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Climate change doubles sedimentation-induced coral recruit mortality

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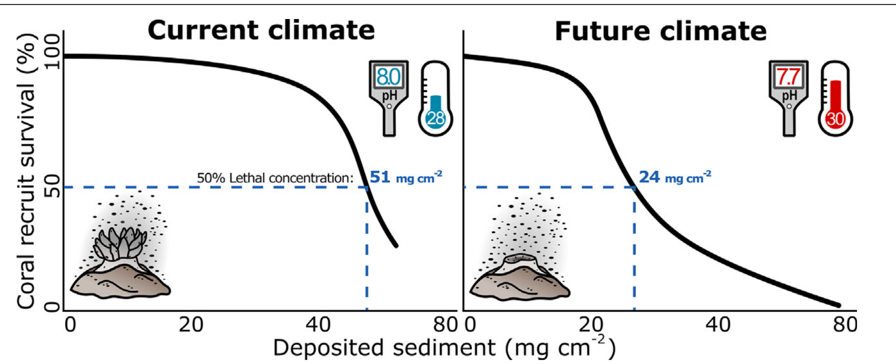
HIGHLIGHTS

- Recruits grown under future climate are twice as sensitive to sediment deposition.
- Older recruits survived higher sediment depositions events.
- Only recruits grown in current climate survived the highest realistic sedimentation.

GRAPHICAL ABSTRACT



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ABSTRACT

Coral reef replenishment is threatened by global climate change and local water-quality degradation, including smothering of coral recruits by sediments generated by anthropogenic activities. Here we show that the ability of *Acropora millepora* recruits to remove sediments diminishes under future climate conditions, leading to increased mortality. Recruits raised under future climate scenarios for fourteen weeks (highest treatment: +1.2 °C, pCO_2: 950 ppm) showed twofold higher mortality following repeated sediment deposition (50% lethal sediment concentration LC_{50}: 14–24 mg cm^{-2}) compared to recruits raised under current climate conditions (LC_{50}: 37–51 mg cm^{-2}), depending on recruit age at the time of sedimentation. Older and larger recruits were more resistant to sedimentation and only ten-week-old recruits grown under current climate conditions survived sediment loads possible during dredging operations. This demonstrates that water-quality guidelines for managing sediment concentrations will need to be climate-adjusted to protect future coral recruitment.

1. Introduction

The future of coral reefs is under threat from multiple pressures, including ocean acidification, rising water temperatures and mass bleaching events which are becoming more severe and frequent as the climate changes (Hoegh-Guldberg et al., 2017; Hughes et al., 2018; Lough et al., 2018). These global pressures, in combination with local water-quality degradation (i.e., sediment and nutrient runoff), are

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primary causes of the 'coral crisis' (Bellwood et al., 2004), and the recovery and replenishment of disturbed coral populations is critically dependent on successful coral recruitment (Hughes et al., 2000; Randall et al., 2020). To predict the resilience of coral reefs in future climate scenarios, experimental and monitoring studies often focus on ocean warming, ocean acidification, or their interaction (Foster et al., 2015; Hoegh-Guldberg et al., 2007). However, with over 39% of the human population living within 100 km of the ocean (Cesar et al., 2003), coastal development increasingly contributes to declining water quality in near-shore reef systems (Doney et al., 2012; McCulloch et al., 2003). Therefore, the effects of water-quality degradation and climate change must be investigated jointly for accurate predictions of future coral reef resilience (Doney et al., 2012; Uthicke et al., 2016). Cumulative pressures of poor water quality with ocean warming and/or ocean acidification can have more severe effects (either additive or synergistic) on corals than individual pressures alone (Ban et al., 2014; Uthicke et al., 2016). At present, however, most environmental management regulations are only directly applicable to the current state of the environment (Bruno et al., 2018), and consequently, strategies for sustainable management of reef ecosystems will require water-quality guidelines to be adjusted to account for future climate scenarios (Bruno et al., 2018; Doney et al., 2012; Duarte et al., 2020; Uthicke et al., 2016).

A primary cause of poor water quality is the increasing release of sediment from human activities (i.e., dredging operations, river runoff from agriculture and coastal development) (Erftemeijer et al., 2012; GBRMPA, 2018; Jones et al., 2016; McCulloch et al., 2003). Sediments harm marine organisms, including corals, through a variety of pathways depending on whether the particles are suspended (e.g., light attenuation reducing autotrophic production) or deposited (e.g., smothering) (Anthony and Fabricius, 2000; Jones et al., 2016). In the coral life cycle, post-settlement survival represents a critical bottleneck for the replenishment of reefs (Randall et al., 2020), since coral recruits are particularly sensitive to being smothered by deposited sediments due to their small size (<1 mm) (Jones et al., 2015b; Moeller et al., 2017). A review of coral heat-stress experiments found that only about 1% of the studies published within the last thirty years investigated effects on early coral life-stages in general, and on coral recruits specifically (McLachlan et al., 2020), highlighting the need of more studies focusing on this vulnerable life-stage. Although additive and synergistic effects of temperature-sediment interactions have been identified for coral recruits (Fourney and Figueiredo, 2017), the combined effects of sedimentation on coral recruits raised under future climate scenarios (ocean warming and ocean acidification) are unknown. Here, we quantified the interactive impacts of climate and sediment stress on coral recruit survival, investigated potential additive, sub-additive and synergistic responses, and tested whether recruit age, size and capacity to remove sediments are mechanisms that promote sedimentation resistance.

2. Materials and methods

Recruits of *Acropora millepora*, a branching coral species that is abundant in shallow habitats on the Great Barrier Reef, were raised for 4 months in 'current' as well as realistic 'medium' and 'high' climate scenarios (ocean warming and ocean acidification combined), and were exposed to six environmentally relevant sediment deposition loads typical of flood plumes and dredging operations near inshore reefs (Table 1). The exposure to the sediment loads occurred at different recruit ages: (Experiment 1) five- and ten-weeks following larvae settlement, or (Experiment 2) after ten weeks only. One-hour following sediment exposures, photographs were taken to quantify the sediment removal capability. After a four-week recovery phase, survival and size responses were documented photographically (Fig. 1 a). These experiments were carried out at the National Sea Simulator located at the Australian Institute of Marine Science, Townsville, between November 2017 and February 2018.

