge and Vaisnys, 1977; Bak, 1978; Jones et al., 2015b; Jones et al., 2016). High sedimentation rates require corals to self-clean, i.e. to keep their surfaces sediment-free and prevent sediment accumulation and 'smothering' of the underlying tissue (Philipp and Fabricius, 2003; Weber et al., 2006; Weber et al., 2012). If smothering occurs (see Fig. 1), sediments could build up on a coral over successive days, decreasing solute and metabolite exchange and feeding. It will prevent light from reaching the symbiotic dinoflagellates in the coral tissue (Riegl and Branch, 1995; Weber et al., 2006). Once smothering has occurred, partial mortality (lesion formation) can sometimes occur in a few days (Philipp and Fabricius, 2003; Weber et al., 2006; Piniak, 2007; Weber et al., 2012). Estimating the sedimentation rate where the self-cleaning ability of corals is exceeded is a priority for impact prediction assessment during dredging programs.

Corals routinely experience periods of increased sedimentation associated with storms and natural resuspension events (Larcombe et al., 1995; Ogston et al., 2004; Storlazzi et al., 2004; Verspecht and Pattiaratchi, 2010). They have a range of different mechanisms for shifting sediments, primarily involving mucus entrapment and ciliary action (muco-ciliary transport), hydrostatic inflation and tentacle movement (Duerden, 1906; Marshall and Orr, 1931; Hubbard and Pocock, 1972; Rogers, 1983; Rogers, 1990; Stafford-Smith and Ormond, 1992). These 'active' (energy-requiring) processes work in combination with 'passive' forces associated with gravity. Both the macroscale morphology (growth form, branch thickness and spacing) and microscale morphology (corallite size and shape) affect how sediments settle, collect and are cleared from the surface (Hubbard and Pocock, 1972; Stafford-Smith and Ormond, 1992).

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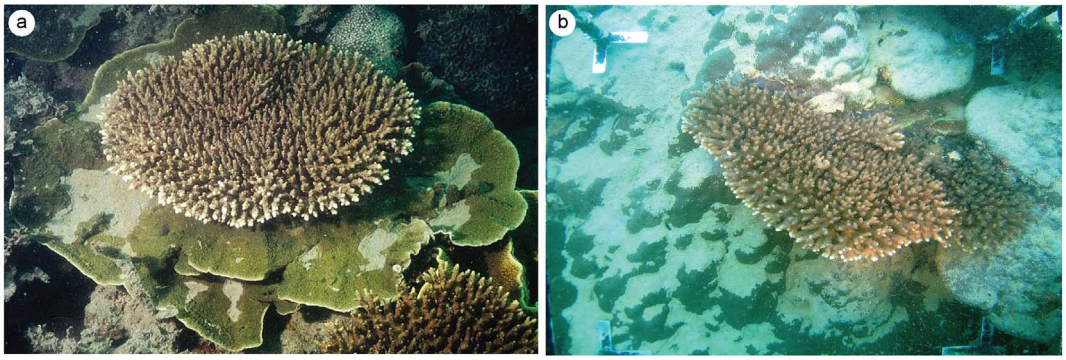


Fig. 1. Smothering of corals during dredging projects (a) near Magnetic Island (Central Great Barrier Reef, Queensland, Australia) in January 2001 at depth of 5–6 m (Jones et al., 2004; Jones, 2008) and (b) near Barrow Island (Pilbara coast of Western Australia, Australia) in April 2011 at a depth of ~11 m (Fisher et al., 2015; Jones et al., 2015a) showing a build-up of sediment on foliose *Montipora* spp. corals and massive *Porites* spp. but no sediment build-up on the branching *Acropora* spp. Corals were located < 100 m from (image a) and 1.5 km (image b) from dredging activities.

Different coral species have different inherent abilities to clean themselves of sediments (Stafford-Smith and Ormond, 1992) with some species, such as *Turbinaria mesenterina* known to be particularly hardy (Sofonia and Anthony, 2008). Other factors which could influence the ability of corals to self-clean include sediment type, particle size and water movement, with the latter factor not only affecting the particle settling velocity, but also providing an additional force to compliment the active and passive removal processes.

In nearshore locations, corals can be exposed to different types of sediment particles, from primarily calcium carbonate (i.e. the skeletal remains of animals and plants), to more terrestrially-derived siliciclastic sediment (Larcombe and Carter, 1998). It is most likely corals will be exposed to a mixture of the two depending on location, distance from shore and proximity to river mouths (Furnas, 2003; Piniak, 2007). The different types of sediments will vary in their density, sphericity and angularity. In addition to different geochemical properties, the sediments will also differ in their organic and nutrient-related properties, which can mediate effects once smothering has occurred (Piniak, 2007; Weber et al., 2012).

A number of studies have examined the difference in sediment rejection ability of corals in response to fine and coarse sediment. However, as noted in Jones et al. (2016), these studies have frequently used sands, whereas even close to a working dredge the particle sizes are typically in the silt range (< 62 μm). Many studies examining the sediment shifting ability of corals have also used silicon carbide (carborundum) (Yonge, 1930; Bak and Elgershuizen, 1976; Stafford-Smith and Ormond, 1992; Junjie et al., 2014; Browne et al., 2015) and as with the use of sands the relevance of these studies for impact prediction with dredging is uncertain.

As part of a sequence of experiments examining the effects of dredging pressures (i.e. suspended sediments, light reduction sedimentation) on corals, alone and in isolation, and over different time periods, in this study the short-term self-cleaning capabilities of a range of coral species was examined. The species included different families and morphologies and were tested with different sediment types (carbonate and siliciclastic and mixed sediments) and different particle sizes (median diameter 10–60 μm), sedimentation rates (0.5–40 mg cm^{-2} d^{-1}) and flow rates (0–17 cm s^{-1}), while a long-term (16 d) experiment examined the consequences of sediment smothering on survival. One of the problems of relating coral health and sedimentation is accurately measuring sedimentation rates at scales that are physiologically relevant i.e. mg cm^{-2} d^{-1}. In this study, two new measuring techniques were used that can provide better estimates of net sedimentation rates — SedPods which are flat, cement filled PVC pipes with a roughened surface (Field et al., 2012), and optical back scatter (OBS) sensors (Ridd et al., 2001; Whinney et al., 2017) which are autonomous in situ instruments capable of measuring deposition over periods of minutes to weeks.

2. Materials and methods

2.1. Coral species

Experiments were conducted with 8 common Indo-Pacific coral species, representing 5 families and 3 morphologies (see Table 1), although not all species were used in each experiment (see Table 3). *Porites lobata* and *Porites lutea* are morphologically similar and difficult to identify underwater due to their small and variable corallites (Veron, 2000), and therefore a mixture of species were used and referred to as *Porites* spp.

For the branching and foliose species, up to 10 colonies were collected and fragmented into replicates using a mallet and cold chisel. The *Porites* spp. cores were removed from > 10 large *Porites* spp. colonies using a pneumatic drill. All coral species were collected between depths of 4–10 m from the lagoon at Davies Reef (a mid-shelf reef of the central (18°S) Great Barrier Reef). *M. aequituberculata* is reported as occurring at Davies Reef, but could not be located during collections, and instead was collected from a coastal fringing reef at Magnetic Island (in Cleveland Bay (18°S), inshore, central GBR) at depth of 4 m. Corals were collected separately for each experiment, with an average of 30

Table 1
Coral species, family, morphology and size, used in the clearance and smothering experiments.

Species (author)	Family	Morphology	Size
Pocillopora damicornis (Linnaeus, 1758)	Pocilloporidae	Branching	Small 4–5 cm (width) fragments containing ≥ 3 branches from 10 + colonies
Acropora millepora (Ehrenberg, 1834)	Acroporidae		
Montipora aequituberculata (Bernard, 1897)		Foliose	Small ~50 cm^{-2} (area) fragments collected from 10 + colonies
Montipora capricornis (Veron, 1985)			
Turbinaria reniformis (Bernard, 1896)	Dendrophylliidae		
Goniastrea retiformis (Lamarck, 1816)	Merulindae	Massive	Small ~50 cm^{-2} whole colonies
Porites lutea (Milne Edwards & Haime 1851)	Poritiidae		Small ~50 cm^{-2} whole colonies and 50 mm diameter cores.
Porites lobata (Dana, 1846)			

replicates per species used in each clearance rate experiment and 120 replicates used in the smothering experiment. Each replicate was individually glued onto a numbered aragonite coral plug and left to heal for > 3 weeks in 200 L holding tanks. Corals were fed daily using enriched *Artemia*.

