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Effects of sediment resuspension on the larval stage of the model sponge *Carteriospongia foliascens*

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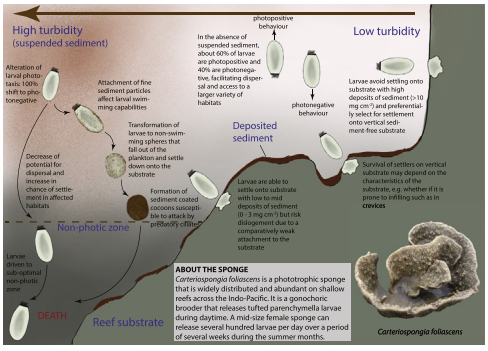
HIGHLIGHTS

- >50% larvae survived exposure to suspended sediment concentrations up to 300 mg L^{-1}.
- Suspended sediment caused homogenisation of larval negative phototaxic behaviour.
- Larvae could not remove attached sediment that affected dispersal and led to death.
- Larvae settled onto surfaces with up to 3 mg cm^{-2} sediment but risk dislodgment.
- Larvae avoided surfaces with deposited sediment >10 mg cm^{-2} but settled nearby.

GRAPHICAL ABSTRACT



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ABSTRACT

Sponges are important components of many marine communities and perform key functional roles. Little is known on the processes that drive larval dispersal and habitat selection in sponges, and in particular under stress scenarios. The increase in sediment in the marine environment is a growing concern for the health of ecosystems, but scarce information exists on the effects of sediment on sponge larvae. This study assessed the effects of suspended and deposited sediment on the larva of *Carteriospongia foliascens*. A suspended sediment concentration (SSC) of 100 mg L^{-1} caused homogenisation of the natural pattern of phototactic responses, leading to 100% of photonegative behaviours and a reduction of swim speeds by 27%. After 24 h exposure to suspended sediments, fine particles were found attached to larval cilia, causing abnormal swimming behaviours. Larvae did not have the ability to remove the attached sediment that led to a transformation of the larval body into a cocoon-like morphology and death. Mortality tripled from 3 mg L^{-1} (9%) to 300 mg L^{-1} (30%) and the relative SSC EC_{10} and EC_{50} values corresponded to 2.6 mg L^{-1} and 17.6 mg L^{-1} respectively. Survival, as determined by live swimming larvae, exceeded 50% even in the highest SSC of 300 mg L^{-1}, however settlement success decreased by ~20%. Larvae were able to settle onto substrate having deposited sediment levels (DSLs) up to 3 mg cm^{-2} (~24%), but recorded a 25 × chance of dislodgement compared to settlers on substrate with DSL of 0.3 mg cm^{-2}. Larvae avoided settling onto substrates with DSLs >10 mg cm^{-2} and preferentially settled onto alternative vertical substrate that

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were free of sediment. While *C. foliascens* larvae have some ability to survive and settle through conditions of elevated sediment, detrimental effects are also clear.

1. Introduction

Sponges are key components of marine benthic communities, from tropical coral reefs, to temperate and polar seabeds, and can form impressive aggregations and dominate communities in abundance and biomass (Heyward et al., 2010; Dayton et al., 2016; Maldonado et al., 2017). Sponges are crucial to ecosystem functioning and underpins local food webs through their large capacity for water filtration and bentho-pelagic coupling of organic and inorganic nutrient cycles (Reiswig, 1971; Wulff, 2006; Bell, 2008; Maldonado et al., 2012; de Goeij et al., 2013). As sponges are relevant components to both the physical 3-dimensional structure and the functioning of many marine communities, assessing their responses to anthropogenic stressors is pivotal to anticipate how marine communities may shift under scenarios of disturbances.

The increase in sediment in the marine environment, both as suspended and deposited sediment, is one of the rising stressors identified as a major global threat to benthic marine ecosystems (Fabricius, 2005; Halpern et al., 2007). Through time, many species have evolved to tolerate episodic and/or periodic natural events of local sediment resuspension and increased turbidity caused by turbulent hydrodynamics from atmospheric low pressure systems (Wulff, 1995; Anthony and Larcombe, 2000) and other processes, such as riverine discharges (Moura et al., 2016; Abdul Wahab et al., 2017). However, the level of sediment in the world's oceans has also progressively increased in the past decades as the result of a combination of local and regional coincidental human-driven processes (Airoldi, 2003). These include continental run-offs derived from major changes in land use (McCulloch et al., 2003), resuspension and land-slides from trawl fishing (Churchill, 1989; Dellapenna et al., 2006), and more importantly, sediment resuspension from coastal and offshore industrial activities, including dredging, mining, drilling and a growing panoply of natural resource explorations and extractions (Davies et al., 1984; Jones et al., 2016; Levin et al., 2016). This increasing turbidity and sediment resuspension are known to operate as acute and chronic ecosystem pressures, both at the local and regional scales (Airoldi, 2003; Fabricius, 2005; Fisher et al., 2015; Jones et al., 2015).

Sediment can affect marine communities in multiple ways. The fine fraction of suspended sediment can remain in the water column for extended periods and be transported over large areas (e.g. see satellite images in Abdul Wahab et al., 2017). As a result, light penetration is reduced, which reduces primary productivity and the survival of phototrophic benthic taxa, such as macroalgae, seagrasses, corals and many sponges (Airoldi and Cinelli, 1997; Erftemeijer and Lewis III, 2006; Fabricius et al., 2016; Pineda et al., 2016; Bessell-Browne et al., 2017b). Additionally, elevated fine suspended sediment can directly clog the feeding apparatus of filter feeders, but also suffocate the respiratory system of many other organisms (Fabricius and Wolanski, 2000; Armsworthy et al., 2001; Tompkins-MacDonald and Leys, 2008; Bell et al., 2015). As sediment falls out of suspension and is deposited onto the seabed, sessile organisms can be affected negatively by smothering and the increased energetic needs for active clearing of sediment from exposed surfaces (e.g. mucus production, Bessell-Browne et al., 2017a; Pineda et al., 2017c).

Investigations into the responses to sediment and siltation of ecologically relevant habitat-building organisms such as corals and sponges have largely focussed on either adult life stages (Jones et al., 2016; Pineda et al., 2017a) or early settlers (Maldonado et al., 2008). Recent works have progressed our understanding of the consequences of sediment resuspension on the gametic and larval ecology of scleractinian corals (Ricardo et al., 2015; Ricardo et al., 2016a; Ricardo et al., 2016b; Ricardo et al., 2017; Ricardo et al., 2018). In comparison, how sediments influence sponge larvae is very poorly understood (Bell et al., 2015). Sponge larvae are lecithothropic and, in most groups, possess limited dispersal capabilities and are free swimming from hours to a few days (Maldonado, 2006; Whalan et al., 2008). Nevertheless, the motile larval stage is critical in ensuring the success of sponge populations in the long term by enabling species to migrate away from suboptimal habitats that are under disturbance or re-populate once the disturbance is removed (Pineda et al., 2010). The role of larvae for population connectivity is therefore important in maintaining inter-population genetic exchanges, minimising intra-population inbreeding, and limiting the risks of local population extinction (Cowen and Sponaugle, 2009).

Carteriospongia foliascens is an abundant sponge across the Indo-Pacific (Wilkinson, 1988; Abdul Wahab et al., 2014c), easy to maintain in aquaria, and capable of producing thousands of larvae over several weeks under controlled laboratory conditions (Abdul Wahab et al., 2014b). *Carteriospongia foliascens* larvae are highly photoresponsive and may utilise this behaviour for vertical migration and appropriate water column placement for dispersal (Abdul Wahab et al., 2014b). Any changes in this photoresponsiveness and swimming speed may lead to changes in the range of dispersal and in the chance of encountering suitable habitats. Given all these features, *C. foliascens* is viewed as a suitable proxy to both assessing environmental impacts on the larval stage of invertebrates and refining management strategies in a large variety of Indo-Pacific shallow-water systems. Therefore, the objective of this study was to assess the larval responses of *C. foliascens* to increases in both suspended and deposited sediment. Herein we have documented, for the first time, how a variety of sediment resuspension scenarios affect patterns of larval swimming and orientation, larval survival, larval settlement success, and the growth and survival of early juvenile stages.

2. Materials and methods

2.1. Species selection, collection and spawning

Carteriospongia foliascens occurs on tropical reefs in the Indo-Pacific region across the Western Pacific Ocean to the Red Sea (van Soest et al., 2005). Adults sponges inhabiting intertidal habitats can be exposed to air during spring tides (Abdul Wahab et al., 2014b), thus allowing short durations of exposure of individuals to air in experiments with no subsequent detrimental effects on sponge performance. *Carteriospongia foliascens* is gonochoric and viviparous, and trickle spawns tufted parenchymella larvae during daytime hours (Abdul Wahab et al., 2014a, 2014b). Peak release of larvae in the wild occurs during the Austral summer months between October and December, and reproductive female sponges can be identified in the field by the presence of developing eggs, embryos and larvae that appear as cream-coloured particles in the mesohyl (sizes ca. 0.5 mm). In controlled laboratory conditions, a single brooding female may release >750 larvae a day; and larvae are, on average, about 850 μm long and 560 μm wide and exhibit strong phototactic responses during their planktonic swimming phase that is no longer than 24 h (Abdul Wahab et al., 2014b; Whalan et al., 2015).

Over 3000 larvae were collectively used for the various experiments in this study. Larvae were obtained from thirty reproductive *C. foliascens*

individuals, which were collected from depths of <3 m from south Juno Bay (Fantome Island, 18°41.1309S, 146°30.8809E;) on the 8th of November 2018 and transported to the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS, Queensland). Sponges were maintained in groups of 7–8 individuals in 4 × 884 L rectangular aquaria (930 mm width × 1440 mm length × 760 mm height; water height = 660 mm) supplied with flow-through 0.4 μm filtered seawater (FSW; flow rate = 2 L min^{-1}, ~3 × 100% water exchange per 24 h) in an environment controlled room maintained at 27.5–28 °C. Unfiltered seawater (1 L min^{-1}) was also supplemented to each aquaria to supply dissolved and particulate organic matter as nutrition to sponges. *Carteriospongia foliascens* contains symbiotic cyanobacteria and requires light for additional phototrophic nutrition (Wilkinson, 1983; Luter et al., 2015). Photosynthetically active radiation (PAR) was supplied to the aquaria using LED aquarium lights (Hydra, AquaIllumination), reproducing a natural irradiance and lighting regime. The lighting regime comprised of a linear ramp-up period of 6.5 h from darkness (0530 h) to a maximum of 100 μmol quanta m^{-2} s^{-1} (1200 h), a ramp-down over 6.5 h to darkness (1830 h) resulting in a daily light integral (DLI) of 2.8 mol quanta m^{-2} d^{-1}. Water temperature profiling in aquaria followed daily average temperature from the field at 5.8 m collected from 2016 to 2017 (Orpheus Island, Palm Island Group, central Great Barrier Reef) and was controlled by mixing two streams of temperature controlled FSW using automatic valves regulated through a Siemens PCS7 SCADA system. All larval experimental conditions were maintained at 28 °C and corresponded to average natural values during the November–December months.

For spawning, each reproductive female was transferred to a 15 L white polyvinyl chloride (PVC) container filled with FSW in the morning (0830 h) and exposed to light conditions simulating maximum daily irradiance. In these static water conditions, larvae were released from the sponges within 2–3 h of isolation. Swimming larvae were collected by careful pipetting to avoid structural damage and transferred to 0.3 L PVC bowls filled with 0.4 μm FSW. For experiments, larvae from multiple sponges (n = 6–12) were randomly pooled.