Table 1
Climate and sediment treatments. The applied current temperature was based on the historic daily mean reef temperature at Davies Reef between 1991 and 2012 (Australian Institute of Marine Science, 2020) which increased from 26.2 to 28.7 °C between November and February. In the high climate treatment, the increased temperature was adjusted to reach 8 degree heating weeks by the end of the experiment (Hughes et al., 2017a; Kayanne, 2017). $pCO_2 \pm$ SE was based on monitoring data (Uthicke et al., 2014) and on RCP8.5 (IPCC, 2014). Sediment loads resembled conditions in calm inshore reefs (Jones et al., 2016; Tebbett et al., 2017; Wolanski et al., 2005), as well as near river runoff (Lewis et al., 2018; Wolanski et al., 2008) and dredging operations (Jones et al., 2016; Nichols et al., 1990).

Climate	Temp (°C)	pCO_2 (ppm)	Sediment (mg cm^{-2})					
			Calm inshore reef			River runoff		Dredging
Current	26.2–28.7	410 ± 50	0	5	10	20	40	80
Medium	Current + 0.6	680 ± 50	0	5	10	20	40	80
High	Current + 1.2	940 ± 50	0	5	10	20	40	80

2.1. Spawning and larvae rearing

In November 2017, gravid *A. millepora* colonies were collected from 2 to 6 m water depth near Falcon Island in the central Great Barrier Reef (18°45′ 57.0″S 146°31′ 57.0″E) and transported to the National Sea Simulator. After collection, the coral colonies were maintained in outdoor flow-through aquaria in unfiltered seawater under ~50% shading. Egg and sperm bundles from eight colonies were collected and cross-fertilized as per Guest et al. (2010). After two hours (>90% of cleavage), the embryos were rinsed twice in 50 L filtered seawater (0.04 μm) and transferred into 440 L flow-through larval rearing aquaria with circular water flow (Guest et al., 2010). The embryos were left to develop for 18 h after which gentle aeration was introduced.

2.2. Coral larvae settlement

Disc-shaped experimental substrates (2 cm diameter × 1 cm height) for recruit exposures were manufactured from polyvinyl chloride (PVC) and sanded on the upper surface to accelerate biofilm formation (Lee et al., 2009; Ricardo et al., 2017). In order to initiate settlement and metamorphosis of *A. millepora* larvae, the discs were conditioned for two months in an indoor flow-through aquarium (daily light integral: 4.0 mol m^{-2} d^{-1}, photosynthetic active radiation: 100 μmol photons m^{-2} s^{-1}) together with the crustose coralline algae *Porolithon onkodes* and *Titanoderma prototypum*, which are known coral settlement inducers (Harrington et al., 2004; Heyward and Negri, 1999).

Following coral spawning, daily assays were performed to assess when the coral larvae were competent to settle. In each well of a six-well tissue culture plate ($n = 3$), settlement of ten larvae was tested in 10 mL filtered seawater (0.04 μm) along with one ~9 mm^2 chip of live *P. onkodes* (Harrington et al., 2004). Once the assays indicated a settlement response of at least 90% (7 days after spawning), all coral larvae were presented with the conditioned discs in static tanks (120 discs per 50 L at approximately 2 larvae mL^{-1}). From these discs, 576 discs were selected that had an average of six uniformly settled recruits across the disc surface (i.e., no settlement close to other recruits or the disc rim). The selected discs were haphazardly distributed among 12 filtered seawater-filled (0.04 μm) climate-controlled 50 L indoor flow-through aquaria (48 discs per aquarium, 24 discs per experiment). One week after settlement, the coral recruits were inoculated with cultured Symbiodiniaceae (Fig. 1 a) as per Chakravarti et al. (2019) [*Cladocopium goreaui*, ID: SCF055-01.10, formerly known as *Symbiodinium clade* C1 (LaJeunesse et al., 2018), isolated from *Acropora tenuis* from Nelly Bay, Magnetic Island].

2.3. Climate treatments

Three climate scenarios were tested in this study: referred to as 'current', 'medium' and 'high' (Table 1). Each scenario was based on a