2.2. Experimental design

A series of 4 laboratory-based experiments were conducted in the SeaSim aquarium facilities of the Australian Institute of Marine Science (AIMS, Townsville, Queensland). These included 3 clearance rate experiments (C1, C2, C3) which involved exposing corals to different levels of sedimentation using different sediment types, particle sizes and under different flow speeds, and a smothering experiment (S1) which involved examining the response of corals to long term sediment smothering.

The clearance rate experiments were conducted in a large (1500 L) fibreglass tank, holding 1200 L of 0.4 μm filtered seawater at salinity of 33‰ and temperature of 27 °C. Experiments were typically conducted under static (no flow) conditions or under different flow rates created using submerged pumps (Hydrowizard ECM63, Panta Rhei, Germany) used in wave mode (0.6 s pulse: 0.6 s no pulse, at 5% and 50% power). Flow rates in the tank were measured using acoustic Doppler techniques with a 16-MHz MicroADV (Sontek, USA). The smothering experiment (S1) was conducted in 18 × 115 L PVC tanks, filled with 100 L of 0.4 μm filtered seawater pumped into each tank at 400 mL min^{-1} to ensure 6 complete water changes every day. An underwater pump (VorTeck, EcoTech Marine, USA) circulated water (~9 cm s^{-1}) throughout each tank to ensure it was evenly mixed.

In all experiments high suspended sediment concentrations (SSCs) were created in the tanks (see below) and sediments allowed to settle out of suspension onto corals which were located on a fibre reinforced plastic grating 50 cm below the surface (experiments C1, C2 and C3) or 25 cm below the surface (experiment S1). The false bottom floor (grating) had an open area of 70% and was designed to allow sediments to fall past the corals down to the container floor. The tanks were illuminated with Photosynthetically Active Radiation (PAR, 400–700 nm) with a custom-made LED light (experiments C1, C2 and C3) or Hydra FiftyTwo™ HD LED lights (Aquaria Illumination, IA, US) (experiment S1) suspended above the tanks. Lights provided an even illumination with an equal mix of white, blue, and red light of ~6.5 mol m^{-2} d^{-1} (measured using a LI-190R Quantum PAR Sensor, LI-COR, USA).

2.3. Sediments types and sizes

Experiments were conducted with sediments collected from 3 different coastal reef settings in Australia (Table 2) including light grey, predominantly carbonate (biogenic) sediments from the central GBR (Davies Reef), yellow-brown, mixed terrigenous mud and carbonate sediments from coastal GBR (near Middle Reef, Cleveland Bay), and red-brown, predominantly siliciclastic sediment from the nearshore environment of north west Australia (Onslow, Pilbara region). Several hundred kilograms of each sediment type was collected using a Smith-McIntyre grab or by SCUBA divers from depths < 10 m, screened to 2 mm, and then ground with a rod mill grinder to reduce the mean particles sizes to a silt and clay fraction. After grinding, approximately 50 kg of each sediment type was passed through a series of industrial sieves to create fine and coarse silt fractions. Particle size distributions (PSDs) were measured using laser diffraction techniques (Mastersizer 2000, Malvern instruments Ltd., UK). The total organic content and carbon content of the sediment was analysed using the Shimadzu TOC-L analytical method, while metal analysis used the ICP-OES analytical method (Supplementary information, Table S1). Particle size, shape and texture of the different sediment types was also examined by scanning electron microscopy (SEM).

2.4. Sediment addition and measurement

For all experiments sediment of a known weight was mixed with 2 L of 0.4 μm filtered seawater in a domestic blender for 2 min at 15,000 rpm to create a concentrated slurry. The slurry was then added to the tank, mixed thoroughly for 30 s using the recirculating and submersible pumps, and in experiments with no water flow the pumps were turned off to allow the sediment to settle. Water flow typically ceased within 3 min after pumps were turned off.

Turbidity was measured using nephelometers (Turbimax CUS31, Endress & Hauser, Switzerland) and SSCs were determined by taking 3 × 200 mL water samples at set times. Sediment deposition in each experiment was measured using SedPods randomly placed throughout each tank on the fibre reinforced plastic grating. These were capped and removed for sediment weighing after 24 h. The SedPods had a surface area of 25.2 cm^2 and were created with a rough surface by imparting a plywood imprint as described by Field et al. (2012). In the clearance rate experiments, a deposition sensor (Whinney et al., 2017) was placed in the middle of the tank to examine temporal changes of deposition. All water and sediment samples were filtered through pre-weighed 0.4 μm 47 mm diameter polycarbonate filter, placed back into numbered scintillation vials and dried for 60 °C for ≥ 24 h, and weighed (to 0.0001 g) to determine sediment weight.

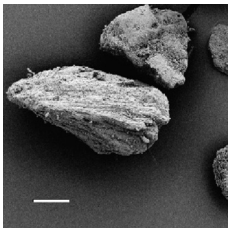
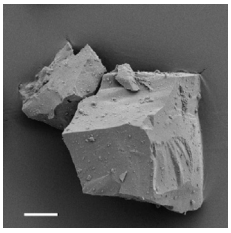
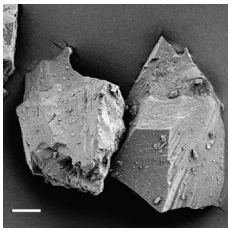
2.5. Coral clearance measurement

To examine the role of active versus passive sediment rejection, the weight of sediment that remained on live corals versus dead skeleton was examined, as well as the % of the colony surface area covered in sediment in the various treatments. For the dead skeleton measurements, replicates of each species were cleaned of their live tissue using dilute sodium hypochlorite, washed, dried, and then spray-painted several times using a non-toxic and waterproof paint (Dy-Mark Enamel, Australia) to seal the surface (hereafter referred to as 'skeleton-only'). Before each experiment all live corals and skeleton-only corals were placed beside a scale bar and photographed from above. The images were used to calculate the 2-dimensional surface area (cm^2) or 'projected area' using image processing techniques (ImageJ, Version 1.49, Schneider et al., 2012). All corals were also photographed inside the tanks at the end of the experiments and the images used to determine the proportion (%) of their surface covered by sediment.

Corals in all experiments were positioned as close as possible to their natural orientation and placed randomly throughout tank on the plastic grating, ≥ 8 cm from other replicates. Coral replicates are therefore statistically independent. To measure the weight of sediment remaining on the surfaces at the end of the experiment, a plastic bag was placed around each live coral (and skeleton-only coral) and the bag then sealed and shaken to dislodge all sediment that had settled. The suspension was then emptied into a measuring cylinder, the volume recorded, and the sediment mass determined by filtration, drying and weighing as described previously. Since the water surrounding the coral at the time it was placed in the bag may also have had measureable concentrations of suspended sediments, the weight of sediments in suspension was calculated from the water volume taken during the sampling process and subtracted from the sediment that had deposited. The mass of sediment that had settled on the corals was then normalized to the projected area (mg cm^{-2}). A self-cleaning index (SCI) was also calculated based on the ratio of the amount of sediment accumulated on the live tissue (mg cm^{-2} live tissue) to the amount collecting on the enamel-sealed skeleton of the same species (mg cm^{-2} skeleton).

$$\text{Self} - \text{Cleaning Index (SCI): } 1 - \left(\frac{(\text{mg cm}^2 \textit{ live tissue})}{(\text{mg cm}^2 \textit{ skeleton only})} \right) \quad (1)$$

Table 2
Characteristics of the 3 different sediment types used in the clearance rate (C1, C2, C3) and smothering (S1) experiments including the collection locations, type, Munsell soil colour chart hue, value, and chroma score. Scale bar is 10 μm in all SEM images. Summary statistics for particle size where: D_{50} is the median particle size by volume, and D_{10} and D_{90} are commonly reported percentiles describing a range encompassing 80% of the sediment particle sizes. Span is a measure of the width of distribution, skewness is a measure of the distortion from a symmetrical distribution, and kurtosis is a measure of the peakedness (shape) of the distribution. The fine, medium and coarse classification is based on the Wentworth grade scale scheme for sediment (Wentworth, 1922). Note for simplicity the fine-medium Davies Reef sediment is labelled as fine silt throughout the manuscript.