2.2. Sediment types

Sediment was collected from the seabed by SCUBA divers ~100 m from Middle Reef, Cleveland Bay, Townsville, Queensland (19°11.657S, 146°48.825E) in March 2018. Fine sediments on the upper surface of the benthos were targeted, as these most often persist in the water column following resuspension. The sediment was primarily composed of siliciclastic minerals (~58% quartz, ~25% microcline) with a smaller proportion of carbonate minerals (~17%). The organic characteristics of this sediment, with a total organic carbon as low as 0.35%, were reported in Duckworth et al. (2017). Sediment was shipped to ALS (Perth, Western Australia) where it was milled, screened to two grain size ranges (<38 μm and <53 μm) and dried. Size distributions in each of these two sediment size ranges were determined using 1 μm resolution laser diffraction techniques (Mastersizer 2000, Malvern Instruments Ltd), and yielded modal sizes of 25 and 40 μm respectively. The <38 μm sediment size range was subsequently used for experiments associated to suspended sediment concentrations (SSCs), and the <53 μm sediment size range was used for experiments associated with deposited sediment. The rationale for using two separate sediment size classes is explained in detail in the respective corresponding methodological sections.

2.3. Larval swimming and photobehaviour in suspended sediment

To assess changes in larval swimming behaviours and speeds, we used 4 h-old larvae, which were known to exhibit a marked swimming response to light (Abdul Wahab et al., 2014b), swimming in a direct trajectory either towards or away from a light source. Larval swim speed and phototactic behaviours in clean FSW (0 mg L^{-1}; control) and seawater containing a nominal SSC of 100 mg L^{-1} were tested. This SSC was chosen because such a concentration can commonly be achieved in dredging projects (Fisher et al., 2015). Tests were conducted in a swim chamber (100 × 10 × 10 cm, L × W × D) filled to 4 cm. The swim chamber was placed within a larger aquaria, which provided 5 cm of water jacket that buffered light transmission and internal reflection within the swim chamber, minimising confounding larval photoresponsive behaviours (as recommended by Forward Jr et al., 1984; Fig. 1). An intensity controllable LED light source was externally positioned at one end of the swim chamber and the light extinction within the chamber with increasing distance to the light source measured using a LICOR meter (LI-250A with LI-192; Fig. 1). The experiment was performed in a dark room and larvae that had been maintained in darkness were individually pipetted into the swim chamber at a distance from the light source where irradiance was adjusted to attain intensity ~10 μmol quanta m^{-2} s^{-1} in the midpoint of the chamber (i.e. ~50 cm from the light source), irrespective of water turbidity (Fig. 1). The swimming speeds and direction of swimming towards the light (photopositive) or away from light (photonegative) were quantified for 32 independent larvae in each of the two SSC treatments. As larvae swam in a relative straight trajectory towards or away from the light source, swim speeds were quantified through chronometric timing of larvae between two points across a measuring tape (see Supplementary Video 1 of larval unidirectional swimming). Assays for each of the treatment lasted up to 1 h, with minor settling of sediment in the 100 mg L^{-1} treatment.

The difference in average larval swimming speed and swim distance as a function of the presence/absence of suspended sediment was assessed using the Mann-Whitney *U* test. All statistical analyses were performed in SigmaPlot 14.0 unless otherwise stated.

2.4. Effects of larval exposure to SSCs on survival, settlement and early post-settlement juveniles

2.4.1. Larval survival and settlement success during sediment exposure

Shortly after release from the parent sponge, *C. foliascens* larvae were exposed to SSCs of 0, 3, 10, 30, 100 and 300 mg L^{-1} ($n_{replicate}$ = 10) to assess the effects of suspended sediment on survival both during the planktonic life of larvae and at the settlement stage. The SSC treatments were representative of conditions that free-swimming larvae can experience in the field during dredging projects (Jones et al., 2015). To prepare SSCs treatments, a calibration curve of SSC (mg L^{-1}) to nephelometric turbidity units (NTUs) was first produced. Here, very fine particle sized sediment was separated from the <38 μm sediment by first thoroughly and vigorously suspending 100 g of the dried sediment in 20 L of 0.4 μm FSW. Subsequently, the largest sediment particles were allowed to fall out of suspension for 10 min in static conditions and the supernatant (top 15 L) containing the very fine sediment siphoned to a clean container. The supernatant was left overnight in static conditions to concentrate the very fine sediment by siphoning off the clear seawater. The very fine sediment fraction had a modal size of 11 μm (Mastersizer 2000, Malvern Instruments Ltd). Using a turbidity sensor (90-FLT, TPS, Queensland, Australia), the very fine-sediment concentrate was serially diluted in FSW to produce triplicate suspended sediment concentrations of 650, 325, 162.5, 81.25, 40.6, 20.3. 10.16 and 0 NTU. Depending on the SSC, 50 to 200 mL of the sediment solution was individually passed through a 0.4 μm pre-weighed polycarbonate track etched (PCTE) membrane in a vacuum filter to capture the suspended sediment and washed free of salts using ultrapure freshwater (Milli-Q®). The PCTE membrane containing the suspended sediment was then dried at 60 °C to determine the mass of the dried fine suspended sediment at the various NTUs. The SSC treatments were subsequently prepared by following the same procedure to produce the very fine sediment concentrate as described above and using the appropriate NTU values that corresponded to the targeted SSC as per the final

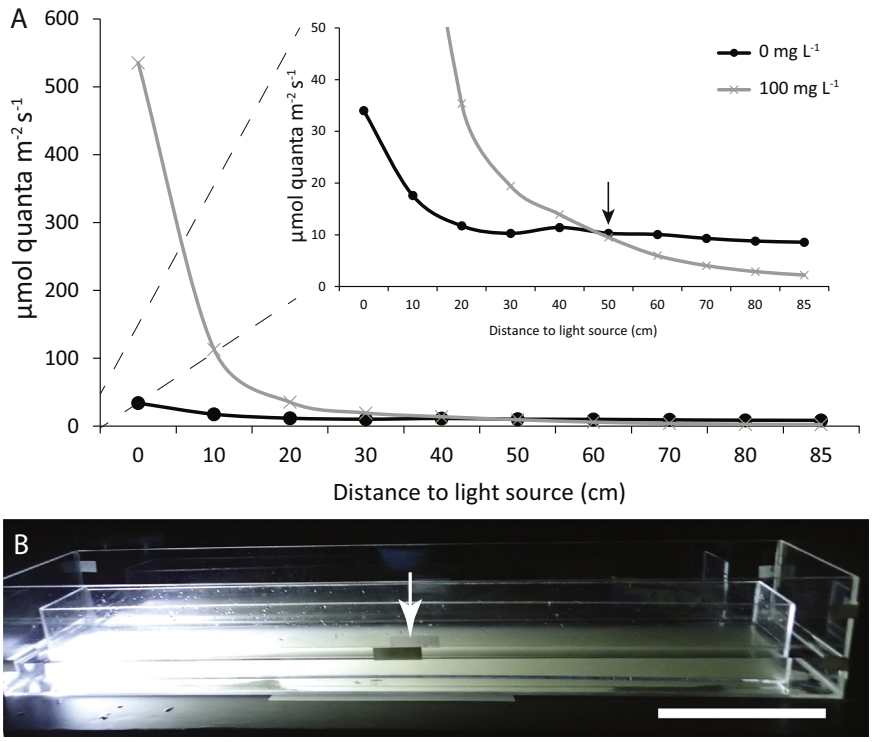

Fig. 1. A) Light irradiance (µmol photons m^{-2} s^{-1} measured at distances to the light source) through suspended sediment concentrations (SSCs) of 0 (black lines) and 100 mg L^{-1} (grey lines). Inset shows the finer patterns of light irradiance (between 0 and 50 µmol photons m^{-2} s^{-1}, y-axis truncated at 50 µmol photons m^{-2} s^{-1}) through the two SSC treatments. The intersect of light irradiance curves (~10 photons m^{-2} s^{-1} at 50 cm to the light source, see black arrow) served as a starting point for each larva being introduced into the swim chamber for the swimming assays. To achieve similar light irradiance levels in the 100 mg L^{-1} to the 0 mg L^{-1} treatment at 50 cm, light intensity was increased at the source to account for light attenuation through the suspended sediment. B) Set-up of the experimental swim chamber with 100 mg L^{-1} SSC treatment and light source to the left and external of outer aquaria, showing the gradient of irradiance from one to another end of the swim chamber. White arrow represents the starting point where each larva was introduced (50 cm mark). White scale bar = 20 cm.

linear SSC-NTU calibration curve (SSC = 1.1095*NTU, R^2 = 0.9986; Supplementary Fig. 1).

Twenty to 24 larvae ($\tilde{X}$ = 21) were introduced to clear 400 mL wide mouthed, cylindrical polystyrene containers (8 × 10 cm, d × h) containing the SSC treatments. The containers were laid horizontally on a series of 3 cm diameter mechanical rollers that continuously rotated, keeping the larvae and sediments in suspension (Supplementary Video 2). The mechanical rollers were set to 0.3 revolutions s^{-1} and were kept in an environmental controlled room at 28 °C with a 12 h diel light cycle. Exposures lasted for ~21.4–23.7 h. At the end of the exposure period, the conditions of larvae and settlers were examined using a dissecting microscope and larvae assigned to one of the following categories: swimming larvae, alive but non-swimming larvae, larvae that had settled on the substrate, larvae that had settled at the air-water interface, and dead (see Supplementary Table 1 for the detailed categories). Settled larvae (hereafter referred to as 'settlers') were defined as larvae that had attached to the substrate (or air-water interface) and whose pigmented posterior ring was no longer perceptible because metamorphosis had started. Experimental replicates were performed in two independent batches, each starting on a different day. This two-batch design was necessary, due to the time needed to accurately score larval conditions in every container without exceeding a total exposure time of 24 h for each container.

To assess if SSC treatments had an effect on larval mortality, a two-way ANOVA having 'experimental batch' (1 and 2) and 'SSC treatment' as factors was performed on the percentage data of larvae that had died. As the 'batch' factor had only a marginal effect on mortality (Supplementary Fig. 2), data were subsequently pooled across batches, and a one-way ANOVA performed to examine the effects of SSCs in greater power. The Tukey's HSD post-hoc test was used to identify pairwise differences in larval mortality between the levels of the SSC treatment. The same procedure was performed to assess whether batch and SSC factors had any effect on the success of settlement within the experimental containers. Additionally, we used non-linear regression to examine how the average levels of pre-settlement mortality in the different SSC treatments were related.

2.4.2. Settlement, post-settlement survival and growth after pre-exposure to suspended sediment

To assess whether the exposure of larvae to SSCs during their planktonic life negatively affected subsequent larval settlement ability or the survival of the early settlers, larvae that were identified as healthy swimmers after the SSC exposure were pipetted out of their corresponding treatment container and introduced into pre-conditioned polystyrene well plates containing 10 mL of FSW (Sarstedt, well dimension – 3.4 × 1.5 cm, w × h; n_{larvae} per plate = 5–12, $\tilde{X}_{larvae}$ = 10; 10 replicate wells per SSC treatment). The wells were pre-conditioned by immersing them for ~14 d in aquaria receiving similar environmental conditions to adult sponges; as conditioned surfaces can improve larval settlement rates and simulate substrates that occur naturally in the wild (Abdul Wahab et al., 2011). The successful settlement of larvae to the substrate, as percentages to the initial number of larvae introduced, was assessed 55 h after introduction to the wells. A two-way ANOVA was first performed on the percentage settlement data to test the combined effects of SSCs and batch on larval settlement. A one-way ANOVA was then performed to assess the effects of SSCs on larval settlement in isolation using data that were pooled across batches. A Tukey's HSD test was performed to identify pairwise differences in settlement between the SSC treatments.