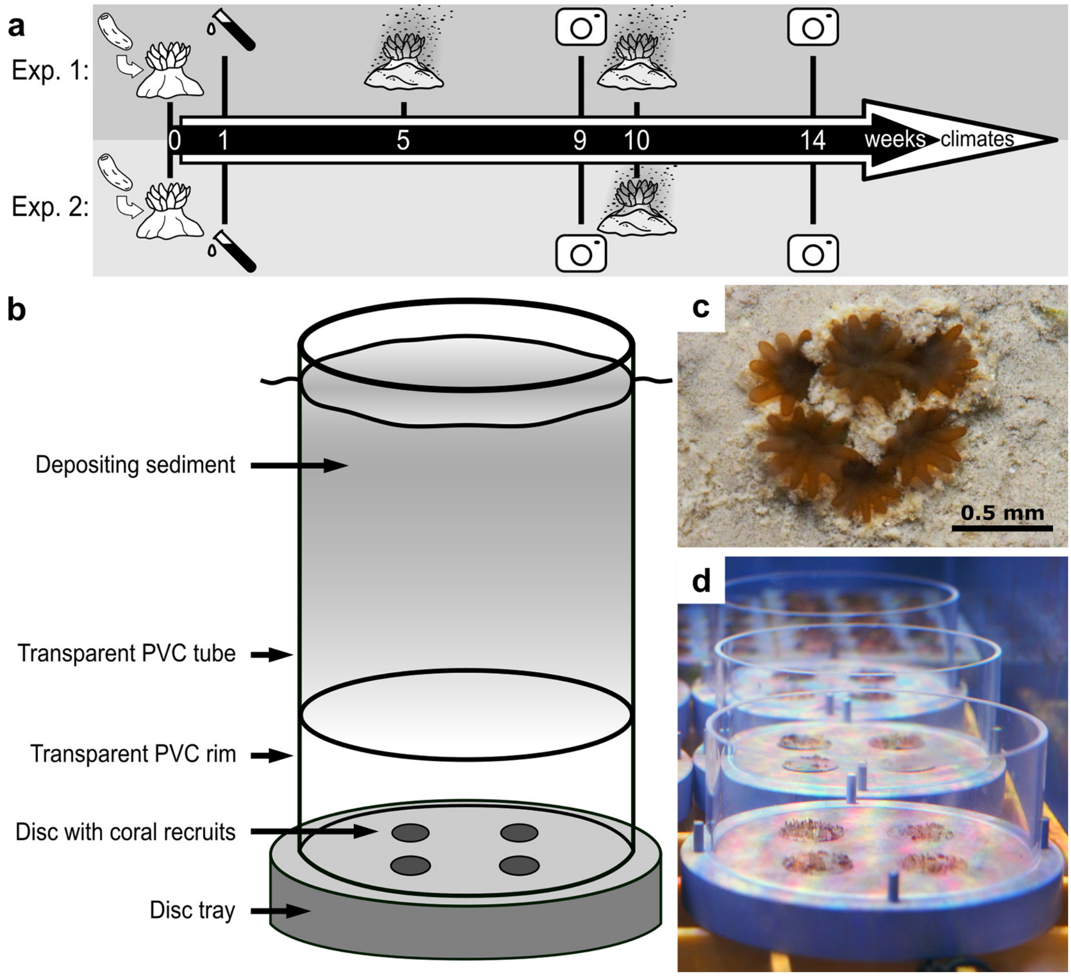

Fig. 1. Experiment timeline and setup. a: Timeline for Experiment 1 (top) and Experiment 2 (bottom), illustrating the settlement of *Acropora millepora* larvae (represented by a larvae and coral recruit in week 0) and when the recruits were inoculated with cultured Symbiodiniaceae (test tube in week 1), when they were smothered for three days with six environmentally relevant sediment loads (smothered recruit in week five and ten), and when responses (survival and polyp numbers) were photographically captured (camera in week nine and fourteen). The sediment removal capability was recorded one hour after every sediment deposition. Exposure to three climate scenarios (4 replicate tanks per climate) occurred just after settlement until the end of the study. b: Setup during sediment application with a removable transparent PVC tube guiding the sediment from the water surface to the discs with coral recruits. c: Ten-week-old coral recruit 1 h after being covered by 40 mg cm^{-2} sediment. d: Four discs with coral recruits placed respectively in disc trays. Sediment deposited on the entire surface surrounded by a transparent PVC rim.

different combination of temperature and carbon dioxide partial pressure (pCO_2). The temperature of the current day climate scenario was based on the historic daily mean reef temperature at a typical mid-shelf coral reef in the central Great Barrier Reef (Davies Reef, 18°49′ 52.7″S 147°38′ 07.8″E). Temperature data (4 m water depth) from 1991 to 2012 (Australian Institute of Marine Science, 2020) were used to calculate the historic average water temperature for every day of the experimental period. At the typical spawning time of *A. millepora* in November (Harrison, 2011), the calculated historic daily average temperature was 26.2 °C, which increased to the annual maximum of 28.7 °C at the end of the experiment in February. The mean pCO_2 used for the current climate treatment (450 ± 50 ppm) was based on mean sea surface pCO_2 monitoring data of inshore reefs (Uthicke et al., 2014).

The temperature of the medium and high climate scenarios were based on degree heating weeks (DHW), a measure for accumulated heat stress at a given location and time (Kayanne, 2017). In the Great Barrier Reef, elevated temperatures over extended periods demonstrated that more than 8 DHW cause extensive coral mortality (70–>90%) (Hughes et al., 2017a; Kayanne, 2017). To generate a maximum of 8 DHW by the end of this experiment, a temperature of 1.2 °C above the calculated historic daily mean reef temperature was selected for the high climate treatment. For the medium climate treatment, a temperature increase of 0.6 °C, half that of the high climate treatment, was applied. Given the water temperature of the Great Barrier Reef already increased by ~0.9 °C since pre-industrial conditions (Lough et al., 2018), our temperature treatments roughly correspond to the +1.5 and +2.0 °C targets of the IPCC Paris Agreement (IPCC, 2014). The pCO_2 concentrations used for the medium and high climate scenarios were based on the representative concentration pathway model RCP8.5 that predicts pCO_2 levels of 680 ppm and 940 ppm for the years 2050 and 2100 (IPCC, 2014; Meinshausen et al., 2011). Immediately after settled recruits were transferred into the climate-controlled aquaria, the climate conditions were ramped over a period of one week to reach these three climate scenarios (Table 1).

The three climate scenarios were created by manipulating the temperature and pCO_2 of filtered seawater (0.04 μm) and then distributing it between four 50 L replica aquaria for each of the three climate scenarios (see supplementary material for details). Temperature and pCO_2 sensor data were automatically monitored and logged every 10 min by a SIMATIC WinCC SCADA system (Siemens AG, Munich, Germany) (Fig. S1). Before and after the sediment deposition experiments, water samples were collected and preserved with mercury chloride for the determination of total alkalinity (TA) and dissolved inorganic carbon (DIC) using a Vindta 3C (Marianda, Kiel, Germany). The pCO_2 and saturation state of aragonite (Ω_{Arag}) were calculated from the pH, TA, salinity and temperature data with the R package Seacarb version 3.2.13 (Gattuso et al., 2020) (Table S1).

A diurnal light cycle was applied (12:12 h day and night) including a three-hour linear ramping time after sunrise and before sunset using one Hydra FiftyTwo HD LED (Aquaria Illumination, Allentown, USA) per aquarium. This resulted in a daily light integral of 4 mol m^{-2} d^{-1} and a maximum photosynthetic active radiation of 124 μmol photons m^{-2} s^{-1} which together with a calibrated light spectrum (JAZ spectrometer, Ocean Insight, Florida, USA) resembled conditions found at 4 m water depth in a typical inshore reef according to measurements at Middle Reef, Magnetic Island. Coral recruits were fed daily with 10 mL newly hatched *Artemia* sp. per 50 L aquarium.

2.4. Sediment treatments

The effects of sediment deposition on coral recruits developed under three climate scenarios were tested with two simulated sediment deposition events. Based on monitoring data from nearshore environments, six sedimentation intensities ranging from 0 to 80 mg cm^{-2} were used, as this spectrum represents values observed at calm inshore reefs (Jones et al., 2016; Tebbett et al., 2017; Wolanski et al., 2005), following wet-season river runoff (Lewis et al., 2018; Wolanski et al., 2008) and near dredging operations (Jones et al., 2016; Nichols et al., 1990) (Table 1). Coarse silt sediment (median particle size: 53–75 μm) was used for the simulated depositions, which equates to the most common particle size (~60 μm) in close proximity (125 to 200 m) to dredging operations (Jones et al., 2016). The mixed carbonate-siliciclastic sediment was collected (Middle Reef, 19°11′ 43.3″S 146°48′ 49.3″E), dried and sieved by Duckworth et al. (2017) (total organic content of the sediment mixture: 0.35% and complete sediment characteristics in Table 2 of their study). The dried sediment and unfiltered seawater were used to create a sediment slurry, which was conditioned for two days in an aerated aquarium prior to the exposure to the coral recruits.