Composition		Primarily carbonate			Mixed carbonate/siliciclastic			
Location		Davies Reef			Middle Reef		Onslow nearshore	
Lats/long		18° 49.507′S, 147° 38.826′E			19° 11.722′S, 146° 48.822′E		21° 37.940′S, 115° 0.175′E	
SEM images								
Munsell colour		10YR 8/1			10YR 6		10YR 5/3	
Colour								
RGB		231, 231, 239			124, 104, 54		100, 74, 39	
Density (Kg m^3)		1.4			1.27		1.30	
C (mg Kg^{-1})		11.45			2.77		5.26	
TOC (%)		0.25%			0.35%		0.16%	
Silt classification		Medium	Fine-Med.	Coarse	Fine	Coarse	Fine	Coarse
PSD	D_{50}	24	17	55	9	58	14	53
	D_{10}	2	2	36	2	31	2	34
	D_{90}	64	45	84	31	102	42	83
Span		2.1	2.5	0.9	3.3	1.2	2.9	0.9
Skewedness		1.0	1.0	0.8	1.5	0.7	1.1	0.8
Kurtosis		0.8	0.7	6.5	3	0.6	0.8	0.4

2.6. Experimental program

The effects of increasing sediment deposition (experiment C1) was examined for each of 6 coral species, with 5 live corals and 5 skeleton-only corals exposed for 1 d to 7 nominal sedimentation levels ranging from 0.5–40 mg cm^{-2} d^{-1} using sediment from Davies Reef (Table 3). The sedimentation levels were examined separately, with their order randomised. Because there was insufficient space in the tank for all 60 replicates plus SedPods and a deposition sensor, 2 separate runs were done for each sedimentation level. Each run had 1 species per morphology.

The effects of water flow (experiment C2) was examined for 4 corals species whose clearance rates varied most between treatments in experiment C1, with 4 live corals and 4 skeleton-only corals exposed to 20 mg cm^{-2} d^{-1} of Davies Reef sediment for 1 d at 3 flow rates: 0 (no flow), 2–3 cm s^{-1} (low flow) and 9–17 cm s^{-1} (high flow) (Table 3). The flow rates used are based on estimates made in the Davies reef lagoon where the corals were collected using a drag-tilt current meter (see Fig. S1), where the 50th percentile (P_{50}) was 5.3 cm s^{-1}, P_{80} 10.4 cm s^{-1}, P_{95} 16.1 cm s^{-1} and maximum 24.5 cm s^{-1}. The effects of sediment type and size (experiment C3) was examined for 2 branching and 2 foliose coral species, with 4 live and 4 skeleton-only corals exposed for 1 d to 20 mg cm^{-2} d^{-1} of fine and coarse silt from Davies Reef, Middle Reef and Onslow (Table 3) at no flow.

Table 3
Sediment type, particle-size distribution (PSD, μm), flow rates (cm s^{-1}), nominal deposition rates (mg cm^{-2} d^{-1}), experimental duration (d) and species used in the 3 clearance rate experiments (C1, C2, C3) and 1 smothering experiment (S1).

Experiment	Sediment type	PSD D_{50}	Flow (cm s^{-1})	Nominal deposition rate (mg cm^{-2} d^{-1})	Length (d)	Coral species
C1: effects of different sedimentation levels on self-cleaning	Davies Reef	24	0 (zero)	0.5, 1, 2, 5, 10, 20, 40	1	*A millepora* *P. damicornis* *T. reniformis* *M. aequituberculata* *G. retiformis* *Porites* spp.
C2: effects of current flow on self-cleaning	Davies Reef	24	0 (zero) 2–3 (low) 9–17 (high)	20	1	*A. millepora* *P. damicornis* *T. reniformis* *M. aequituberculata*
C3: effects of different sediment types and sizes on self-cleaning	Davies Reef Middle Reef Onslow	17, 55 9, 58 14, 53	0 (zero)	20	1	*A. millepora* *P. damicornis* *T. reniformis* *M. capricornis*
S1: effects of smothering on long term survival	Davies Reef	17, 55	9	235	0, 1, 2, 4, 8, 16[a]	*A. millepora* *T. reniformis* *M. capricornis* *Porites* spp.

[a] + 42 d observation period.

The effects of sediment size and smothering time (experiment S1) was examined using a single sediment deposition of 235 mg cm^{-2} day^{-1} of fine or coarse silt that was left on 4 coral species for 0 (control), 1, 2, 4, 8 or 16 d, followed by a 42 d observation period (Table 3) when their tissue was sediment-free. The 2 sediment sizes were examined separately, with each smothered treatment having 3 experimental tanks, randomly ordered, and with each containing 3 replicates per species. Although a very high deposition level was used, all corals had some tissue not smothered by sediment with temporal variation in tissue colour and chlorophyll fluorescence measured for both smothered and non-smothered tissue. Tissue colour was determined by photographing corals next to a colour health monitoring chart (Siebeck et al., 2006) where the coloured squares are a guide of symbiont concentration.

Chlorophyll fluorescence of the symbiotic dinoflagellate algae was measured over time using a Mini-PAM fluorometer (Walz GmbH, Germany) with a 6 mm fibre-optic probe placed 3 mm away and perpendicular to the surface of the corals. All corals were dark-adapted for ≥ 1 h, with initial fluorescence (F_o) measured by applying a weak pulse-modulated red light (650 nm, ~0.15 μmol photons m^{-2} s^{-1}), and maximum fluorescence (F_m) measured after a saturating pulse of white light to calculate maximum quantum yield as the ratio of variable fluorescence F_v (i.e. F_m–F_o) to F_m (i.e. F_v/F_m). Each coral was measured at the start of the experiment, immediately after sediment removal, and then every week.

2.7. Data analysis

ANOVA's statistically tested for differences of each parameter (e.g. sedimentation rate, percent sediment cover, final dark-adapted F_v/F_m) among factors (e.g. species, sedimentation level, days-smothered). Analysis was done separately for live corals and skeleton only corals in the clearance rates experiments, and separately for smothered and non-smothered tissue in the smothering experiment. Data was log transformed when needed to meet assumptions, while percentage or proportion data was arcsine transformed. When a data set had many zeros (i.e. zero-inflated data) and thus violating the ANOVA assumption of normality, a zero-inflated Poisson regression (with robust standard error option) was used instead. Statistical analyses were done using NCSS (version 9) and STATA (version 14).

3. Results

Preliminary studies with the sediment deposition sensor in the 1500 L tank showed that a well-mixed homogeneous suspension of very fine sediment (D_{50} < 25 μm, calcium carbonate) rapidly settled out of suspension when the pumps were turned off (Fig. 2). In the first 3 h, as much as 50% of the sediment in suspension had settled under gravitational forces past the grating where the sensor (and corals) was located (50 cm below the surface), and the majority (~99%) had settled by 20 h (Fig. 2B). Settling rates are affected by water flow with sediment deposition slower at high water flow (9–17 cm s^{-1}). Sediment PSDs in seawater sampled from 10 cm depth also showed a rapid initial loss of larger sized particles and a transition to finer PSDs (Fig. 2C) and a decrease in SSCs in the upper water column (Fig. 2A). Using this principle it was possible to create a range of 'nominal' sedimentation levels from 0.5–40 mg cm^{-2} d^{-1}, by adjusting the starting SSCs concentrations and allowing the sediments to fall from suspension. SedPod accumulation rate was measured in each experiment.

3.1. C1 (clearance rate experiment 1): effects of increasing sediment deposition

Mean SedPod accumulation rates in experiment C1 were 0.5, 1.1, 5.1, 9.3, 18.2 and 37.9 mg cm^{-2} d^{-1}, < 10% from the nominal sedimentation rate (0.5, 1, 5, 10, 20, 40 mg cm^{-2} d^{-1}). For the skeleton-only corals, all surfaces were covered with a thin veneer of sediment after 24 h, but accumulation was observed in local depressions on the foliose species, and at the intersection of branches for *A. millepora* and *P. damicornis*, and in some cases inside the corallites for *G. retiformis* and *A. millepora*. The amount of sediment settling on the surfaces increased in proportion to the starting SSCs in the tanks, and varied significantly among species (Table 4). On an areal basis, sediments accumulated on skeleton-only corals in the following manner: *A. millepora* > *M. aequituberculata* = *T. reniformis* = *P. damicornis* > *G. retiformis* = *Porites* spp. (Fig. 3). For live corals there was a significant species × sedimentation level interaction (Table 4), indicating that the relationship of sedimentation rates on corals exposed to increasing sediment deposition varied among species. Overall, the amount of sediment remaining on the live corals also increased with increasing starting SSC but, because of active removal of the sediment by the coral polyps (i.e. self-cleaning), accumulation values were lower than on the skeleton only corals. Each species differed in their ability to actively remove sediment, highlighted by differences in their self-cleaning index (Eq. (1)) where a high value indicates a greater ability to shift sediment. Average SCIs ranged from 0.3 in *A. millepora* (poor shifting ability) to as high as > 0.9 in the dome shaped *G. retiformis*.