Plates containing successful settlers were subsequently placed within a flow-through aquaria receiving similar water temperature,

light regime and food supply to those experienced by adult sponges. The initial number of settlers in a well ranged from 3 to 12 individuals ($\tilde{X} = 8$, $\bar{x} = 8$). The survival and size of these settlers, larvae of which had been previously exposed to SSCs of 0, 3, 10, 30, 100 and 300 mg L^{-1} was assessed after a 30 d grow-out period in an aquarium provided with a continuous flow of unfiltered seawater. Survival was recorded as a percentage (%) of the initial number of living settlers. The size of settlers after 30 d of growth was assessed by considering only those settlers established on horizontal surfaces and away from the vertical walls of the wells, which provide reliable comparable morphometric data over time. These settlers were photographed and their size as surface area (mm^2) quantified in ImageJ (Schneider et al., 2012).

For size comparisons between SSC treatments, the surface area at the moment of settlement was assumed to be equal (or non-significantly different) for all settlers. Individual size data of settlers after 30 d of growth was pooled across the two experimental batches, and individual settlers treated as replicates within levels of the SSC treatment. To assess the effects of SSC treatment on settler survival and growth, two-way ANOVA was first performed to assess the combined effects of SSCs and experimental batches on survival and size separately. Subsequently, data across experimental batches were pooled and used to perform one-way ANOVAs for each of the survival and size datasets. Where a significant difference was detected, a Tukey's HSD test was then performed to identify pairwise differences between SSC treatments.

2.5. Larval settlement onto sediment covered surfaces

The ability of larvae to successfully attach to and metamorphose on surfaces covered with deposited sediment was assessed. Larvae were offered substratum that had deposited sediment levels (DSL) ranging from 0, 0.3, 1, 2, 3, 10 to 30 mg cm^{-2} and representing a two order of magnitude range. Settlement assays were performed in clear, conditioned 400 mL polystyrene containers (8 × 10 cm, d × h). Containers were conditioned following the same procedure described previously. The <53 μm sediment was used as the slightly larger particle sizes facilitated quicker deposition onto test substrates. Sediment loads were prepared by introducing 100 mL FSW containing the known homogenous sediment mass to the experimental containers. The suspended sediment completely settled out of suspension in ~20 h. By using 100 mL of water, larvae were presented with approximately equal area for settlement (50.3 cm^2) on (1) the bottom substrate of the containers (with settled sediment), (2) the vertical wall of the container (with no settled sediment) and (3) the air-water interface (with no settled sediment).

Fifteen to twenty ($\tilde{X} = 18$) competent, swimming larvae (22–24 h old) were introduced to each of the containers at random, and 10 replicate containers were used to evaluate each settled sediment treatment (see Supplementary Video 3 of larvae swimming over the sediment covered substrate). After 48 h in the treatments, the percentage of successfully settled larvae was scored for each of the three substrates. For the bottom and vertical surfaces, the success of the attachment was assessed by gentle pipetting the incubation water over the larvae. Any settlers that were dislodged were assumed to have partially settled onto the layer of sediment, rather than directly to the underlying container floor and were not considered viable in the long run in natural conditions, and would not progress to recruitment into wild populations. In addition, any larvae that were unattached were counted and any larvae that had died on substrate, on sediment, or were missing due to disintegration into smaller fragments (see Results and Discussion), were categorized as dead.

To assess the settlement ability of larvae, a one-way ANOVA was first performed on the sum of all successful settlement, including onto the air-water interface, bottom substrate and vertical wall across the experimental treatments. This was to ensure that the overall settlement was not affected by any effects of residual water column turbidity. To assess settlement behaviours of larvae, the Vanderploeg and Scavia relativized electivity index (E^*) was calculated for each of the test surface at each of the DSL. This index incorporates a selectivity coefficient and the number of settlement substrate that are offered, such that: $E^* = [W_a - (1/n)] / [W_a + (1/n)$, where n is the total number of substrate types available to the larvae for settlement, and W is the selectivity coefficient for substrate type 'a' determined by $W_a = [r_a/p_a]/\sum(r_a/p_a), (r_b/p_b)\ldots(r_z/p_z)$, where r is the proportion of larvae that had settled onto substrata a to z, and p is the proportion of substrata a to z that is available to the larvae for settlement (Lechowicz, 1982). E^* of ~0 indicates random settlement on a substrata, $E^* < 0$ when a substrata is avoided, and $E^* > 0$ when a substrata is preferred. Permutational ANOVA (PERMANOVA) was performed to assess the effects of DSLs on larval settlement behaviours, using 9999 permutations of the Euclidean resemblance matrix of the raw multivariate electivity index data in PRIMER PERMANOVA+ v7.

3. Results

3.1. Larval swimming and photobehaviour in suspended sediment

Each of the 32 larvae placed in the swim chamber with the 100 mg L^{-1} SSC exhibited a photonegative behaviour and swam away from the light source when initially exposed to an irradiance of ~10 μmol quanta m^{-2} s^{-1}. In contrast, only 12 out of 32 larvae in the 0 mg L^{-1} (control) treatment were photonegative, with the rest of the larvae swimming towards the light source, showing a natural variability in the sign (positive or negative) of larval photoresponse during the first hours of swimming life. Several repeated tests using the same larvae gave consistent behaviours in both treatments (data not shown).

Larvae swam significantly faster (0.48 ± 0.01 cm s^{-1}, mean ± SEM; n = 32) in the absence of suspended sediment than through seawater with 100 mg L^{-1} SSC treatment (0.35 ± 0.01 cm s^{-1}, n = 32; Mann-Whitney: U = 71.00, $p < 0.001$). On average, 100 mg L^{-1} of suspended sediment induced a 27% reduction in swimming speeds, although larvae swam similar distances in both treatments (0 mg L^{-1} = 49.44 ± 0.67 cm, 100 mg L^{-1} = 50.06 ± 3.84 cm; Mann-Whitney: U = 511.00, p = 0.995; Fig. 2A & B).

There was no difference in the speed between photopositive (0.48 ± 0.01 cm s^{-1}, n = 20) and photonegative larvae (0.48 ± 0.01 cm s^{-1}, n = 12; Mann-Whitney: U = 108.5, p = 0.668), even when average swimming distance was a few centimetres longer in photopositive larvae (50.4 ± 0.95 cm) than photonegative larvae (47.8 ± 0.63 cm; Mann-Whitney: U = 42.00, p = 0.002; Fig. 2C & D).

3.2. Effects of larval exposure to SSCs on survival, settlement and early post-settlement juveniles

3.2.1. Larval survival and settlement success during sediment exposure

The fate of larvae after 24 h exposure to the SSC treatments included a variety of outcomes (Figs. 3 and 4). Some larvae were still healthy and swimming actively after 24 h (Fig. 3A, sw) and some showed a slightly abnormal swimming, likely resulting from some sediment particles that had attached to their cilia interfering with the metachronal wave propagation of ciliary beating (Fig. 3B). Other larvae were alive, but not swimming any longer because they had initiated the process of attachment onto the bottom of containers (demersal exploratory phase). Some larvae had already successfully settled on either the air-water interface or the plastic substratum of the containers (Figs. 3A and 4A, st; see Supplementary Table 1 for the numerical summary of the various larval fates by batch and SSC treatments). As larvae that had settled to the water surface had no chance to survive, these larvae were scored as 'dead' (ecologically unviable). Some larval outcomes required further assessment as sometimes it was unclear whether they were still viable. For example, in the suspended sediment treatments, some unattached larvae had regressed their body into a non-swimming, ball-like morphology that was scored as 'spheres' and often these spheres were

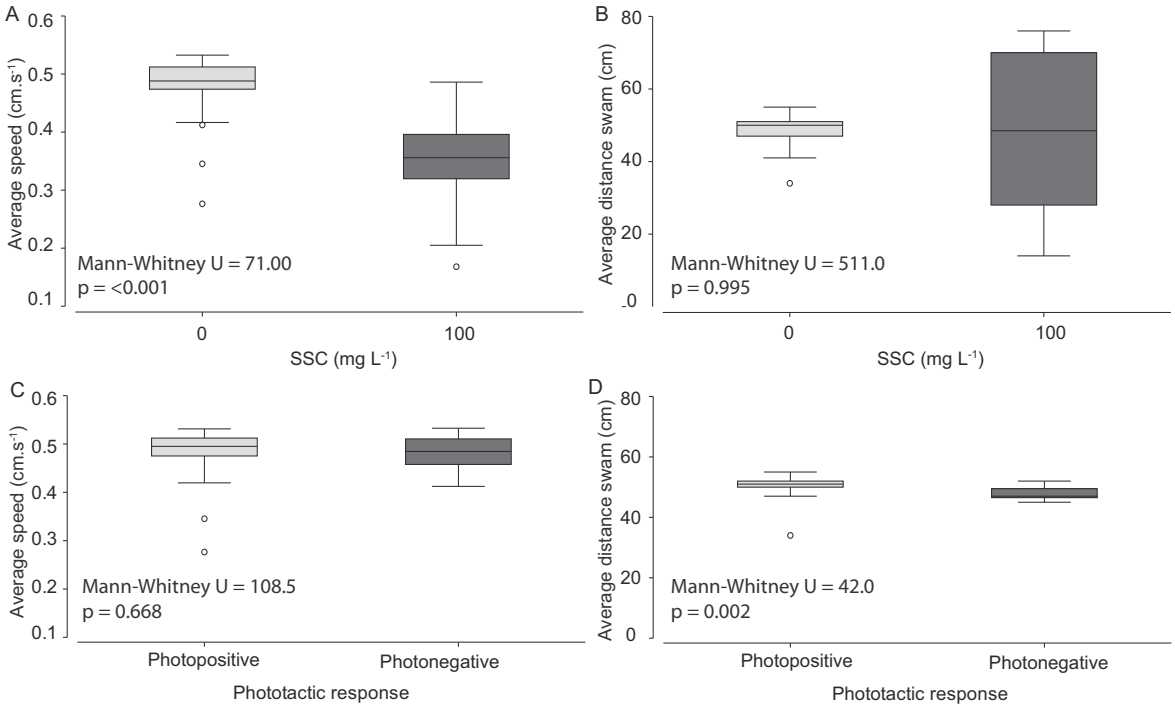

Fig. 2. A) Average swimming speeds (cm s^{-1}) and B) average distance swam (cm) of larvae in the 0 mg L^{-1} (n = 32) and 100 mg L^{-1} SSC treatments (n = 32). C) Average swimming speeds (cm s^{-1}) and D) average distance swam (cm) of photopositive (n = 20) and photonegative larvae (n = 12) in the 0 mg L^{-1} SSC treatment (control).

lightly coated with sediment (Fig. 3C). When they were transferred to unconditioned polystyrene wells filled with FSW, the "sphere-like" larvae were all able to attach and spread out on the bottom within 24–48 h (Figs. 3D and 4B), resulting in healthy, viable juvenile sponges. The percentage of larvae that formed spheres was consistently low, ranging from 1.4 ± 0.7 (3 mg L^{-1} treatment) to 2.7 ± 1.2% (300 mg L^{-1} treatment) Figs. 3.