Sediment depositions were simulated by enclosing four discs with settled recruits per sediment treatment with a transparent PVC tube (∅ = 96 mm) (Fig. 1 b). Five sediment slurries and one control were created using the conditioned sediment mixture, filtered seawater (0.04 μm) and a nephelometer (Turbimax CUS31, Endress & Hauser, Reinach, Switzerland). The six sediment deposition treatments were generated by respectively pouring 100 mL of these well-mixed slurries into the transparent PVC tubes, and allowing the sediment to settle for 12 h (Table 1, Fig. 1 c & d). After this time elapsed, the upper part of the PVC tubes were removed to allow water circulation, with a 35 mm tall transparent PVC rim left around the discs (≥10 mm distance to discs) so that the sediment would not be immediately carried away by the current (Fig. 1 d). Based on preliminary experiments, three days following the initial sediment deposition, the deposition event was stopped by removing the transparent PVC rims and carefully collecting the sediment remaining on the discs by individually placing them in glass jars and gently rinsing the sediment off with filtered seawater. The cleaned discs were then placed back into the aquaria. The collected sediment of every disc was filtered through pre-weighed 0.4 μm polycarbonate filters, dried at 60 °C for ≥24 h, and weighed (±0.0025 mg, BM-20 Micro Analytical Balance, A&D Ltd., Tokyo, Japan) to validate the amount of deposited sediment (Table S2).

2.5. Sampling

The capability of recruits to remove sediment was documented by photography one hour after the sediment exposure (STYLUS TG-3 Tough, Olympus, Tokyo, Japan). Coral survival and size (number of polyps) were documented with high resolution images (Nikon D810 with Nikon AF-S 60 mm f/2.8G ED macro lens, Tokyo, Japan with four Ikelite DS161 strobes, Indianapolis, USA) four weeks after every sedimentation event. During every photo-documentation, the orientation of the discs relative to the camera was kept constant, allowing accurate recording of recruit sediment removal capabilities, recruit survival and number of polyps (as a proxy for recruit size) using the software ImageJ Fiji version 1.52u (Schindelin et al., 2012).

Coral recruits were excluded from the dataset if they fused with neighboring recruits during settlement or throughout the experiment. Recruits were classified as alive when they featured at least one living polyp. For the recruit size and sediment removal analyses, only live recruits were investigated. Due to mortality following the first sediment exposure at week five in Experiment 1, 20% less recruits were included in the recruit size and sediment removal analyses four weeks after the second sediment exposure (week fourteen in Experiment 1). The sediment load of 80 mg cm^{-2} was also excluded from analyses of recruit size because less than 3 recruits were alive in each of the treatment groups at this sediment load after the first sediment deposition. Overall, the fate of 2582 *A. millepora* recruits was recorded over the duration of the experiment ($n = 43$ to 118 per sediment-climate treatment in each experiment).

2.6. Calculations

Statistical analyses were performed using R version 4.0.2 (R Core Team, 2020). Initial data exploration was conducted following the protocols in Zuur et al. (2010) and subsets of the data were created based on experiment type and recruit age. The subsets were separately analyzed using Generalized Linear Mixed-Effects Models (GLMMs) with the package glmmTMB (version 1.0.1) (Brooks et al., 2017). For the survivorship (percentage of survival) and sediment removal data (probability of sediment removal) a Binomial model was applied, and for the recruit size data (polyp counts of surviving corals) a Poisson model was used. The uneven numbers of recruits on each disc at the commencement of the experiments was accounted for by including this variable as a weighting within the GLMM and is represented graphically by the size of the data points in the figures. Sediment loads were treated as a continuous fixed factor and climate scenario was used as a categorical fixed factor. 'Aquaria' ($N = 12$), 'disc trays' ($N = 72$), and 'discs' ($N = 288$) were treated as random factors. Assumptions of the statistical analysis, including homogeneity of variances and distribution of residuals, together with other model validation metrics including assessment of overdispersion, were verified using simulation-based approaches with the package DHARMa (version 0.2.7) (Hartig, 2020). Statistically significant differences between the treatments were identified using the Anova and summary function of the package car (version 3.0.7) by deriving chi squared values (Fox and Weisberg, 2020). Lethal concentrations (LC_{50}) (for recruit survival) and effect concentrations (EC_{50}) (for sediment removal), that describe the sediment deposition loads that cause a 50% change in response from control (current climate at 0 mg cm^{-2}), were estimated from the GLMMs by calculating at what sediment load (intercept with x-axis) a 50% decrease in the control occurred (Blasco et al., 2016). Separate LC_{50s} and EC_{50s} were generated for each climate scenario relative to the current climate at 0 mg cm^{-2}. Interactive effects of climate scenario and sedimentation on recruit survival were evaluated using the independent action (IA) model (de Zwart and Posthuma, 2005; van Dam et al., 2012). The combined effects on survival predicted by the IA model from individual sediment deposition and climate treatment survival data were plotted against the measured survival means for all sediment-climate combinations. Additivity is indicated when the measured vs predicted effects overlap with the zero-interaction line; sub-additivity when the measured effect < predicted effect; and synergistic when the measured effect > predicted effect.

3. Results

3.1. Coral recruit survival

The exposure to two future climate conditions and six sediment deposition loads, alone and in combination, led to significant decreases in

A. millepora recruit survival in both experiments and for both tested recruit ages (Fig. 2, Table 2). For example, in Experiment 1 the survival decreased by 16.6% in the high climate treatment alone (sediment-free conditions: 0 mg cm^{-2}) in comparison to survival in the current climate (assessed at week nine, Fig. 2). Sediment depositions of ≥40 mg cm^{-2} significantly decreased the survival of recruits ($p < 0.001$) across all climate scenarios (Fig. 2). In every case, lowest recruit survival was observed when the greatest sediment deposition was combined with the high climate conditions, reducing survival by at least 85 ± 2% compared to the control (current climate, 0 mg cm^{-2}). The climate by sediment interaction on coral recruit survival was statistically significant following the initial sediment exposure in each experiment (assessed at week nine in Experiment 1 and week fourteen in Experiment 2) (Table 2). However, there was no interaction following a subsequent sediment exposure (week fourteen in Experiment 1) (Table 2). The interaction of climate and sediment effects (i.e., additive, sub-additive or synergistic) on coral recruit survival was evaluated by comparing measured effects with predicted additive effects using the independent action (IA) model (de Zwart and Posthuma, 2005; van Dam et al., 2012). The effects of climate and sediment were generally additive and greater than for any pressure individually (Fig. S2).