For the percent cover of sediment on live corals, there was a significant species × sedimentation level interaction (Table 4), indicating that the relationship of percent sediment cover to increasing sediment deposition varied among coral species. This was most noticeable for *M. aequituberculata* (Fig. 3C), as the proportion of its surface covered by sediments dramatically increased as sedimentation levels increased. Among species, mean percent cover was highest for *M. aequituberculata* and lowest for *P. damicornis* (Fig. 3). For example, at the highest SedPod accumulation rate (39.7 mg cm^{-2} d^{-1}), 32% of each *M. aequituberculata* was covered, compared with only 4% for *P. damicornis*. Among the 3 general morphologies, sediment cover was highest on foliose corals, with % cover generally increasing with increasing sediment level. Remaining sediment (after 1 d) was generally trapped in mucous bundles or sheets for both foliose corals and *Porites* spp., located at the intersection of branches for *A. millepora* and *P. damicornis*, and found in some corallites for *G. retiformis*. For all coral species, apart for *M. aequituberculata* in the highest treatment, most (> 90%) of their surfaces were free of sediment (see inset graphs in in Fig. 3).

3.2. C2 (clearance rate experiment 2): effects of water flow

The accumulation rate of sediment on the SedPods varied greatly among flow rates (ANOVA: $F_{(2,12)} = 6.96$; $P = 0.0099$). Compared to the accumulation rate under still (no flow) condition (19.3 mg cm^{-2} d^{-1}), the accumulation rate was ~20% lower in low flow (2–3 cm s^{-1}) and ~50% lower at high flow (9–17 cm s^{-1}) (Fig. 4). For the skeleton-only corals, the amount of sediment accumulating on their surfaces varied significantly only among species (Table 3), and for *A. millepora* was close to 20 mg cm^{-2} d^{-1} (Fig. 4B). Water flow did not significantly influence the accumulation rate on the skeleton-only corals for any species (Table 3), although less sediment remained on *P. damicornis* exposed to high water flow than at low or no flow (Fig. 4A). For all species, the sediment accumulation rates were considerably higher on skeleton-only corals than on live corals, indicating that each species was actively removing sediment.

For live corals, there was a significant species × water flow interaction (Table 4), with patterns of sediment accumulation across flow grouping into their general coral morphologies. For the two foliose species, there was an inverse relationship between water flow and sediment accumulation, with less sediment remaining on their surfaces at the highest flow rate (Fig. 4). For the two branching species, sediment accumulation rates on their tissues were stable and largely unaffected by increasing flow rates (Fig. 4). This variation among morphologies is reflected in the SCIs, which were similar across flow rates for *A. millepora* and *P. damicornis*, and increased with increasing water flow for *M.*

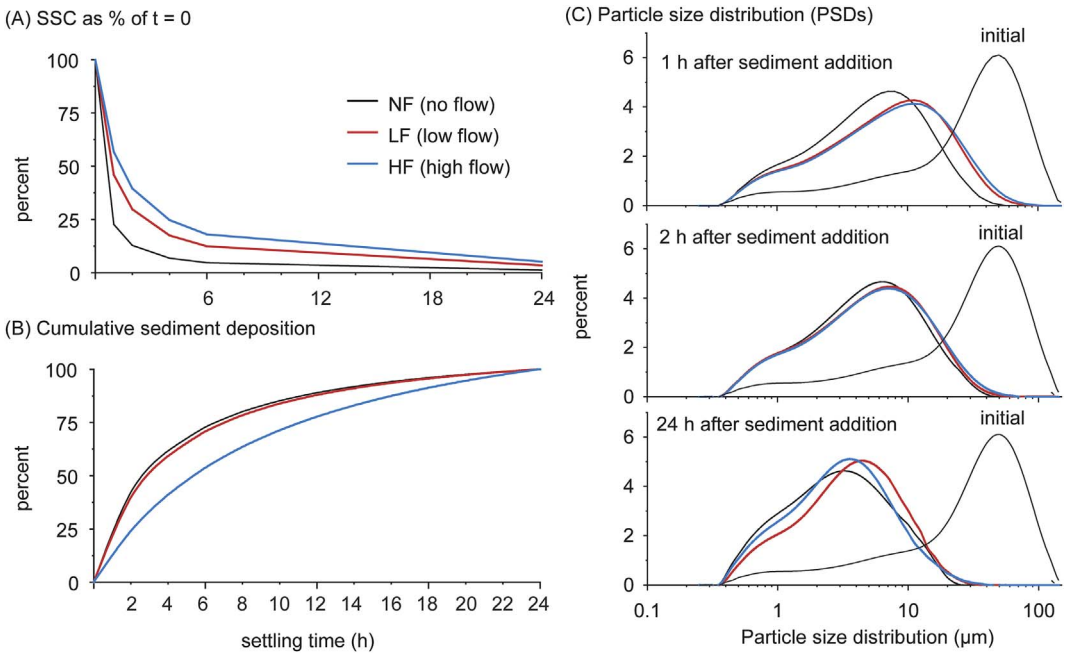


Fig. 2. Effects of water flow on (A) suspended sediment concentration and (B) sediment deposition over 24 h, and (C) particle size distributions of Davies Reef sediment 1, 2 and 24 h after sediment was added compared to its initial size range. Note Log scale on x-axis for (C).

Table 4
Summary statistical tables for each 24 h clearance rate experiments (C1–C3), showing all main and any significant interaction factors for each analysis. Crossed ANOVAs tested effects separately for the projected area sedimentation rate of live and skeleton-only corals, and percent sediment cover of live corals. Degrees of freedom (df) are the same across each row. P values highlighted in bold are significant.

	Projected area sedimentation rate				Percent sediment cover	
	Live corals		Skeleton-only corals		Live corals	
	$F_{(df)}$	P	F	P	F	P
Clearance Expt. C1						
Species	$23.84_{(5168)}$	**< 0.0001**	11.51	**< 0.0001**	56.20	**< 0.0001**
Sediment level	$76.67_{(6168)}$	**< 0.0001**	688.79	**< 0.0001**	34.18	**< 0.0001**
Species * level	$1.91_{(30,168)}$	**0.0056**	0.59	0.9555	2.17	**0.0011**
Clearance Expt. C2						
Species	$6.02_{(3,36)}$	**0.0020**	3.38	**0.0286**	14.93	**< 0.0001**
Water flow	$9.77_{(2,36)}$	**0.0004**	1.07	0.3523	9.07	**0.0006**
Species * flow	$2.96_{(6,36)}$	**0.0186**	1.19	0.3344	3.23	**0.0121**
Clearance Expt. C3						
Species	$9.21_{(3,72)}$	**< 0.0001**	23.70	**< 0.0001**	9.24	**< 0.0001**
Sediment type	$6.59_{(2,72)}$	**0.0023**	1.28	0.2838	2.13	0.1257
Sediment size	$0.20_{(1,72)}$	0.6568	54.30	**< 0.0001**	0.06	0.8029

aequituberculata and *T. reniformis*.

For percent sediment cover on live corals, there was a significant species × water flow interaction (Table 4) with percent cover decreasing greatly with increasing flow for both foliose species but varying little across flow for the two branching species (Fig. 4). Overall, percent sediment cover was highest on *M. aequituberculata*, and similar to *T. reniformis* any remaining sediment was often wrapped in mucous bundles. Mucous was generally not observed on *A. millepora* or *P. damicornis*, regardless of flow. Instead, sediment was generally located (after 1 d) at the intersection or base of branches. For all species, mean percent sediment cover was < 10% in all treatments indicating that most (> 90%) of their surfaces areas were free of sediments.