A number of larvae that had regressed into spheres, in addition, were heavily coated by sediments (Figs. 3E, F & 4C). These were referred to as 'cocoons' and were never viable in terms of either progressing to any sort of attachment or producing settlers. Microscopic assessments showed that 'cocoons' were larvae that had died under a thick sediment coat and were being internally predated on by ciliates (Supplementary Video 4). Therefore, cocoons were placed in the category of dead larvae. Cocoon occurrence increased with increasing SSC, from 9.3 ± 2.2% in the 3 mg L^{-1} treatment to 30.5 ± 3.7% in the highest, 300 mg L^{-1} treatment. We hypothesize that the initial regression of the larval body to a spherical morphology, while non-fatal, represents an intermediate step of damage to the larva from the SSCs, following sediment attachment to cilia. The cocoon-like condition represents a more advanced stage of damage where smothering of the larva with sediment made it more susceptible to ciliate predation. Of note, the initial stage of damage by suspended sediment was represented by swimming larvae with abnormal swimming trajectories as the result of just a few sediment particles attaching to their cilia (Fig. 3B; Supplementary Video 5). A proportion of larvae were 'lost' from the containers during the experiments. These represented ~5% of the total (range 0–35% per container, Fig. 4C) and it is assumed that these larvae had settled rapidly to the air-water interface during the experiment and subsequently disintegrated by the agitation of the water during sediment exposure, or had died before attaching and similarly disintegrated.

A two-way ANOVA on the percentage of mortality, i.e. the sum of cocoon, settlers at the air-water interface and lost records, as a function of batch and SSC treatments revealed that the SSC treatment had a strong effect on mortality (Two-way ANOVA: $F_{(5, 48)} = 3.86$, $p = 0.005$). The effect of the experimental batch was only marginally significant from the statistical point of view ($F_{(1, 48)} = 4.16$, $p = 0.046$; Supplementary Fig. 2), with no significant interaction between both factors ($F_{(5,48)} = 0.63$, $p = 0.67$). The largest difference in larval mortality between experimental batches occurred in SSCs ranging from 10 to 100 mg L^{-1}, and they both were only slightly higher in experimental batch one (differences ranged from 10 to 14% across levels of SSC, Supplementary Fig. 2). As the effect of batch was minor and not consistent across levels of SSC, the data were pooled and collapsed across the batch factor to allow for a one-way ANOVA analysis with greater power only on the effects of sediment concentrations. This analysis corroborated a significant effect of SSCs on larval mortality (One-way ANOVA: $F_{(5, 54)} = 3.77$, $p = 0.005$) and the Tukey's HSD pairwise tests identified that mortality was significantly different only between the control and the highest SSC treatment (300 mg L^{-1}, $p = 0.01$).

A regression analysis revealed that the best fitting model for average larval mortality (%) was a 3-parameter exponential function of SSC ($f = 17.88 + 17.32^{*}(1-\exp(-0.04 \times SSC))$, $R^2 = 0.906$; $p < 0.001$), with mortality increasing quickly from 0 to 30 mg L^{-1} SSC, and moving asymptotically above 30 mg L^{-1} (Fig. 4D). According to this model, the concentration at which suspended sediment induced 50% and 10% mortality from the control level (0 mg L^{-1}) was 17.6 mg L^{-1} (relative EC_{50}) and 2.6 mg L^{-1} (relative EC_{10}) respectively.

The larvae of *C. foliascens* were able to attach in some SSC treatments to a plastic surface that was in continuous movement for 24 h. When examining the effects of batch and SSC factors on the success of larval settlement on the moving container substrate, the two-way ANOVA revealed a significant effect of SSCs but not of the experimental batch (Two-way ANOVA: SSC: $F_{(5, 48)} = 8.164$, $p < 0.0001$, batch: $F_{(1, 48)} = 2.555$, $p = 0.116$). In addition, there was no significant interaction between the main factors ($F_{(5, 48)} = 2.384$, $p = 0.052$). The main pattern reflected a decrease in settlement success with increasing SSCs, decreasing from 8.9 ± 2.5% in the 0 mg L^{-1} SSC, to 1.0 ± 1.0% settlement in the 30 mg L^{-1} SSC, and then to 0% in SSCs of 100 mg L^{-1} and above (Fig. 4A). An additional one-way ANOVA for the SSC factor (One-way ANOVA: $F_{(5, 54)} = 7.056$, $p < 0.0001$) and its associated Tukey HSD pairwise tests corroborated a significant reduction in larval settlement in all SSCs

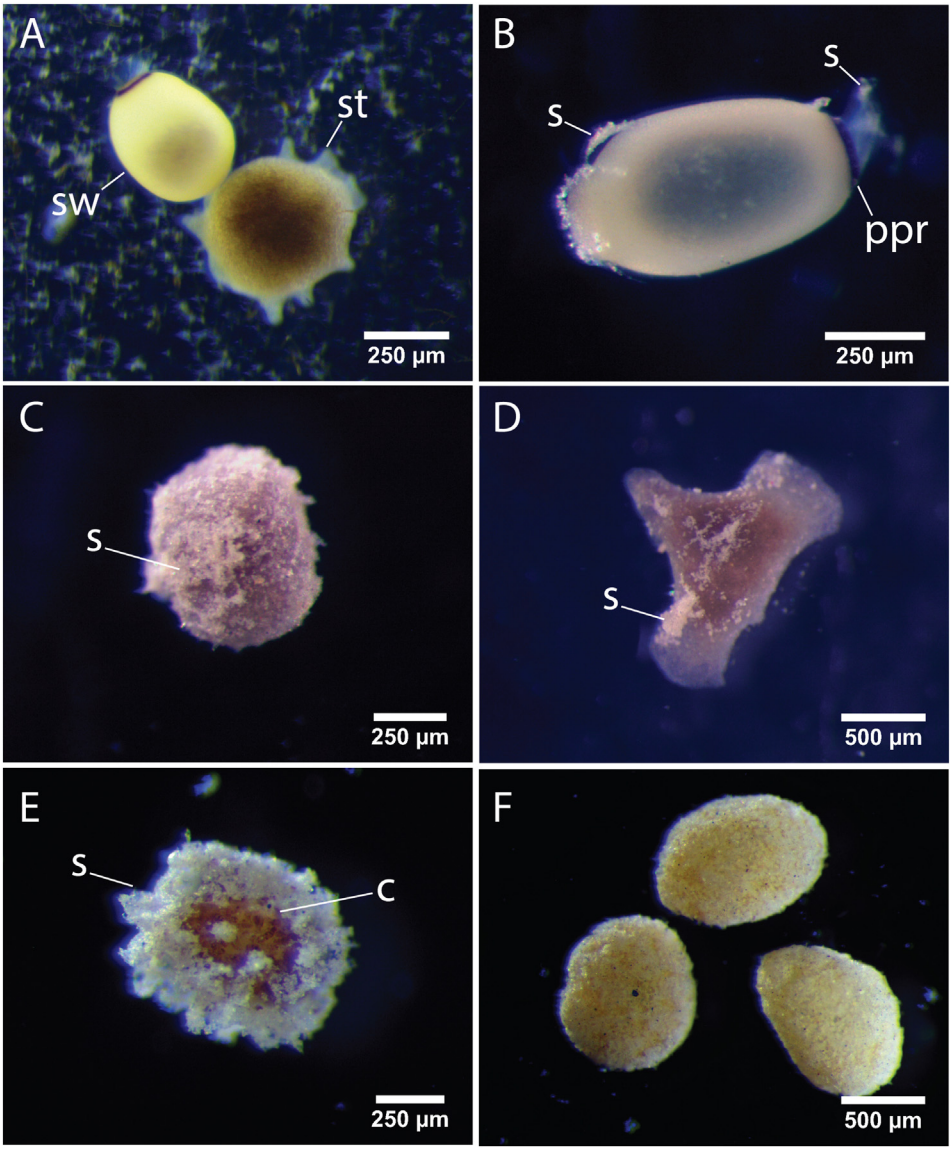

Fig. 3. Larval planktonic and settlement responses when exposed to elevated suspended sediment concentrations (SSCs). A) Swimming (sw) and settled larvae (st) in settlement assays after exposure to a 30 mg L^{-1} SSC. B) Swimming larva after exposure to a 300 mg L^{-1} SSC with sediment (s) attached to the larval anterior end and to the tufted cilia of the pigmented posterior ring (ppr). C) Live unattached sphere-like morphology slightly coated with sediment after exposure to a 300 mg L^{-1} SSC; the viability of the individual was confirmed by successful attachment to substrate and progression towards a settled larval morphology. D) Settled larval morphology derived from the sphere-like larval condition that was slightly coated in sediment. Sediment (s) can still be seen on the surface of the settler. E) Health compromised larval sphere structure that was coated by abundant sediment (s) and started being predated on by ciliates (c) after exposure to a 300 mg L^{-1} SSC. F) Larvae regressed to a ball-like morphology and severely covered by sediment (cocoon stage) after exposure to a 300 mg L^{-1} SSC; internally, the cocoons contained a larval sphere structure that was predated on by ciliates (see Supplementary Video 4).

compared to the control (0 mg L^{-1}, $p < 0.01$), but no significant differences among treatments with suspended sediment, irrespective of their concentrations.

3.2.2. Settlement, post-settlement survival and growth after pre-exposure to suspended sediment

When the settlement success of larvae that had previously been exposed to the SSC treatments was examined, the highest settlement was found in the control treatment (0 mg L^{-1}, 84.1 ± 2.3%; Fig. 5A; see Supplementary Table 2 for the detailed data). Successful larval settlement remained at acceptable levels across all SSC treatments, being consistently above 75% for SSCs up to 100 mg L^{-1}. Yet, a comparatively reduced settlement of 67.3 ± 4.9% was found in the highest SSC treatment (300 mg L^{-1}). Two-way ANOVA showed a significant effect of SSC pre-exposure on successful larval settlement, but not experimental batch (Two-way ANOVA: SSC: $F_{(5, 48)} = 2.15$, $p = 0.023$, batch: $F_{(1, 48)} = 0.18$, $p = 0.673$, interaction: $F_{(5, 48)} = 2.155$, $p = 0.075$). Similarly, a significant effect of SSC on successful larval settlement was found when data across experimental batches were pooled (One-way ANOVA: $F_{(1, 54)} = 2.644$, $p = 0.033$), with a Tukey's HSD tests identifying a significant reduction in larval settlement at the highest 300 mg L^{-1} treatment ($p < 0.05$).