The sediment deposition loads that caused 50% mortality (LC_{50}) decreased under future climate scenarios in both experiments (Fig. 2, Table 3). A comparison of LC_{50}s suggests that coral recruits raised under high climate conditions were approximately twice as sensitive to sediment deposition than those raised under the current climate scenario. Recruits raised under medium conditions exhibited intermediate sensitivity and this overall pattern was consistent in both experiments and for both age classes of recruits (Table 3). The sediment deposition LC_{50}s were similar (within a climate scenario) regardless of recruit age or whether there were one or two deposition events (Table 3). At the highest sediment deposition tested (80 mg cm^{-2}), the only recruits that survived were those raised under current climate conditions and exposed only to sediment at ten weeks of age: 30 ± 9% (mean survival ± SE, Fig. 2).

3.2. Sediment removal

The probability that recruits were able to completely remove sediments within an hour from their tissues decreased with increasing sediment loads (Fig. 3). Sediment removal by recruits exposed to sedimentation for the first time was greatly impacted by the climate

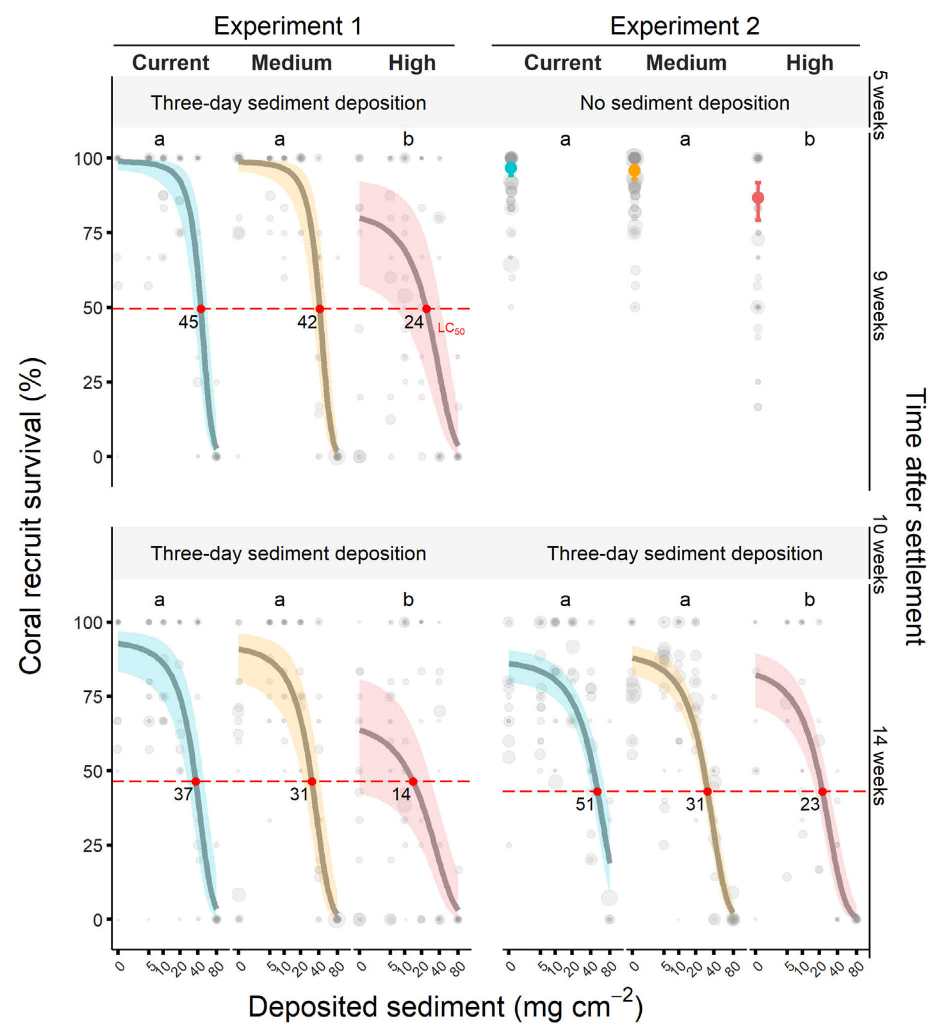

Fig. 2. *Acropora millepora* recruit survival following continuous climate stress and exposure to three-day long sediment deposition events at different ages. Experiment 1: Survival of coral recruits exposed to six different sediment deposition intensities at five and ten weeks of age and assessed at nine and fourteen weeks after settlement, respectively. Experiment 2: Coral recruit exposure to sedimentation after ten weeks only and survival assessed at nine and fourteen weeks. Ribbons and error bars illustrate 95% confidence intervals of predicted mean sediment effects under each climate treatment. Grey bubbles are percentage survival of corals settled on the same settlement disc. The greater the bubble diameter, the more coral recruits were present per settlement disc. On the 16 settlement discs per climate-sediment treatment combination, numbers of recruits ranged from 1 to 17. Red dotted lines with annotation (sediment mg cm^{-2}) illustrate the Lethal Concentration of 50% (LC_{50}), which is based on the control (current climate at 0 mg cm^{-2}) in each week. Different lowercase letters indicate significant differences between the climates in each week (Table 2).

Table 2
Analysis of Deviance results for the probability that *Acropora millepora* recruits are sediment-free one hour following sediment exposure, as well as for recruit survival and recruit size (number of polyps) respectively four weeks after sedimentation. 'Deposition' indicates how often the coral recruits were exposed to sediment in each experiment. Interactions are illustrated with an '×' and significant results ($p < 0.05$) are in bold.