3.3. C3 (clearance rate experiment 3): effects of sediment type and size

Sediment accumulation rates on SedPods varied significantly between sediment sizes only (ANOVA: $F_{(1,24)} = 5.57$; $P = 0.0268$), being 13% lower for fine than for coarse silt. Overall, sedimentation rates on SedPods were similar among sediment types, averaging around 20 mg cm^{-2} d^{-1} (Fig. 5). For skeleton-only corals, the sediment accumulation varied significantly among species (Table 4), and was highest on *T. reniformis* and lowest on *P. damicornis* (Fig. 5). The sediment accumulation rate on the skeleton-only corals varied greatly among sediment sizes (Table 4), and was on average 20% lower for fine than coarse silt. Sediment type did not influence sediment accumulation rates on skeleton-only corals (Table 4), as rates for each coral species were similar among the different sediments types (Fig. 5). For all species, sediment accumulation rates were again substantially higher on the skeletons than on live corals, indicating active sediment rejection by corals.

For live corals, sediment accumulation rates varied significantly between species (Table 4) and was highest for *M. capricornis* (Fig. 5C), averaging 4.9 mg cm^{-2} d^{-1} across sediment types. Mean sediment accumulation rates for *T. reniformis*, *A. millepora* and *P. damicornis*

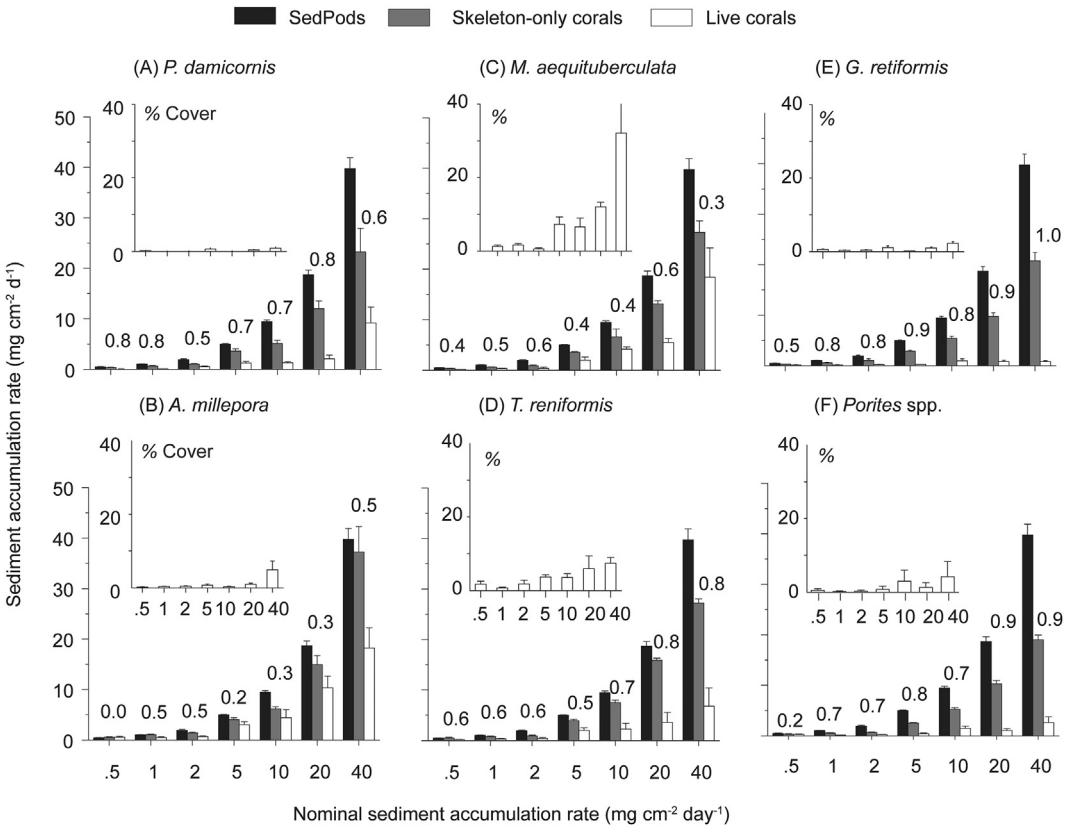


Fig. 3. Experiment C1. Mean sediment accumulation (mg cm^{-2}) on the projected area of the skeleton-only corals (grey bars) and live corals (white bars) or on flat, cement filled PVC pipes with a roughened surface (SedPods, black bars) under different sedimentation rates. The number above the bars is the self-cleaning index (SCI) ranging from 0.0 (low) to 1.0 (high). The numbers on the x-axis represent the nominal sedimentation rate (mg cm^{-2}) which was similar to the SedPod accumulation rate (black bars). Species are grouped into their general morphologies, with *A. millepora* and *P. damicornis* being branched, *M. aequituberculata* and *T. reniformis* being foliose, and *G. retiformis* and *Porites* spp. being massive shaped. Inserts show the mean % cover of sediments remaining on live corals for each species after 24 h. All error bars represent 1 standard error.

were > 50% lower — 2.4, 1.5 and 0.6 mg cm^{-2} d^{-1}, respectively. Sediment accumulation rates on live corals also varied significantly among sediment types (Table 4), being highest for Davies Reef and Middle Reef sediment and lowest for the Onslow sediment (Fig. 5). Differences in clearances rates among sediment types were most noticeable for *M. capricornis* and *T. reniformis* as SCI values showed both foliose species cleared considerably more Onslow sediment than Davies Reef and Middle Reef sediment (Fig. 5). Sediment accumulation rates

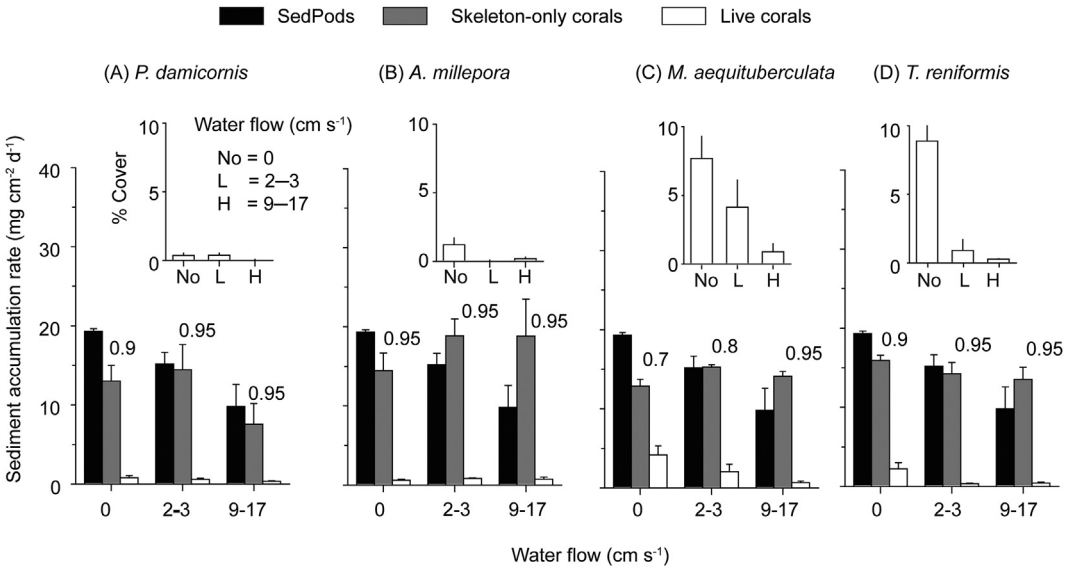


Fig. 4. Experiment C2. Mean sediment accumulation (mg cm^{-2}) on SedPods (black boxes) and the projected area of the skeleton-only corals (grey boxes) and live corals (white boxes) for each species across the flow rates of 0 cm s^{-1} (Zero, 0), 2–3 cm s^{-1} (Low, L) and 9–17 cm s^{-1} (High, H). The number above the grey-white box pair is the self-cleaning index (SCI) ranging from 0.0 (low cleaning ability) to 1.0 (high cleaning ability). Inserts show the mean % cover of sediments remaining on live corals for each species after 24 h. All error bars represent 1 standard error.