The survival of *C. foliascens* settlers after the 30 d grow-out period, from the pooling of data across experimental batches, was variable and not linearly related to the magnitude of the SSC treatments, with the highest survival found in the 30 mg L^{-1} treatment (48.8 ± 6.2%) and lowest survival found in the 300 mg L^{-1} treatment (39.4 ± 2.6%; Fig. 5B). There was a significant effect of experimental batches on the survival of *C. foliascens* recruits but not the different treatments (Two-way ANOVA: batch: $F_{(1, 48)} = 8.431$, $p = 0.006$; SSC: $F_{(5, 48)} = 0.626$, $p = 0.681$), with a significant interaction of SSC and experimental batches (interaction: $F_{(5,48)} = 4.964$; $p < 0.001$). When experimental batches were considered separately, there was a significant effect of SSCs on the survival of settlers only for the first experimental batch

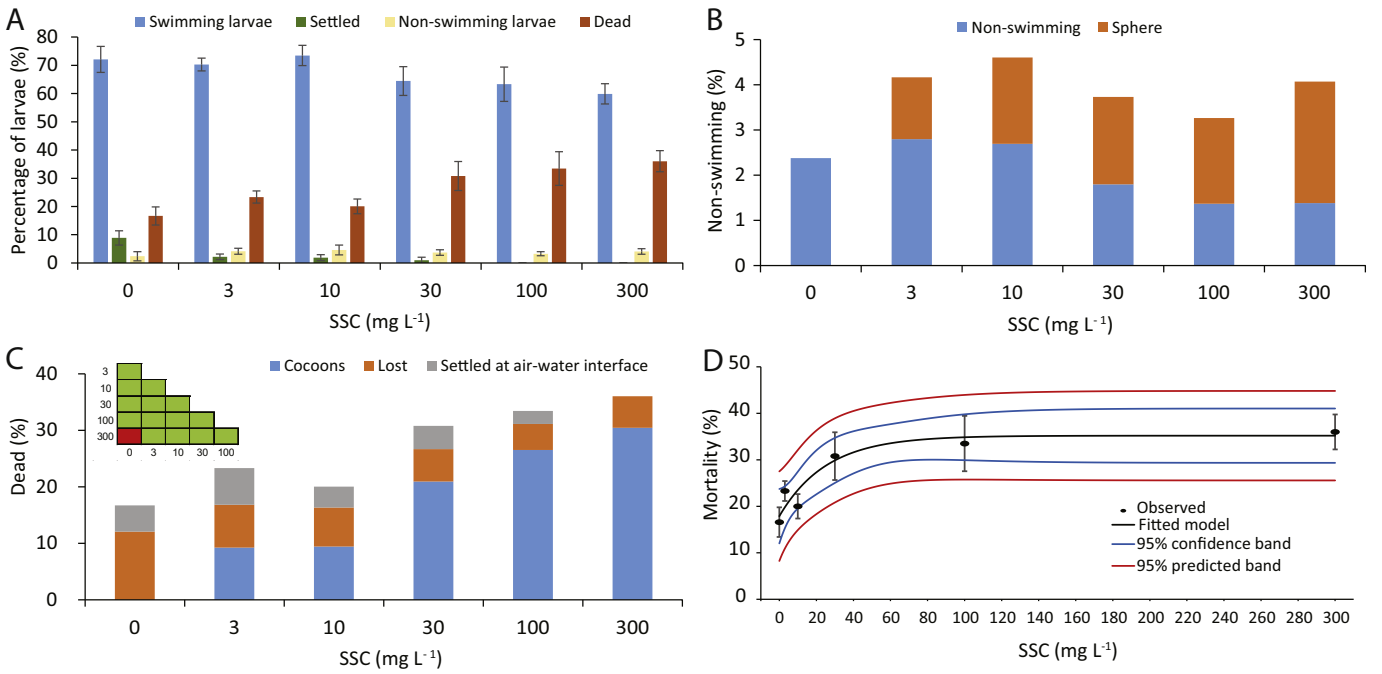

Fig. 4. Summary of data for larvae exposed to SSCs. A) Mean percentages (%, ± SE) of larvae that were swimming, had settled, were not swimming, or had died after exposure to SSC levels of 0, 3, 10, 30, 100 and 300 mg L^{-1} of up to 24 h. B) The composition of larval conditions that were not-swimming, comprising non-swimming larvae (demersal exploratory phase) and the spherical morphology across the SSC treatments. C) The composition of larvae that were considered dead, comprising sediment coated cocoons, larvae that were lost and those that had settled at the air-water interface. Tukey's pairwise tests significance matrix for total % of larvae that had died is shown, with significant differences indicated as red cells and non-significant differences as green cells. D) Larval mortality as a function of SSC, derived from the average % (± SE) dead data. Error bars indicate standard error of the means for % dead at each of the SSC. Black line represents the fitted model, blue line the 95% confidence band and red line the 95% predicted band. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(One-way ANOVA: $F_{(5, 24)} = 3.653$, $p = 0.013$), with a Tukey's HSD tests detecting a significant difference between the 30 and 100 mg L^{-1} treatments, and the 0 and 100 mg L^{-1} treatments ($p < 0.05$). The variability between experimental batches and the lack of a clear trend of the SSC treatment within the first experimental batch suggests that patterns of survival in the settlers were likely due to natural variability.

There were no statistically significant difference in the surface areas attained by the settlers after the 30 d grow-out period as a function of SSC treatments (Fig. 5C), irrespective of experimental batches being considered together or separately (Two- and one-way ANOVA: SSC: $p > 0.05$). Typically, the largest individuals were found in the 10 mg L^{-1} treatment (2.18 ± 0.36 mm^2) and smallest individuals found in the 30 mg L^{-1} treatment (1.82 ± 0.28 mm^2).

3.3. Larval settlement onto sediment covered surfaces

There were no swimming larvae remaining at the end of the 48 h assay and all larvae were either settled, unattached but alive (sphere-like morphology) or dead (see Supplementary Table 3 for the detailed data). The total larval settlement onto all surfaces combined (air-water interface, bottom substrate and vertical wall) were consistent across DSL treatments and ranged from 55.6 ± 4.9% to 66.4 ± 3.6% (One-way ANOVA: $F_{(5, 54)} = 0.669$, $p = 0.6485$; Fig. 6A), indicating that the overall settlement capability of larvae was unaffected by any residual water column turbidity or deposited sediment on the bottom substrate. PERMANOVA on the untransformed electivity index data showed a significant effect of DSL treatments on the settlement preferences of larvae, with the strongest effects found at DSLs of 10 and 30 mg cm^{-2} (PERMANOVA: pseudo-$F_{(6, 63)} = 7.75$, $p = 0.0001$; Fig. 6B). At the lower DSLs (0–3 mg cm^{-2}), larvae preferentially settled onto the bottom substrate and recorded mean electivity indices ranging 0.31 ± 0.05 to 0.42 ± 0.03 (Fig. 6B). At the higher DSLs (10 and 30 mg cm^{-2}), larvae preferentially settled onto the vertical walls of the container that were free of sediment, with mean electivity indices to the vertical wall ranging 0.20 ± 0.06 to 0.34 ± 0.02; settlement to the bottom substrate was random (mean electivity indices = −0.05 ± 0.04 to 0.06 ± 0.07; Fig. 6B).

The total larval settlement onto the bottom substrate prior to hydrodynamic agitation across DSL treatments was 57.1 ± 5.4% settlement in the 0 mg cm^{-2} DSL treatment and gradually decreased with increasing DSLs to 43.6 ± 5.2% in the 3 mg cm^{-2} treatment (Fig. 6C). A 44% reduction in initial settlement was found from the 3 mg cm^{-2} to 10 mg cm^{-2} treatment, with settlement in the 30 mg cm^{-2} treatment recorded at 19.0 ± 2.2% (Fig. 6C). For these settlers, it appeared as if they were able to wedge themselves under the sediment after attachment to the substrate and were capable of clearing the surrounding sediment from the substrate (Fig. 7A). This can be achieved because the larval cilia continue beating during larval attachment until the onset of metamorphosis, when cilia start disappearing from the external epithelium. Surprisingly, some larvae were able to attach to the underlying plastic under the sediment in the highest treatment of 30 mg cm^{-2}, corresponding to a sediment thickness of ~200 μm, although such a success occurred in rare instances (total of 3 larvae). The strength (or effectiveness against dislodging) of larval attachment to the bottom substrate decreased with increasing DSLs, the ratio of mean settler dislodgement (by gentle wafting using a pipette) to final successful attachment being 0, 0.1, 0.4, 1.0, 2.6, 22.1 and 10.3, for DSLs 0, 0.3, 1, 2, 3, 10 and 30 mg cm^{-2}, respectively (Fig. 6C).

Similar to the previous experiment on suspended sediment, we found larvae that were unattached and displayed the sphere-like morphology (Fig. 7B). The abundance of spheres was found to vary between 10.2 ± 3.1 to 12.6 ± 3.1% in intermediate DSLs of 0.3 and 3 mg cm^{-2}, but was lower in the higher DSLs of 10 mg cm^{-2} (7.4 ± 1.7%) and 30 mg cm^{-2} (6.6 ± 3.2%). Even though the sphere stage was viable (as shown in the previous experiment; see Fig. 3C and D), we assumed here that spheres will have little or no chance for survival in the long run under natural conditions, similar to settlers that were dislodged after initial settlement from hydrodynamic agitation.

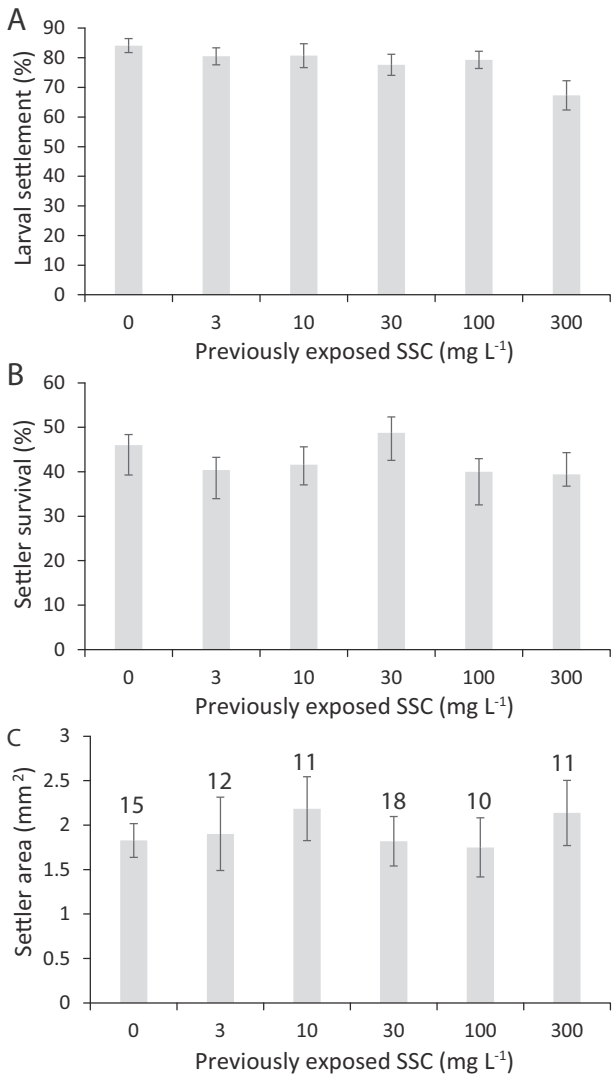

Fig. 5. Settlement, survival and growth of larvae that had been previously exposed to SSCs of 0, 3, 10, 30, 100 and 300 mg L^{-1} for 24 h and then placed in conditioned 6-well plates. A) Mean successful settlement (%, ± SE) of swimming larvae after a 55 h post-introduction. B) Mean survival (%, ± SE) of settlers after a 30 d grow-out period. C) Mean area (mm^2, ± SE) of settlers after a 30 d grow-out period across the SSC treatments. The numbers over the error bars represent the total number of settlers that could be reliably processed for size analyses at 30 d. Data from the two experimental batches were pooled to derive the mean values presented here.