	Experiment	Age	Deposition	χ^2			n	
		(weeks)		Sediment	Climate	Sediment × climate	Number of discs per treatment	Number of recruits per disc
Sediment-free	1	5	1	**<0.001**	**0.008**	0.730	16	1–10
		10	2	**<0.001**	0.121	0.131	16	1–9
	2	5	0					
		10	1	**<0.001**	**0.008**	0.179	16	1–14
Recruit survival	1	9	1	**<0.001**	**0.008**	**0.002**	16	1–15
		14	2	**<0.001**	**0.010**	0.230	16	1–15
	2	9	0		**<0.001**		16	1–17
		14	1	**<0.001**	**0.001**	**0.003**	16	1–17
Recruit size	1	9	1	**<0.001**	0.093	0.486	16	1–10
		14	2	**<0.001**	0.408	0.971	16	1–9
	2	9	0		0.095		16	1–17
		14	1	**0.011**	0.579	0.410	16	1–14

scenario and sediment load, independent of the recruit age (Table 3). Sediment deposition loads that could be cleared by 50% of recruits (50% effect concentration: EC_{50}) were highest for recruits grown under current climate conditions in each experiment (Table 3). Following the first deposition events, the sediment clearance EC_{50}s for high climate scenario recruits were reduced by 49% and 20% in comparison to control climate recruits in Experiments 1 and 2 respectively (Table 3). Survivors of the first sedimentation event demonstrated a much greater capacity to remove sediments following a subsequent deposition with EC_{50} values doubling for all climate scenarios (Fig. 3, Table 3).

3.3. Coral recruit size

Acropora millepora recruits that survived until the end of the experiment were slightly larger (had more living polyps) at increased sediment loads (Fig. S3). This effect was the same under all three climate treatments (no climate effect or interaction, Table 2). In Experiment 1, corals surviving high sediment deposition (40 mg cm^{-2}) for the first time were 1.7-times larger (more polyps) than those that were not exposed to sediments (0 mg cm^{-2}, Fig. S3). After the second sediment-deposition, the survivors were 2.4-times larger in the 40 mg cm^{-2} treatment. A similar trend of 1.3-times larger survivors following higher sediment exposures was observed in Experiment 2 (after a single exposure at ten weeks) (Fig. S3).

Table 3
Sediment depositions that cause a 50% change in response (±SE) of *Acropora millepora* recruits for survivorship (lethal concentration: LC_{50}, Fig. 2) and sediment removal (effect concentration: EC_{50}, Fig. 3). For all climates and ages, the calculations of the lethal concentrations were based on the respective control (current climate at 0 mg cm^{-2}), whereas the sediment removal effect concentration was based on a probability of 0.5. Survival was quantified four weeks after the sedimentation events (Experiment 1: week nine and fourteen, Experiment 2: week fourteen). The sediment removal capability was recorded one hour after the sediment deposition (Experiment 1: week five and ten, Experiment 2: week ten).

Climate	Experiment 1		Experiment 2	
	Survival	Sediment-free	Survival	Sediment-free
	LC_{50} [mg cm^{-2}]	EC_{50} [mg cm^{-2}]	LC_{50} [mg cm^{-2}]	EC_{50} [mg cm^{-2}]
	1st sediment deposition			
Current	45 ± 13	37 ± 11		
Medium	42 ± 13	31 ± 10		
High	24 ± 12	19 ± 10		
	2nd sediment deposition		1st sediment deposition	
Current	37 ± 10	>80	51 ± 6	51 ± 10
Medium	31 ± 9	71 ± 24	31 ± 5	32 ± 8
High	14 ± 9	61 ± 20	23 ± 6	41 ± 9

4. Discussion

This study illustrates that *A. millepora* recruits were sensitive to sediment deposition loads well within the ecologically relevant range (i.e., inshore reefs, during river runoff and near dredging operations). The negative effects of sedimentation were strongly exacerbated when coral recruits were raised under future climate scenarios. This trend of decreasing recruit survival was apparent at both recruit ages tested (nine and fourteen weeks), and regardless of whether recruits were exposed to sediment depositions once (Experiment 2) or twice (Experiment 1). Survival of coral recruits is critical for the maintenance of coral populations, and for the recovery of coral reefs following disturbance (Hughes et al., 2000; Randall et al., 2020). Therefore, the strong effects of realistic future climate conditions on sediment deposition thresholds for recruit survival revealed here indicate that environmental management regulations and guidelines for sedimentation will need to be adjusted under different future climate scenarios, as recognized for other stressors (Bruno et al., 2018; Flores et al., 2020; Negri et al., 2020).

4.1. Effects of future climate scenarios on recruits

Pressures related to future climate scenarios can affect the survival of coral recruits (Albright et al., 2008; Randall et al., 2020). In the present study, the highest climate scenario (temperature: +1.2 °C to 29.9 °C, pCO_2: 950 ppm), comparable with the business-as-usual scenario RCP 8.5 (Meinshausen et al., 2011), decreased recruit survival by 17% nine weeks after settlement, and by at least 32% fourteen weeks after settlement in comparison to current climate conditions, even in the absence of sediments. Previous studies illustrated that elevated temperature alone can lead to a >20% decrease in survival of *Porites astreoides* recruits (+4 °C to 30 °C) (Fourney and Figueiredo, 2017). Mortality following thermal stress events is generally linked to both acute oxidative stress in the host and symbiont as well as energy limitation in heavily bleached corals (Lough and van Oppen, 2018). The effects of ocean acidification on the health of coral recruits may also have contributed to mortality as calcification becomes more difficult at low aragonite saturation levels, leading to deformed skeletons (Foster et al., 2016) and potentially exhausting the recruit's energy reserves (Albright et al., 2008). Other studies also reported negative synergistic interactions of ocean warming and ocean acidification on recruit calcification in *Porites panamensis* (+1.2 °C to 29.6 °C, pH reduced by −0.2 to −0.25) (Anlauf et al., 2011) and skeletal weight of *Acropora spicifera* (+3 °C to 27 °C, pCO_2: ~900 µatm) (Foster et al., 2015) even though no significant effect on post-settlement survival was identified in both studies. For adult corals, there is no clear consensus about the cumulative effects of ocean warming and ocean acidification. For example,