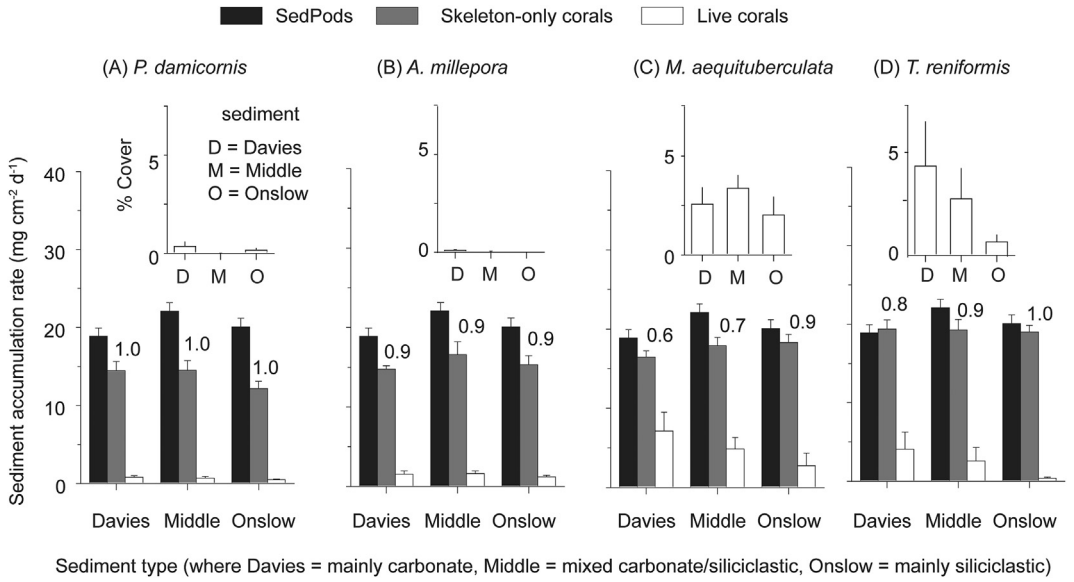


Fig. 5. Experiment C3. Mean sediment accumulation (mg cm^{-2}) of Davies Reef (D), Middle Reef (M) and Onslow (O) sediment on SedPods (black boxes) and the projected area of the skeleton-only corals (grey boxes) and live corals (white boxes) for each species. The number above the grey-white box pair is the self-cleaning index (SCI) ranging from 0.0 (low cleaning ability) to 1.0 (high cleaning ability). Inserts show the mean % cover of sediments remaining on live corals for each species after 24 h. Results for fine and coarse silts are combined to sediment type because sediment size was not significant for live corals. All error bars represent 1 standard error.

on live corals were similar between sediment sizes (Table 4).

Percent sediment cover varied significantly only among coral species (Table 4) and grouped into general morphology, with percent cover a magnitude higher on the two foliose species than on the two branching species. On average, percent cover was 2.6% for both *M. capricornis* and *T. reniformis*, and < 0.2% for *A. millepora* and *P. damicornis*. Although percent sediment cover varied among species, it was universally low across treatments with most (> 95%) of a corals surface free of sediment.

3.4. S1 (smothering experiment): effects of sediment size and smothering time

In the smothering experiment, SedPod accumulation rates were statistically similar between fine and coarse silt (P > 0.05), averaging 235 mg cm^{-2} d^{-1}, and resulted in an approximately 2 mm thick layer of sediment on the SedPods. Instantaneous PAR measured under sediment deposited in glass petri dishes placed next to SedPods, was similar between silt sizes and averaged 3.5% of initial intensity.

Sediment accumulation rate on *A. millepora* varied significantly between sediment sizes (Table 5), and was 6 × higher for corals smothered by fine silt than coarse silt (Fig. 6A). Accumulation rates for *A. millepora* also varied significantly among days-smothered, and was highest for corals smothered for 1 day regardless of sediment size. Accumulation rates on *M. capricornis* varied significantly between sediment sizes (Table 5), and was 2 × higher in corals smothered by fine silt than coarse silt (Fig. 6B), and were similar among days-smothered. Sedimentation rates for *Porites* spp. and *T. reniformis* were similar between sediment sizes and days-smothered (Table 5). For *T. reniformis*, however, there was approximately 80% less fine and coarse silt remaining after 16 d than after 1 d (Fig. 6C). Sedimentation rates varied greatly among species, being a magnitude higher for *M. capricornis* and *Porites* spp. than for *A. millepora* and *T. reniformis*. For all species there was often great variation in clearance rates among replicates within a treatment. For example, accumulation rates for *M. capricornis* smothered by fine silt for 2 days ranged from 0.3–99.1 mg cm^{-2} Replicates of *Porites* spp. smothered by coarse silt for 1 day had accumulation rates ranging from 0.6–83.7 mg cm^{-2}. Thus, some coral replicates were very effective at removing deposited sediment while neighbouring conspecifics were not.

Table 5
Summary statistics table for the smothering experiment (S1), showing individual analyses for the accumulation rate, % sediment cover, % bleaching and final dark-adapted F_v/F_m of smothered tissue per coral species. No *A. millepora* bleached or sufficiently smothered to obtain meaningful dark-adapted F_v/F_m value so analyses were not possible. ANOVAs were used (with degrees of freedom (df) the same across each row except where shown), except for some *A. millepora* and *T. reniformis* data where a zero inflated Poisson regression (z value) was more appropriate. P values highlighted in bold are significant.

		A. millepora		*M. capricornis*		*Porites* spp.		*T. reniformis*	
		F or z	P	F	P	F	P	F or z	P
Accumulation rate	Sediment size	$14.73_{(1,80)}$	**0.0002**	21.78	**< 0.0001**	0.00	0.9782	0.45	0.5049
	Days-smothered	$3.25_{(4,80)}$	**0.0160**	0.44	0.7824	0.60	0.6617	1.20	0.3165
	Size × days	$1.96_{(4,80)}$	0.1083	0.15	0.9623	0.61	0.6554	0.48	0.7474
% cover	Sediment size	− 3.06	**0.002**	$85.29_{(1,80)}$	**< 0.0001**	0.00	0.9942	− 0.53	0.597
	Days-smothered	− 2.32	**0.020**	$0.90_{(4,80)}$	0.4702	0.89	0.4746	− 1.71	0.087
	Size × days			$0.51_{(4,80)}$	0.1650	0.84	0.5013		
% bleaching	Sediment size			$22.63_{(1,80)}$	**< 0.0001**	0.03	0.8671	1.21	0.225
	Days-smothered			$16.24_{(4,80)}$	**< 0.0001**	0.43	0.7870	− 1.08	0.279
	Size × days			$6.30_{(4,80)}$	**0.0002**	0.92	0.4560		
Final dark-adapted F_v/F_m	Sediment size			$27.83_{(1,76)}$	**0.0001**	$14.95_{(1,57)}$	**0.0003**	$12.53_{(1,19)}$	**0.0022**
	Days-smothered			$1.97_{(4,76)}$	0.1085	$2.92_{(4,57)}$	**0.0300**		
	Size × days			$1.61_{(4,76)}$	0.1812	$0.80_{(4,57)}$	0.5321		

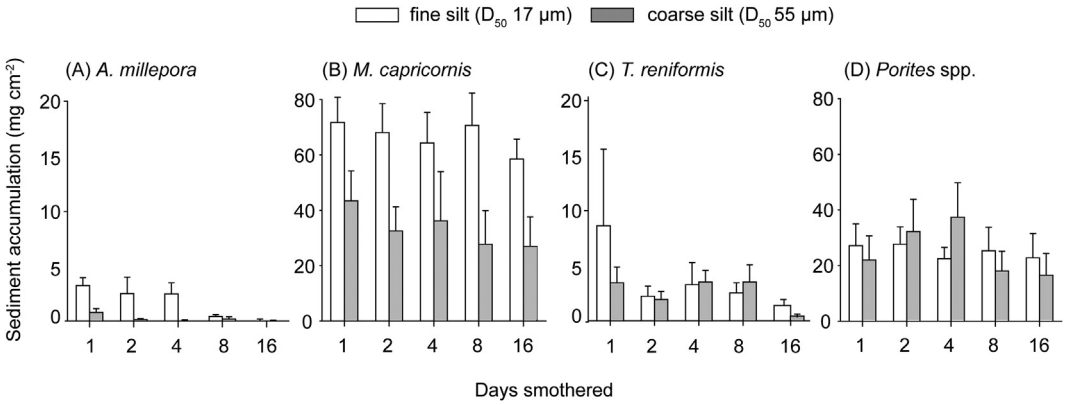


Fig. 6. Experiment S1. Mean weight of fine (white bar) and coarse silt (grey bar) remaining on live *A. millepora*, *M. capricornis*, *T. reniformis* and *Porites* spp. after 1, 2, 4, 8 or 16 days. Note that the y-axis scale varies among species because their sedimentation rates varied greatly. Error bars represent 1 standard error. For all species, patterns of percent sediment cover mirrored patterns for sedimentation rates (Table 5), so results are not graphically presented. For *A. millepora*, percent sediment cover varied significantly between sediment sizes, and was highest for fine silt, and among days, was highest for corals smothered for 1 day. Although percent cover on *A. millepora* varied among treatments, mean values were all < 1%. For *M. capricornis*, percent sediment cover was highest for corals exposed to fine silt, averaging 56%, compared with 16% cover for coarse silt. Percent sediment cover for *Porites* spp. and *T. reniformis* were similar between sediment sizes and days smothered, averaging 21% and 2% respectively. There was a strong and positive relationship between sedimentation rate and percent sediment cover for all coral species ($P < 0.0001$).