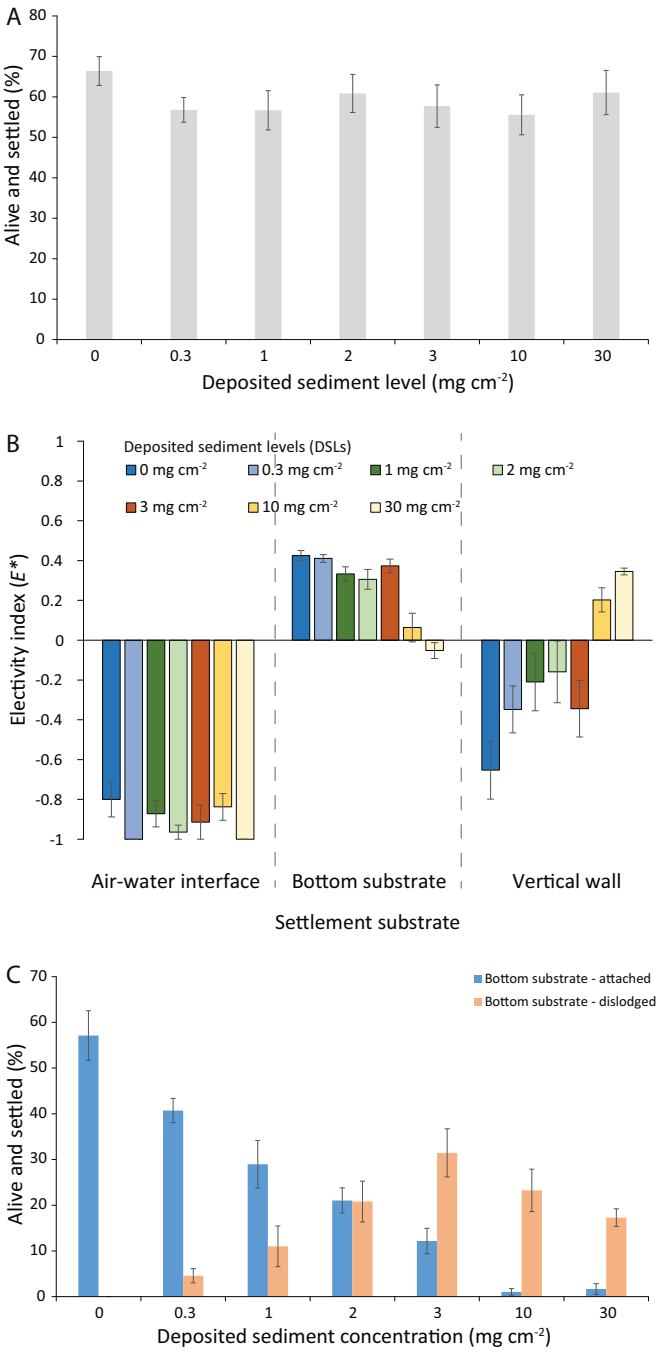

Fig. 6. A) Total settlement success. Mean percentage (%, ± SE) of the sum of larvae that had settled to the air-water interface, bottom substrate and vertical wall at 48 h after introduction to experimental containers containing deposited sediment levels (DSLs) of 0, 0.3, 1, 2, 3, 10 and 30 mg cm^{-2}. B) Settlement behaviours of larvae onto the water-air interface, bottom substrate and vertical wall at deposited sediment levels (DSLs) of 0, 0.3, 1, 2, 3, 10 and 30 mg cm^{-2} using Vanderploeg and Scavia's electivity index (E^*). E^* ~0 indicates settlement onto the substrata was random, $E^* < 0$ indicates settlement to the substrata was avoided and $E^* > 0$ indicates settlement to the substrata was preferred. Data are presented as mean ± SE, n = 10. C) Mean percentages (%, ± SE, n = 10) of larvae that had initially settled onto the bottom substrate across the DSL treatments after the 48 h assay and that had remained attached or dislodged after gentle wafting with a pipette (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

4. Discussion

The responses of sponge larvae to both suspended and deposited sediments were quantified for the first time. When larvae were exposed to suspended sediment in seawater, a number of responses were observed that included changes in their swimming speeds and orientation to light, abnormal swimming behaviours, but also complete loss of swimming capability, regression of the larval body to spherical morphologies, reduction in settlement success, and eventual death. These responses were affected at varying degrees, with the response intensity generally greater with increasing concentrations of suspended sediment. Nevertheless, a considerable proportion of larvae (>50%) survived and were swimming after the SSC treatments, even after 24 h exposure to the highest suspended sediment concentration of 300 mg L^{-1}. When searching for appropriate substrata for settlement, swimming larvae demonstrated their ability to avoid settlement onto exposed horizontal substrate that were heavily covered with sediment, and were able to selectively and successfully settle onto vertical substrate free of sediment. Additionally, settlers derived from larvae that were pre-exposed to sediment did not show any detectable reduction in post-settlement survival or body size attained after 30 days. When these observations are considered together, this study demonstrated that *C. foliascens* larvae are relatively tolerant to some scenarios of elevated sedimentation. However, this study also provides some insight on how sponge

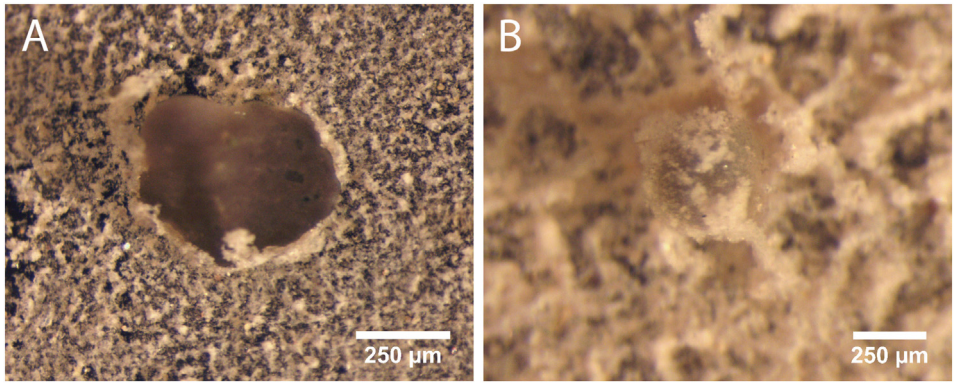

Fig. 7. A) A settler that had successfully attached, settled and metamorphosed onto the bottom substrate through the sediment layer in the 1 mg cm^{-2} deposited sediment level (DSL) treatment. B) A settler that had attached onto the sediment layer in the 3 mg cm^{-2} DSL treatment, but were unable to settle to the bottom substrate. Often these settlers has the sphere morphology that were unable to be dislodged through gentle water movement resulting from moving the experimental containers. However, gentle wafting of the sediment layer caused these settlers to dislodge along with the sediment.

populations may respond to sediment if challenged by higher environmental loads.

Connectivity via the dispersal of larvae is important for the maintenance of sessile populations across spatial and temporal ranges (Pineda et al., 2008). Sponge larvae are relatively weak swimmers, and generally exhibit short competency periods ranging from minutes to less than two weeks (Maldonado, 2006), making dispersal over large geographic ranges unlikely. Nevertheless, as the larvae brooded by *C. foliascens* are released during day time, their ability to perform directional swimming to the surface via positive phototaxis can facilitate dispersal by placement into wind-driven currents (Cowen et al., 2000; Metaxas, 2001). In addition, positive phototactic behaviours may be crucial in the positioning of larvae in optimal photic depths prior to settlement and could translate to higher survival of individuals and the success of juvenile and adult populations for phototropic species such as *C. foliascens* (Wilkinson, 1983; Wilkinson and Evans, 1989). In seawater with suspended sediment concentration of 100 mg L^{-1}, 4 h old *C. foliascens* larvae were slowed down to speeds similar to 12 h old larvae in clean seawater (~0.35 cm s^{-1}; Abdul Wahab et al., 2014b). The reduction in larval swimming speed was likely due to the higher viscosity of the sediment suspension in the 100 mg L^{-1} treatment (Zhu et al., 2017). Previous work by Abdul Wahab et al. (2014b) on the larval behaviours of *C. foliascens* under sediment-free conditions showed that negatively buoyant larvae were able to maintain their position at the water surface at the aforementioned swimming speeds, thus suggesting that newly released larvae have the ability to maintain their vertical position in the water column with SSCs up to 100 mg L^{-1}. However, we also found that suspended sediment caused the phototaxis of *C. foliascens* to be consistently photonegative, compared to larvae in sediment-free water that displayed variability in the photoresponse, with 60% of the tested individuals being photopositive. The pigmented ring at the larval posterior end, which is the light sensory mechanism of the tufted parenchymellae, has been reported to express blue-light receptive cryptochrome genes that are responsible for photodetection and the resulting phototactic behaviours of larvae (Rivera et al., 2012). As suspended sediment could alter the spectral quality of light in water (Jones et al., 2016), this may explain changes in larval phototactic behaviours observed in the present study. While the effects of suspended sediment on larval phototaxis are yet to be fully understood, the homogeneity of a photonegative response when suspended sediment was present indicates the loss of behavioural variability that otherwise could offer respite to the larval pool when encountered with challenging environmental conditions (i.e. not all larvae would be exposed to the same stressor at the same time), and that could facilitate survival of a proportion of the larval pool. The homogenisation of the larval photoresponse in the presence of sediment also means that larvae are more likely to migrate towards the seabed within natural habitats that are affected by suspended sediment. Whether this would translate into a reduction in recruitment success to populations is unknown and would likely be influenced by a combination of additional factors, including the longevity of the stress (acute or chronic) and the sensitivity of juvenile sponges to sediment. The latter issue remains unaddressed for this species, but previous studies have shown that juvenile sponges can survive better if protected from siltation during their first weeks of life (Maldonado et al., 2008). Irrespective of the final consequences, the detected effects of suspended sediment on swimming larvae would reduce the chance of larvae encountering a greater diversity of suitable habitats for recruitment.

Larvae can remain in the water column for 24 h before entering a demersal, exploratory phase (Abdul Wahab et al., 2014b), and thus can be exposed for some time to suspended sediments with potential cumulative effects. We found that exposures to suspended sediment in moving seawater of up to 24 h manifested a number of effects on *C. foliascens* larvae, with the attachment of fine sediment onto larval cilia, which can cause abnormal swimming; this being the onset of a chain of larval health deterioration that led to death. Following sediment attachment, larvae exhibited a sub-lethal condition through the regression of their body shape to a spherical morphology that was present in every treatment with suspended sediment. This spherical morphology had previously been observed in the tufted parenchymella larvae of another Great Barrier Reef sponge species, *Coscinoderma mathewsi*; the sphere-like condition was shown by larvae that had undergone thermal stress (+4 °C ambient), and that similarly could attach and settle onto substrate once the stress was removed (Abdul Wahab unpublished data). Environmentally tolerant morphologies, that could progress with ontogenetic development once conditions are favourable, are known to occur (i.e. diapauses) in gemmules of freshwater sponges (Simpson and Fell, 1974; Reiswig and Miller, 1998) and, more rarely, in marine species (Fell, 1974). The spherical condition of *C. foliascens*, therefore, may represent a physiological attempt to reach diapause-like temporary state that is yet to be described in other tufted parenchymella larvae. Of importance, the formation of this non-swimming morphology under suspended sediment exposure involves the loss of active dispersing capability and eliminates the possibility of larvae to explore the benthos for settlement on optimal substrates and habitats.