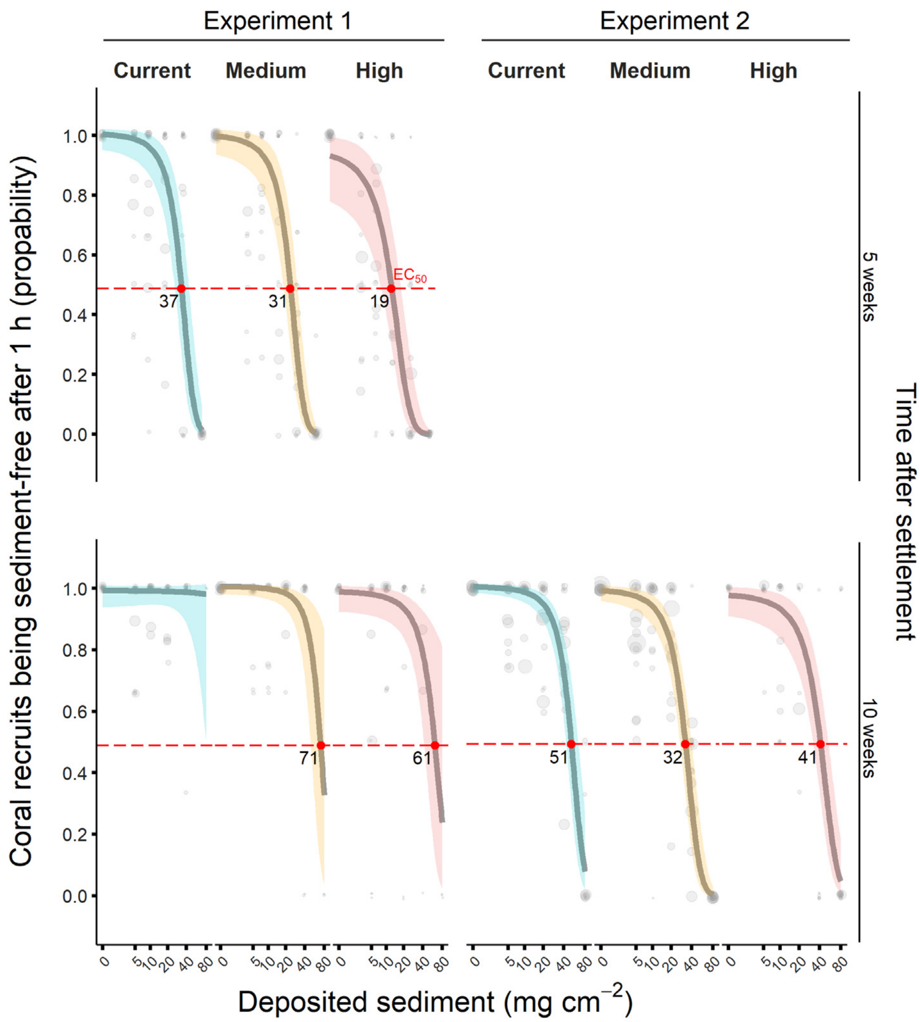

Fig. 3. Probability that *Acropora millepora* recruits grown in three climate scenarios are clear of sediment one hour following the exposure to different sediment loads. Experiment 1: Coral recruits smothered with sediment five and ten weeks after settlement. Experiment 2: Coral recruit exposure to sedimentation after ten weeks only. Ribbons and error bars illustrate 95% confidence intervals. Grey bubbles are percentage of recruits on each disc that had successfully removed sediment after 1 h. The greater the bubble diameter, the more coral recruits were present per settlement disc. On the 16 settlement discs per climate-sediment treatment combination, numbers of recruits ranged from 1 to 17. Red dotted lines with annotation (sediment mg cm^{-2}) illustrate the Effect Concentration of 50% (EC_{50}), which is based on a probability of 0.5.

temperature stress (+2.5 °C to 31 °C) had a greater impact on the survival of *Acropora* spp. fragments than ocean acidification alone or in combination with ocean warming (Anderson et al., 2019). In contrast, the combined exposure to ocean acidification and ocean warming generally leads to additive impacts on calcification and survival of adult corals as identified by other studies (McCulloch et al., 2012; Reynaud et al., 2003). Further studies are therefore required to elucidate the conditions under which future ocean acidification and ocean warming cause corals, and particularly vulnerable coral recruits, to be more susceptible to additional stressors.

4.2. Effects of sediments on recruits

Corals are able to actively remove sediments from their tissues via ciliary activity, hydrostatic expansion, tentacle movement and mucus production (Jones et al., 2016; Stafford-Smith and Ormond, 1992). However, this diversity of sediment-removal mechanisms can be overwhelmed as the intensity of sedimentation increases, leading to mortality via smothering and/or by preventing tentacle expansion for particle feeding (Jones et al., 2016; Stafford-Smith and Ormond, 1992). In the present study, only half of the five-week-old recruits were able to survive the single sediment deposition pulse of 45 mg cm^{-2} (i.e., LD_{50}) under current climate conditions, a sediment load typical near river runoff (Lewis et al., 2018; Wolanski et al., 2008) or dredging operations (Jones et al., 2016; Nichols et al., 1990). Other studies have reported mortality in *Leptastrea purpurea* and *Acropora hyacinthus* recruits of different ages at lower sediment deposition loads, when sediment pulses were repeated every three days over several weeks (Moeller et al., 2017). Five-week-old recruits in the present study were able to remove half the deposited sediment at 37 mg cm^2 (i.e., EC_{50}) after one hour, a concentration very similar to the LD_{50} for the same recruits. Collectively these results indicate that inability to remove sediment was the main driver of mortality.

Lowest recruit survival was observed in greatest sediment loads. The few recruits which survived high sediment depositions were on average larger than those that died, which we interpret as 'escape by size' from the effects of sedimentation due to a presumably greater capacity of larger recruits to clear sediments. Consistent with this result, recruits were more resistant to sediment deposition (higher LD_{50}, and higher EC_{50}) when exposed to sediments for the first time at ten weeks, opposed to recruits exposed after five weeks. However, we cannot rule out more complex trade-offs between sediment-induced mortality and increased growth not investigated here. The greater vulnerability of younger (smaller) recruits to sediments was also reported for other coral species during laboratory (Moeller et al., 2017) and monitoring studies (Wittenberg and Hunte, 1992), highlighting the importance of rapid recruit growth to survive sediment deposition events. This 'escape by size' from sediment deposition events indicates that the timing of anthropogenic activities that increase sediment levels in reef waters (e.g., dredging) (Jones et al., 2015a) should be regulated to prevent periods of high sediment levels coinciding with recruitment (Jones et al., 2015b).

4.3. Effects of climate scenarios on sedimentation thresholds

Recruits raised under future climate scenarios were more vulnerable to sediment deposition stress. The lethal sediment deposition loads (LC_{50}) showed consistent decreases by about 50% under high future climate conditions for both five- and ten-week-old recruits, and after either one or two deposition events. In the high climate scenario, recruits were approximately twice as sensitive (LD_{50}: 23 mg cm^{-2}) to sediment deposition as those raised under the current climate scenario (LD_{50}: 51 mg cm^{-2}). The reduced ability of recruits raised under future climate scenarios to clear sediments was a likely cause of higher sedimentation-related mortality observed under 'medium' and 'high' ocean warming and ocean acidification conditions. This result is consistent with a previous study in which the thermally bleached adult corals *A. millepora* (branching), *Porites* spp. (massive) and *Turbinaria reniformis* (plating) showed 3 to 4-fold lower sediment clearance compared to corals not affected by temperature (Bessell-Browne et al., 2017). Finally, the only recruits to survive the highest tested sediment load (80 mg cm^{-2}) were grown under current climate conditions and were not exposed to sedimentation until ten weeks of age (Experiment 2), highlighting the influence of both climate and recruit age.