Immediately after sediment was removed, bleaching was most common on *M. capricornis* and *Porites* spp., uncommon on *T. reniformis* and not observed in *A. millepora*. For *M. capricornis* there was a significant sediment size × days-smothered interaction (Table 5), with corals smothered for ≥ 4 d by fine silt having about 3 × as much bleaching as recorded for coarse silt. A few of these replicates had some dead tissue after 6 weeks free of sediment. Although, final colour of smothered *M. capricornis* tissue after the 6 week recovery period was generally lighter for corals smothered for ≥ 4 d than ≤ 2 d, tissue was returning to its natural dark brown pigmentation. For *Porites* spp. and *T. reniformis*, the amount of bleaching was similar between sediment sizes and days-smothered (Table 5) and final colour was similar among treatments.

Initial dark-adapted F_v/F_m was, on average, 0.68 for *A. millepora*, 0.64 for *M. capricornis*, 0.61 for *Porites* spp., and 0.64 for *T. reniformis* and decreased by < 10% over the experiment for non-smothered tissue. Dark-adapted F_v/F_m of smothered tissue immediately after sediment was removed were generally lower the longer fine and coarse silt remained on corals, particularly for *M. capricornis* and *Porites* spp. (Fig. 7). Dark-adapted F_v/F_m for coral tissue smothered for ≤ 8 d generally returned to control or normal levels within 2 weeks while tissue smothered for 16 d took longer to fully recover. After 6 weeks of recovery, however, dark-adapted F_v/F_m values varied significantly among days-smothered for *Porites* spp. only (Table 5). Sediment size also affected the final dark-adapted F_v/F_m values (Table 5), and was 12–15% lower for *M. capricornis*, *Porites* spp. and *T. reniformis* smothered by fine than coarse silt. *A. millepora* were not covered in enough sediment to obtain meaningful dark-adapted F_v/F_m values.

4. Discussion

The sediment rejection ability of corals is a dynamic interaction between active (energy requiring) removal processes, coupled to passive process associated with gravitational forces assisted by water flow. In this study sediment accumulation was compared between live corals, enamel covered-skeletons and SedPods (Field et al., 2012). Deposition was expressed on a mass per unit area basis normalized to the projected (2-dimensional) planar total surface area, and also percent cover of the surface area. For the skeleton-only corals, the accumulation rate in static conditions (no water flow) was typically less than on the flat, horizontal surface of the SedPods. This is intuitive, as many of the coral surfaces were subhorizontal and sediments tended to saltate across and to not accumulate on the inclined, sloping surfaces such as the edges of hemispherical, dome shaped corals (e.g. *G. retiformis*). However, counterintuitively, the skeletons of the branching corals, with their many inclined and angular surfaces, accumulated sediments at equivalent levels to the other growth forms. One reason is that on a smaller scale, the *A. millepora* branches are composed of hundreds of scale-like radial corallites that are nevertheless orientated horizontally to maximize capture of downwelling light. The colonies present a large horizontal planar surface area for sediments to accumulate, despite their attachment to in some cases steeply angled branches. For *A. millepora,* the scale like corallites also acted as cups, capturing sediments.

For the live corals the ratio of sediment accumulation on live tissue versus the skeleton, is indicative of the self-cleaning capability of the coral and highlighted significant variation between species and morphology. Despite the same or similar inherent rates of sediment accumulation noted above, the branching species, *P damicornis* and *A. millepora* were very capable of self-cleaning and removing sediments compared to the foliose and massive morphologies. At the highest SedPod accumulation rate tested (235 mg cm^{-2} d^{-1}) the amount of sediment accumulation on the branching *A. millepora* was ~3 × less than on the foliose *T. reniformis*, 8 × less than on the massive *Porites* spp. and 22 × less than on the foliose *M. capricornis*.

Adjusting the degree of water movement led to a consistent reduction in the amount of sediment accumulating on live foliose corals. Compared to static conditions the amount of sediment settling under a flow of 9–17 cm s^{-1} was ~5 × lower on live *Montipora* and *Turbinaria*, and a 10–30 × lower based on percent cover. The amount of sediment depositing on the enamel-covered skeletons did not show a similar, consistent pattern with higher flow. This suggests an interaction between flow and active sediment rejection i.e. elevated flow rates assist the corals in their active sediment shedding.

Observations during the experiments showed that sediment movement was invariably downslope but frequently became trapped in dips, depressions and concave areas (i.e. 'local minima'). There were some areas where sediments tended to accumulate on the branching species, usually at junctions of the branches, but these were much less common than the foliose species. Although different coral species have been categorized and ranked according to their sediment shifting ability, it is not easy to discern whether this is an inherent physiological trait of a species, as opposed to being simply a product of different morphologies having different numbers of low points where sediments can accumulate. While the branching morphology of *A. millepora*, does not inherently result in less sediment accumulation, when combined with

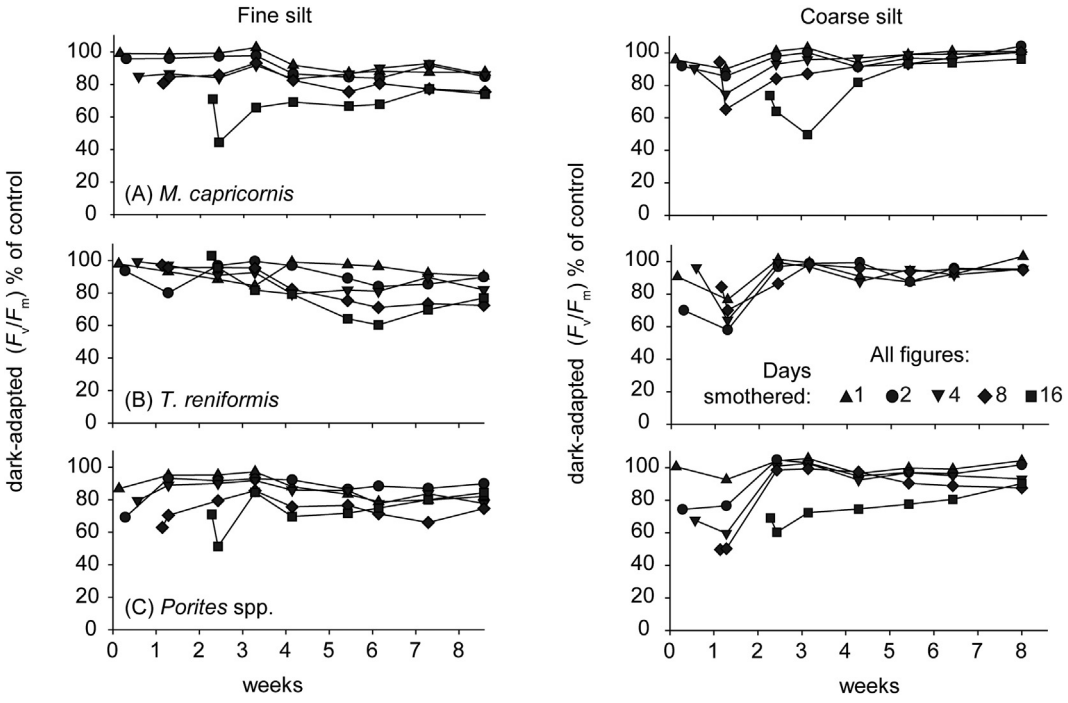


Fig. 7. Experiment S1. Mean maximum quantum yields (dark adapted F_v/F_m) over time for tissue of *M. capricornis*, *T. reniformis* and *Porites* spp. smothered by fine and coarse silt. Dark adapted F_v/F_m for each smothered-day treatment is standardised to control (non-smothered) corals per species. No data is shown for coarse silt × day 16 *T. reniformis* because sediment was mostly cleared from corals making it impossible to obtain relevant F_v/F_m values.

active process such as muco-ciliary transport and the lack of local minima, sediments could easily be moved and ultimately shed from the colony under gravitational forces and assisted by flow.