Prolonged sediment attachment to *C. foliascens* larvae led to sediment encrusted cocoons, similar to that reported for the developing embryos of the scleractinian corals *Acropora millepora* and *A. tenuis* when exposed to suspended sediment for 12 h (Ricardo et al., 2016a). In these coral species, mucous secretion and the beating of cilia by the

larvae that were developing within those cocoons assisted in the removal of attached sediment particles. Similarly, the larvae of these species and another species of brooding coral, *Pocillopora damicornis*, used a similar strategy for sediment avoidance, and their survival were unaffected at SSC exposures of up to 1000 mg L^{-1} and of up to 60 h (Ricardo et al., 2016a). Of note, the ciliated larvae of these coral species did not degenerate into cocoons when exposed to sediment. In contrast, *C. foliascens* spheres and cocoons did not exhibit clear beating of cilia or mucous release. Due to the lack of these mechanisms, sponge larvae often reached the cocoon stage and then became highly susceptible to predation by opportunistic ciliates, so that cocoons suffered total mortality in SSCs as low as 3 mg L^{-1} (9%) and tripling at SSC of 300 mg L^{-1} (30%). This highlights the sensitivity of sponge larvae to suspended sediment compared to coral larvae. It is however important to note that while larval mortality did not exceed 50% even at concentrations of suspended sediment as high as 300 mg L^{-1}, the laboratory use of rollers for simulating experimental sediment exposures may not be representative of sediment suspension under different natural hydrodynamic conditions experienced by larvae in the field, and thus can limit our interpretation of mortality by sediment in this case.

In all the SSC exposures, a considerable percentage of *C. foliascens* larvae (~60–70%) appeared healthy and still swimming in the suspensions. In addition, larvae were able to settle in low numbers (<10%) onto substrate in the rolling experimental containers up to SSC of 30 mg L^{-1}, but were unable to successfully settle in the higher SSCs of 100 and 300 mg L^{-1}. The ability of larvae to attach and successfully settle onto a substrate that was moving is in itself remarkable, although may be analogous to settling onto a substrate in a dynamic, current driven environment. Of note, however, the complete suppression of settlement at these higher SSCs indicates the reduction of larval attachment capacities due to suspended sediment. Swimming larvae that were pre-exposed to SSCs of up to 100 mg L^{-1}, when presented with substrate in sediment-free clean seawater, were able to settle and metamorphose at levels similar to that reported for the coral *A. millepora* (>75%, Ricardo et al., 2016a), however larvae showed a slight reduction in metamorphic success of 20% from control levels at the highest pre-exposure SSC of 300 mg L^{-1}. The reduction in metamorphosis at 300 mg L^{-1}, although not statistically significant in *C. foliascens*, is in the line to previous reports from the coral species *A. tenuis* (Ricardo et al., 2016a), and this effect could be due to structural damage to the larvae from suspended sediment or a reduction in larval energetic reserves from having to maintain swimming at this high SSC that may have compromised metamorphosis. While the upper percentiles of SSCs within a period of 24 h ranged within 10's of mg L^{-1} as determined from logger measurement from a fixed point in a dredging scenario (Jones et al., 2015), larvae may still experience higher levels of suspended sediment as they drift in currents along with suspended sediment. Nevertheless, we did not detect any secondary post-settlement effects on settler survival and growth derived from larvae that had been exposed to SSCs of up to 300 mg L^{-1}, which demonstrate that settlers had an equal chance of surviving and growing after 30 d, regardless of SSC pre-exposures if suitable substrate was available and turbidity returned to ambient levels.

The nature of the available substrate can influence the attachment and settlement success of marine invertebrate larvae (Hodgson, 1990; Webster et al., 2011; Doropoulos et al., 2012; Ricardo et al., 2017). The majority of *C. foliascens* larvae (57%) preferentially settled onto the bottom substrate when sediment was absent. This settlement behaviour was likely influenced by photonegative behaviour of >24 h old larvae (Abdul Wahab et al., 2014b), coupled with a light source from the surface that would promote larval interactions with the bottom substrate. Larvae clearly explored the sediment covered container bottoms, as evidenced by fine tracks across the sediment surface, and were also able to successfully settle onto a sediment load of up to 3 mg cm^{-2} (>10%), and occasionally onto deposits of 30 mg cm^{-2} (<2%). However, in general terms, larvae clearly avoided bottoms that were thickly covered with sediment, and preferentially settle onto the sediment-free vertical surfaces at higher deposited sediment levels of 10 mg cm^{-2} and above. This avoidance behaviour was most pronounced in the highest sediment treatment and interestingly contributed to a final successful settlement that was similar in the 30 mg cm^{-2} concentration to the 1 mg cm^{-2} concentration. The sediment avoidance behaviour here is analogous to that reported for the coral *A. millepora*, whereby, while majority of larvae would preferentially settle onto upward facing surfaces, they would alternatively settle onto downward facing surfaces without incurring any reduction in the total number of settlement should the former is covered by sediment; provided a strong settlement inducer, sufficient light and no space competitor were present (Babcock and Davies, 1991; Ricardo et al., 2017). In nature, and when larvae are presented to habitats having patchy sediment deposition, such as rugose reef substrate, this sediment avoidance behaviour may increase the chances of larvae attaching, settling and surviving through periods of elevated sedimentation, provided the accumulation of sediment that could cause smothering of the settler do not occur (e.g. in shallow crevices susceptible to infilling), and that the alternative habitat meets juvenile and adult physiological requirements (e.g. receive sufficient light for a phototrophic sponge species). Notably, small explants of the sponge *Scopalina lophyropoda* have been shown to survive better when refuge was provided from sediment smothering (Maldonado et al., 2008).

Interestingly, the ability of *C. foliascens* larvae to settle onto surfaces that were covered by sediment at the lower to mid-range DSLs between 0.3 and 3 mg cm^{-2}, may have been facilitated by the corkscrew swimming behaviour of the sponge larvae during substrate exploration up until settlement (Maldonado, 2006) that allowed larval penetration to the substrate. At the higher DSLs of 10 to 30 mg cm^{-2} where sediment thickness was up to ~200 μm, access to the substrate may have likely been facilitated via openings (holes or thinner areas) in the sediment layer that was often observed. Despite the initial successful attachment and settlement of larvae onto substrate with sediment, the final numbers of larvae that remain attached after a sediment clearing procedure (by gentle wafting using a pipette, analogous to the process of natural resuspension by hydrodynamics) decreased with increasing DSL up to 3 mg cm^{-2}, with a ~25× higher chance of dislodgement for settlers on the 3 mg cm^{-2} compared to those on the 0.3 mg cm^{-2} treatment. The dislodgement of settlers here may be due to weaker attachment of some individuals to the substrate resulting from the lower attachment surface area due to sediment acting as a barrier, a concept parallel to the "Attachment Point Theory" developed for fouling marine organisms (Scardino et al., 2008). Whether settlers would be able to better attach to the substrate over a longer period of staticity is unknown from the present study, however could be possible considering the plasticity of the sponge growth form and the ability of sponges to actively transport and eject internal sediment (Strehlow et al., 2017).

Within the context of anthropogenic disturbances such as dredging, while light attenuation associated with the increased turbidity during dredging can cause high levels of bleaching and mortality in adult *C. foliascens*, these sponges were able to survive through periods of up to four weeks in suspended sediment concentrations of up to 30 mg L^{-1} and sediment smothering of 50 mg cm^{-2} when light levels were kept consistent across sediment concentrations, highlighting the capability of adult sponges to withstand low to moderate dredging pressures (Pineda et al., 2016; Pineda et al., 2017a; Pineda et al., 2017b; Pineda et al., 2017c). However, sponges that were exposed to higher levels of dredging scenarios (e.g. SSC of 76 mg L^{-1}) experienced up to 90% mortality (Pineda et al., 2017a). In light of this, the relative EC_{50} and EC_{10} levels of larval mortality to SSCs of 17.6 L^{-1} and 2.6 mg L^{-1} respectively in this study, and LC_{50} and LC_{10} levels for adult sponges of 40.6 L^{-1} and 21.5 mg L^{-1} respectively in Pineda et al. (2017b), could be used in conjunction as technical criterion for future risk modelling of sponge populations to sediment pressures such as during dredging or seabed mining.

5. Conclusion

The larvae of *C. foliascens* responded to elevated SSCs through changes in behaviour, including a reduction in swimming speeds and the loss of positive phototaxis. In addition, larvae did not have the ability to remove sediment particles that were attached to their body that led to the formation of sphere morphologies and the total loss of swimming capability. These effects have repercussions in broader terms by reducing dispersal potential and would mean a higher chance of larvae encountering natal habitats that are already affected by natural and anthropogenic sediment related pressures such as terrestrial run-off, resuspension events and dredging. Majority of larvae (>50%) survived SSC exposures and can settle onto substrate with sediment deposits of up to 3 mg cm^{-2}, however are at greater risk of dislodgement and subsequent mortality from hydrodynamic agitation. Larvae have the ability to avoid settlement onto substrate having sediment deposits of >10 mg cm^{-2}, which can reduce the chance of mortality by settling onto alternative substrate that are sediment-free. While adult *C. foliascens* can persist through periods of elevated sediment from anthropogenic activities (e.g. dredging), nothing is currently known about the responses of juvenile sponges under similar conditions, and about the associated post-settlement vital processes that could be affected.

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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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References