Previous work illustrated that recruit survival is reduced by climate change (Hoegh-Guldberg et al., 2007) and sediment deposition (Jones et al., 2015b) as individual pressures. An additive effect of temperature (+4 °C to 30 °C) and deposition with fine port sediment (30 mg cm^{-2}) was also identified for *P. astreoides* recruit mortality (Fourney and Figueiredo, 2017). For adult colonies, evidence for synergistic impacts of temperature and sediment stress on coral survival were identified during a coral bleaching event that coincided with a 17-month study that monitored dredging operations (Fisher et al., 2019). However, to our knowledge, our study provides the first estimates of how realistic future climate scenarios alter specific thresholds for recruit survival under sediment deposition, information critical for sustainable water-quality management.

The combined effects of the specific climate-sediment treatments are generally additive, based on the independent action (IA) model that describes the joint effects of multiple contaminants (de Zwart and Posthuma, 2005). However, some specific climate-sediment combinations showed sub-additive or synergistic responses that depended on the timing of sediment deposition events (Fig. S2). For example, a change from predominantly additive effects after the first sedimentation event (five weeks) to more sub-additive responses after a subsequent sedimentation event (ten weeks) may reflect a selection pressure for survival of more resilient (larger) corals after the first deposition. While studies on corals exposed to multiple pressures likewise identified additive or synergistic effects, they generally examined very few levels for each pressure (reviewed in Ban et al., 2014; Uthicke et al., 2016). The current study instead demonstrates that response interactions can change between levels of climate and water-quality stress and supports the need for future studies to move beyond simple two-level factorial experiments (Uthicke et al., 2016). Regardless, even when pressures are sub-additive, reef recovery is still affected more intensely under multiple pressures than under either of the individual stressors alone.

4.4. Ecological relevance and application

The future climate scenarios and sediment loads applied in the current experiments are realistic and relevant to managers and policymakers. Our high climate scenario temperature was comparable to the +1.5 and +2.0 °C targets of the IPCC Paris Agreement (IPCC, 2014) given that the Great Barrier Reef water temperature increased already by ~0.9 °C since pre-industrial conditions (Lough et al., 2018), and the applied pCO_2 represents the likely increase by 2100 under RCP8.5 (IPCC, 2014). The highest temperature tested was moderate to ensure survival of enough recruits by the end of the study, and instead equated to an increase of 8 DHW that can cause coral mortality (≥70%) (Hughes et al., 2017a; Kayanne, 2017), with bleaching and mortality sometimes observable after 4 DHW (Hughes et al., 2018). While this temperature is expected to represent typical conditions by 2100 (IPCC, 2014), it is already periodically exceeded during current heatwaves (Hughes et al., 2017a, 2017b; Kayanne, 2017) and therefore represents a conservative temperature when heatwaves are considered into the next century. Stress on coral recruits from higher temperature and pCO_2 conditions than those investigated here are likely to drive thresholds for sediment deposition even lower. The current study applied the elevated temperate and pCO_2 jointly which means that the effects of climate scenario on sediment deposition threshold could not be attributed to either stressor. However, a key strength of the current approach is the ability to calculate LC_{50}s and EC_{50}s for sediment deposition, and this requires using ≥6 sedimentation levels. Quantifying the change in LC_{50} values for coral recruits in this way, and under different scenarios, allows comparison between future studies, as well as being directly applicable in risk assessments and to derive water-quality guideline values (GBRMPA, 2010; Simpson et al., 2013). This is facilitated by the use of sediment deposition values well within the range observed at inshore reefs during wet-season runoff (Lewis et al., 2018; Wolanski et al., 2008) and following dredging operations (Jones et al., 2016; Nichols et al., 1990). Finally, while the current study quantifies for the first time how climate conditions can affect specific sediment deposition thresholds, only one sediment type and grain size was applied. Larger effects of fine port sediment (63–500 μm diameter) than coarse reef sediment (500–2000 μm diameter) was reported for *P. astreoides* recruit mortality (Fourney and Figueiredo, 2017) compared to the effects reported here. Therefore, it remains unclear how future climate will influence sediment deposition thresholds for different sediment types and grain sizes. It is also possible that coral recruits could escape sediment pressure by a transition to settlement on protected surfaces (i.e., downward-facing instead of upward-facing as tested here) (Ricardo et al., 2017). Hence, further studies with a diversity of species and sediment types are needed to address these issues.

5. Conclusion

This study identifies how risks to the vulnerable early life-stage of a reef coral will likely rise in the future. We show, for the first time, that the threshold for coral recruit survival under sediment deposition was approximately halved in 2100-relevant climate scenarios. The climate conditions, and timing of sediment exposure following coral settlement, are important factors, as only at least ten-week-old recruits grown under current climate conditions were able to survive elevated sedimentation loads frequently observed near river runoff and dredging operations. This informs environmental management by demonstrating which, and to what extent, local co-stressors would need to be managed to protect coral recruitment that is critical to the sustainability of reefs (Duarte et al., 2020). For example, metrics such as LD_{50}s are readily incorporated into spatial risk assessments that inform the scale of expected disturbance from sediment-generating activities like dredging (Fisher et al., 2017; GBRMPA, 2010; Simpson et al., 2013). The timing of these activities can be appropriately managed to minimize the influence of co-stressors as the first few weeks of coral recruit development are more vulnerable to sedimentation (Moeller et al., 2017). We therefore stress the importance of sustainable water-quality management efforts, particularly in times of rising temperature and pCO_2 pressure.

CRediT authorship contribution statement

Christopher A. Brunner: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Sven Uthicke:** Conceptualization, Writing - review & editing, Funding acquisition. **Gerard F. Ricardo:** Conceptualization, Methodology, Formal analysis, Writing - review & editing. **Mia O. Hoogenboom:** Conceptualization, Writing - review & editing. **Andrew P. Negri:** Conceptualization, Writing - review & editing, Funding acquisition, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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