Several studies have examined sediment accumulation rates in response to fine and coarse sediments (Lasker, 1980; Stafford-Smith and Ormond, 1992); although, the terms have been used in the context of sand-sized particles (62–250 μm and 500–1000 μm respectively). On a volume basis, sands are orders of magnitude larger than the silts and clay sized particles typically found in sediment plumes (Bainbridge et al., 2012; Jones et al., 2016). Using fine silt (D_{50}, 9–17 μm) and coarse silt (D_{50}, 53–58 μm) and under a 20 mg cm^{-2} d^{-1} SedPod accumulation rate, there was no significant difference in the sediment rejection ability for live corals. Under an order of magnitude higher SedPod accumulation rate (235 mg cm^{-2} d^{-1}), coarse silt was removed on average 3 × more efficiently than fine silt over the 16 d period. It has been suggested that some species use different mechanisms for moving different sized sediments i.e. tentacle movement for coarse sand and muco-ciliary transport for finer particles (Stafford-Smith and Ormond, 1992). However, the differences between coarse and fine silt could also partly reflect differences in the actual number of sediment particles i.e. less particles in the coarser sediment, as opposed to different self-cleaning techniques or differences in the ability to move different particle sizes.

Consistently less siliciclastic (Onslow) sediments was found on the live coral surfaces than either the mixed carbonate/siliciclastic sediments from Middle Reef or the carbonate sediment from Davies Reef. The SEM images showed the Onslow sediments were more angular, as compared to the rounded carbonate grains. This would lessen their ability to be moved over the surface which was opposite to the pattern observed. Similarly, there was no difference in the accumulation rate on the SedPods or the skeletons according to sediment types and these observations suggest the observed pattern was related to preferential movement of the siliciclastic sediments i.e. to active processes. For the foliose species, *M. aequituberculata* and *T. reniformis*, this was 3 × and 10 × faster respectively. The particle size distributions and trace metal concentrations were similar between sediment types and unlikely to have been the cause of this difference. The total organic carbon (TOC) content of the Onslow sediments was the lowest of the 3 sediment types, and differences in coral clearance rates has been suggested to vary according to organic content, with organic-rich coastal silt harder to remove than organic-poor off-shore silt (Weber et al., 2006; Piniak, 2007).

In the longer term smothering experiment, a very high deposition rate of 235 mg cm^{-2} d^{-1} resulted in < ~2% of the planar area of *A. millepora* and *T. mesenterina* covered by sediment. For *M. aequituberculata* and the *Porites* spp. fragments, large expanses of tissue (> 20%) were clearly smothered with sediment in a layer several mms deep. A reduction in chlorophyll fluorescence yields (dark-adapted F_v/F_m) occurred in the smothered tissues and this preceded tissues discolouration (bleaching) within ≥ 4 d. There was no mortality associated with this bleaching, and in the post exposure recovery phase most corals regained their pigmentation without lesion formation. Comparable studies with low organic content sediments have shown a similar time course (Weber et al., 2006; Weber et al., 2012). The bleaching could have been caused by restricted solute exchange but also by reduced light transmission (> 96% reduction in light). Weber et al. (2006) measured very low levels of relative light transmission through multiple types of silt-sized sediment (< 62 μm and with a D_{50} of < 20 μm) in contrast to Riegl and Branch (1995) who measured an order of magnitude higher relative transmission of light (70% under a 200 mg cm^{-2} layer of sediment). Riegl and Branch (1995) used sands (> 125 μm and with a D_{50} of 253 μm) in their study and light transmission is likely to be much higher than the silts and clays which typify sediment plumes. The lack of any mortality associated with smothering in this study is consistent with experiments of Weber et al. (2006) who showed fine sediments poor in organic matter did not cause damage while sediments rich in organic matter caused mortality within 1–2 d of smothering.

4.1. Risks associated with sedimentation

One of the most significant problems in understanding the risk of

sediment deposition on corals is quantifying the normal range of sedimentation for different reef settings. A growing body of evidence now suggest that sediment traps, which have routinely been used to estimate sedimentation rates on reefs, could be overestimating rates by perhaps over an order of magnitude (McClanahan and Obura, 1997; Browne et al., 2012; Field et al., 2012; Jones et al., 2016; Whinney et al., 2017). The recent development of an autonomous sediment deposition sensor, which has the capability of estimate mg cm^{-2} d^{-1} deposition rates over a few hours, has proved useful in this context (Whinney et al., 2017). The sensor, which gives similar values to SedPods in laboratory-based tests, was deployed within a semi-enclosed bay in highly turbid, nearshore environment in the inner-shelf zone of the central Great Barrier Reef (Larcombe et al., 1995; Larcombe et al., 2001; Smithers and Larcombe, 2003). The deployment included periods of exceptionally high turbidity (SSCs > 100 mg L^{-1}) and resulted in a maximum sedimentation rate of ~50 mg cm^{-2} d^{-1}, and an overall average deposition rate of 19 mg cm^{-2} d^{-1} (and median value of 11 mg cm^{-2} d^{-1}) over a 40 d period. For the first half of the deployment, where SSCs ranged from < 1–28 mg L^{-1} and which more closely typifies the highly turbid study area (Macdonald et al., 2013), deposition rate averaged only 8 ± 5 mg cm^{-2} d^{-1}. Browne et al., 2012 reported very similar results from a year-long study at the same location using a different technique (shallow trays).

Sediment deposition can also be expressed in terms of thickness of accumulated sediment and is a useful construct for conceptualizing deposition. Assuming a wet bulk density of 1050 kg m^3 for freshly settled sediments (Van Rijn, 1990), a sedimentation rate of 8 mg cm^{-2} d^{-1} would create a sediment veneer only 80 μm thick (see also SKM, 2013). Using similar calculations for river plumes, Orpin et al. (1999) noted that if all the sediments from a stratified (1–2.5 m thick) low salinity sediment plume (of 3–10 mg L^{-1} SSCs) settled on the seabed, it would only create a sediment deposit of 10 μm thick. The results from this study show that most species tested, which were collected from clear-water mid-shelf reefs of the GBR, were capable under slight flow (< 3 cm s^{-1}), of removing all sediment up to 20 mg cm^{-2} d^{-1} leaving only slight residual deposits typically less than a few % of the surface area. The massive morphologies could do the same up to 40 mg cm^{-2} d^{-1}. The branching species *A. millepora* managed to clear a sedimentation rate (under static conditions) of up to 235 mg cm^{-2} d^{-1}, or ~30 × higher than the typical deposition rate in a naturally highly turbid and marginal nearshore environment (Whinney et al., 2017). Smothering of corals in mms of sediment by natural resuspension or river plumes seems unlikely based on these numbers.

Smothering of corals can occur during dredging programs and is one of the key-cause effect pathways causing mortality to adult and recently settled corals at sites close to excavation activities (Jones et al., 2016). There are many examples of this effect (see images in Bak, 1978; Foster et al., 2010; Jones et al., 2015a; Jones et al., 2016) and also Fig. 1 (for examples of sediment smothering from dredging project in similar species and growth forms used in this study). Why this occurs is because dredging activities can generate very high turbidity levels, i.e. the intensity, duration and frequency of the turbidity events can be 10-, 5- and 3-fold respectively higher natural resuspension (at sites < 500 m from dredging). Dredging also usually occurs in low energy water columns, where the hydrodynamics are insufficient to keep the sediments in suspension (Jones et al., 2016). As shown in these experiments, flow and turbulence also act in concert with active and passive processes to assist sediment shedding from corals. Under low flow, high SSCs and high settling velocities sediment accumulation rates are likely to exceed anything corals have previously experienced. Once smothering occurs sediments will build up sediment covered. Sediment deposition rates have not yet been measured near dredging programs, and understanding how these vary temporally and spatially is critical for impact prediction purposes and understanding the potential scale of likely effects. The studies described here primarily involved very short term sediment exposures and were focussed on sediment rejection abilities, and longer-term, experiments involving repetitive smothering are also needed.

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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.2017.08.036.

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