Abdul Wahab, M.A., de Nys, R., Whalan, S., 2011. Larval behaviour and settlement cues of a brooding coral reef sponge. Coral Reefs 30, 451–460.
Abdul Wahab, M.A., de Nys, R., Webster, N., Whalan, S., 2014a. Phenology of sexual reproduction in the common coral reef sponge, *Carteriospongia foliascens*. Coral Reefs 33 (2), 381–394.
Abdul Wahab, M.A., de Nys, R., Webster, N., Whalan, S., 2014b. Larval behaviours and their contribution to the distribution of the intertidal coral reef sponge *Carteriospongia foliascens*. PLoS One 9, e98181.
Abdul Wahab, M.A., Fromont, J., Whalan, S., Webster, N., Andreakis, N., 2014c. Combining morphometrics with molecular taxonomy: how different are similar foliose keratose sponges from the Australian tropics? Mol. Phylogenet. Evol. 73, 23–39.
Abdul Wahab, M.A., Fromont, J., Gomez, O., Fisher, R., Jones, R., 2017. Comparisons of benthic filter feeder communities before and after a large-scale capital dredging program. Mar. Pollut. Bull. 122, 176–193.
Airoldi, L., 2003. The Effects of Sedimentation on Rocky Coast Assemblages. Oceanography and Marine Biology, an Annual Review. volume 41. CRC Press, pp. 169–171.
Airoldi, L., Cinelli, F., 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. J Exp Mar Biol and Ecol 215, 269–288.
Anthony, K., Larcombe, P., 2000. Coral reefs in turbid waters: sediment-induced stresses in corals and likely mechanisms of adaptation. Proceedings of the Ninth International Coral Reef Symposium, pp. 239–244.
Armsworthy, S.L., MacDonald, B.A., Ward, J.E., 2001. Feeding activity, absorption efficiency and suspension feeding processes in the ascidian, *Halocynthia pyriformis* (Stolidobranchia: Ascidiacea): responses to variations in diet quantity and quality. J. Exp. Mar. Biol. Ecol. 260, 41–69.
Babcock, R., Davies, P., 1991. Effects of sedimentation on settlement of *Acropora millepora*. Coral Reefs 9, 205–208.
Bell, J.J., 2008. The functional roles of marine sponges. Estuar. Coast. Shelf Sci. 79, 341–353.
Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., Shaffer, M., 2015. Sediment impacts on marine sponges. Mar. Pollut. Bull. 94, 5–13.
Bessell-Browne, P., Fisher, R., Duckworth, A., Jones, R., 2017a. Mucous sheet production in *Porites*: an effective bioindicator of sediment related pressures. Ecol. Indic. 77, 276–285.
Bessell-Browne, P., Negri, A.P., Fisher, R., Clode, P.L., Duckworth, A., Jones, R., 2017b. Impacts of turbidity on corals: the relative importance of light limitation and suspended sediments. Mar. Pollut. Bull. 117, 161–170.
Churchill, J.H., 1989. The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. Cont. Shelf Res. 9, 841–865.
Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Annu. Rev. Mar. Sci. 1, 443–466.
Cowen, R.K., Lwiza, K.M., Sponaugle, S., Paris, C.B., Olson, D.B., 2000. Connectivity of marine populations: open or closed? Science 287, 857–859.
Davies, J., Addy, J., Blackman, R., Blanchard, J., Ferbrache, J., Moore, D., Somerville, H., Whitehead, A., Wilkinson, T., 1984. Environmental effects of the use of oil-based drilling muds in the North Sea. Mar. Pollut. Bull. 15, 363–370.
Dayton, P., Jarrell, S., Kim, S., Thrush, S., Hammerstrom, K., Slattery, M., Parnell, E., 2016. Surprising episodic recruitment and growth of Antarctic sponges: implications for ecological resilience. J. Exp. Mar. Biol. Ecol. 482, 38–55.
Dellapenna, T.M., Allison, M.A., Gill, G.A., Lehman, R.D., Warnken, K.W., 2006. The impact of shrimp trawling and associated sediment resuspension in mud dominated, shallow estuaries. Estuar. Coast. Shelf Sci. 69, 519–530.
Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O., Mumby, P.J., 2012. Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. Ecol. Lett. 15, 338–346.
Duckworth, A., Giofre, N., Jones, R., 2017. Coral morphology and sedimentation. Mar. Pollut. Bull. 125, 289–300.
Erftemeijer, P.L., Lewis III, R.R.R., 2006. Environmental impacts of dredging on seagrasses: a review. Mar. Pollut. Bull. 52, 1553–1572.
Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146.
Fabricius, K.E., Wolanski, E., 2000. Rapid smothering of coral reef organisms by muddy marine snow. Estuar. Coast. Shelf Sci. 50, 115–120.
Fabricius, K.E., Logan, M., Weeks, S.J., Lewis, S.E., Brodie, J., 2016. Changes in water clarity in response to river discharges on the Great Barrier Reef continental shelf: 2002–2013. Estuar. Coast. Shelf Sci. 173, A1–A15.
Fell, P.E., 1974. Diapause in the gemmules of the marine sponge, *Haliclona loosanoffi*, with a note on the gemmules of *Haliclona oculata*. Biol. Bull. 147, 333–351.
Fisher, R., Stark, C., Ridd, P., Jones, R., 2015. Spatial patterns in water quality changes during dredging in tropical environments. PLoS One 10, e0143309.
Forward Jr., R.B., Cronin, T.W., Stearns, D.E., 1984. Control of diel vertical migration: photoresponses of a larval crustacean 1. Limnol. Oceanogr. 29, 146–154.
de Goeij, J.M., van Oevelen, D., Vermeij, M.J., Osinga, R., Middelburg, J.J., de Goeij, A.F., Admiraal, W., 2013. Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342, 108–110.
Halpern, B.S., Selkoe, K.A., Micheli, F., Kappel, C.V., 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conserv. Biol. 21, 1301–1315.
Heyward, A.A., Fromont, J.J., Schoenberg, C.C., Colquhoun, J.J., Radford, B.B., Gomez, O.O., 2010. The sponge gardens of Ningaloo reef, Western Australia. The Open Marine Biology Journal 4, 3–11.
Hodgson, G., 1990. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. Coral Reefs 9, 41–43.
Jones, R., Fisher, R., Stark, C., Ridd, P., 2015. Temporal patterns in seawater quality from dredging in tropical environments. PLoS One 10, e0137112.
Jones, R., Bessell-Browne, P., Fisher, R., Klonowski, W., Slivkoff, M., 2016. Assessing the impacts of sediments from dredging on corals. Mar. Pollut. Bull. 102, 9–29.
Lechowicz, M.J., 1982. The sampling characteristics of electivity indices. Oecologia 52, 22–30.
Levin, L.A., Mengerink, K., Gjerde, K.M., Rowden, A.A., Van Dover, C.L., Clark, M.R., Ramirez-Llodra, E., Currie, B., Smith, C.R., Sato, K.N., 2016. Defining "serious harm" to the marine environment in the context of deep-seabed mining. Mar. Policy 74, 245–259.
Luter, H.M., Widder, S., Botte, E.S., Abdul Wahab, M.A., Whalan, S., Moitinho-Silva, L., Thomas, T., Webster, N.S., 2015. Biogeographic variation in the microbiome of the ecologically important sponge, *Carteriospongia foliascens*. PeerJ 3, e1435.
Maldonado, M., 2006. The ecology of the sponge larva. Can. J. Zool. 84, 175–194.
Maldonado, M., Giraud, K., Carmona, C., 2008. Effects of sediment on the survival of asexually produced sponge recruits. Mar. Biol. 154, 631–641.
Maldonado, M., Ribes, M., van Duyl, F.C., 2012. Nutrient fluxes through sponges: biology, budgets, and ecological implications. Advances in Marine Biology. Elsevier, pp. 113–182.
Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E.L., 2017. Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 145–183.

McCulloch, M., Fallon, S., Wyndham, T., Hendy, E., Lough, J., Barnes, D., 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421, 727.

Metaxas, A., 2001. Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. Can. J. Fish. Aquat. Sci. 58, 86–98.

Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva Jr., J.M., Araujo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C., Bahia, R.G., Paranhos, R.P., Dias, R.J., Siegle, E., Figueiredo Jr., A.G., Pereira, R.C., Leal, C.V., Hajdu, E., Asp, N.E., Gregoracci, G.B., Neumann-Leitao, S., Yager, P.L., Francini-Filho, R.B., Froes, A., Campeao, M., Silva, B.S., Moreira, A.P., Oliveira, L., Soares, A.C., Araujo, L., Oliveira, N.L., Teixeira, J.B., Valle, R.A., Thompson, C.C., Rezende, C.E., Thompson, F.L., 2016. An extensive reef system at the Amazon River mouth. Sci. Adv. 2, e1501252.

Pineda, J., Reyns, N.B., Starczak, V.R., 2008. Complexity and simplification in understanding recruitment in benthic populations. Popul. Ecol. 51, 17–32.

Pineda, J., Porri, F., Starczak, V., Blythe, J., 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. J. Exp. Mar. Biol. Ecol. 392, 9–21.

Pineda, M.C., Strehlow, B., Duckworth, A., Doyle, J., Jones, R., Webster, N.S., 2016. Effects of light attenuation on the sponge holobiont- implications for dredging management. Sci. Rep. 6, 39038.

Pineda, M.C., Strehlow, B., Kamp, J., Duckworth, A., Jones, R., Webster, N.S., 2017a. Effects of combined dredging-related stressors on sponges: a laboratory approach using realistic scenarios. Sci. Rep. 7, 5155.

Pineda, M.C., Strehlow, B., Sternel, M., Duckworth, A., Jones, R., Webster, N.S., 2017b. Effects of suspended sediments on the sponge holobiont with implications for dredging management. Sci. Rep. 7, 4925.

Pineda, M.C., Strehlow, B., Sternel, M., Duckworth, A., Haan, J.D., Jones, R., Webster, N.S., 2017c. Effects of sediment smothering on the sponge holobiont with implications for dredging management. Sci. Rep. 7, 5156.

Reiswig, H.M., 1971. Particle feeding in natural populations of three marine demosponges. Biol. Bull. 141, 568–591.

Reiswig, H.M., Miller, T.L., 1998. Freshwater sponge gemmules survive months of anoxia. Invert Biol 1–8.

Ricardo, G.F., Jones, R.J., Clode, P.L., Humanes, A., Negri, A.P., 2015. Suspended sediments limit coral sperm availability. Sci. Rep. 5 (18084).

Ricardo, G.F., Jones, R.J., Clode, P.L., Negri, A.P., 2016a. Mucous secretion and cilia beating defend developing coral larvae from suspended sediments. PLoS One 11, e0162743.

Ricardo, G.F., Jones, R.J., Negri, A.P., Stocker, R., 2016b. That sinking feeling: suspended sediments can prevent the ascent of coral egg bundles. Sci. Rep. 6, 21567.

Ricardo, G.F., Jones, R.J., Nordborg, M., Negri, A.P., 2017. Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces. Sci. Total Environ. 609, 277–288.

Ricardo, G.F., Jones, R.J., Clode, P.L., Humanes, A., Giofre, N., Negri, A.P., 2018. Sediment characteristics influence the fertilisation success of the corals *Acropora tenuis* and *Acropora millepora*. Mar. Pollut. Bull. 135, 941–953.

Rivera, A.S., Ozturk, N., Plachetzi, D.C., Degnan, B.M., Sancar, A., Oakley, T.H., 2012. Blue-light-receptive cryotochrome is expresses in a sponge eye lacking neurons and opsin. J. Exp. Biol. 215, 1278–1286.

Scardino, A., Guenther, J., De Nys, R., 2008. Attachment point theory revisited: the fouling response to a microtextured matrix. Biofouling 24, 45–53.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671.

Simpson, T.L., Fell, P.E., 1974. Dormancy among the Porifera: gemmule formation and germination in fresh-water and marine sponges. Trans. Am. Microsc. Soc. 544–577.

van Soest, R., Boury-Esnault, N., Hooper, J., Rützler, K., De Voogd, N., Alvarez, B., Hajdu, E., Pisera, A., Vacelet, J., Manconi, R., 2005. World Porifera database.Available on-line at. http://www.vliz.be/vmdcdata/porifera (Consulted on 23:2007).

Strehlow, B.W., Pineda, M.C., Duckworth, A., Kendrick, G.A., Renton, M., Abdul Wahab, M.A., Webster, N.S., Clode, P.L., 2017. Sediment tolerance mechanisms identified in sponges using advanced imaging techniques. PeerJ 5, e3904.

Tompkins-MacDonald, G.J., Leys, S.P., 2008. Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. Mar. Biol. 154, 973–984.

Webster, N.S., Soo, R., Cobb, R., Negri, A.P., 2011. Elevated seawater temperature causes a microbial shift on crustose coralline algae with implications for the recruitment of coral larvae. ISME J 5, 759–770.

Whalan, S., Ettinger-Epstein, P., Battershill, C., de Nys, R., 2008. Larval vertical migration and hierarchical selectivity of settlement in a brooding marine sponge. Mar. Ecol. Prog. Ser. 368, 145–154.

Whalan, S., Abdul Wahab, M.A., Sprungala, S., Poole, A.J., de Nys, R., 2015. Larval settlement: the role of surface topography for sessile coral reef invertebrates. PLoS One 10, e0117675.

Wilkinson, C.R., 1983. Net primary productivity in coral reef sponges. Science 219, 410–412.

Wilkinson, C.R., 1988. Foliose dictyoceratida of the Australian Great Barrier Reef: II. Ecology and distribution of these prevalent sponges. Mar. Ecol. 9, 321–327.

Wilkinson, C.R., Evans, E., 1989. Sponge distribution across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. Coral Reefs 8, 1–7.

Wulff, J., 1995. Effects of a hurricane on survival and orientation of large erect coral reef sponges. Coral Reefs 14, 55–61.

Wulff, J.L., 2006. Ecological interactions of marine sponges. Can. J. Zool. 84, 146–166.

Zhu, Z., Wang, H., Peng, D., 2017. Dependence of sediment suspension viscosity on solid concentration: a simple general equation. Water 9, 474. https://doi.org/10.3390/w9070474.