Impacts of water quality on *Acropora* coral settlement: The relative importance of substrate quality and light

Gerard F. Ricardo[1*], Charlotte E. Harper[1,2], Andrew P. Negri[1], Heidi M. Luter[1], Muhammad Azmi Abdul Wahab[1], Ross J. Jones[1]

[1]Australian Institute of Marine Science, Townsville, 4810, Queensland, Perth, 6009, Western Australia, and Darwin, 0810, Northern Territory, Australia

[2]University of Plymouth, Drake Circus, Plymouth, Devon, PL4 8AA, UK

[*]Corresponding author: G.F. Ricardo, email: g.ricardo@aims.gov.au, ph: (07) 4753 4423

Abstract

A vast array of factors are associated with coral larval settlement patterns; however, the relative roles of individual factors are rarely tested in isolation, leading to confusion about which are most crucial for settlement. For example, direct effects of light environment are often cited as a major determinate of settlement patterns, yet this has not been demonstrated under environmentally realistic lighting regimes in the absence of confounding factors. Here we apply programmable multispectral lights to create realistic light spectra, while removing correlating (but not obvious) factors that are common in laboratory settlement experiments. Using two common species of *Acropora* – key framework builders of the Great Barrier Reef – we find little evidence that light intensity or changes in the spectral profile play a substantial role in larval settlement under environmentally realistic settings, but can under more extreme or artificial settings. We alternatively hypothesise and provide evidence that chronic conditions of light and recent sediment exposures that impact benthic substrates (e.g. crustose coralline algae) preceding settlement have a greater impact, with up to 74% decrease

in settlement observed on substrates with prior exposure and poor water quality conditions. Management of water quality conditions that impact the quality of benthic-settlement substrates therefore should present a priority area of focus for improving coral recruitment.

Keywords: Coral settlement – water quality– sediment – spectral patterns – light intensity

Introduction

Understanding the relative importance of drivers affecting recruitment has been a fundamental objective of marine ecology for many decades (Giese 1959, Roughgarden et al. 1988), and is of critical importance for predicting how reefs will recover following disturbances, and aiding intervention efforts such as translocation of progeny to damaged reefs (Randall et al. 2020, Vanderklift et al. 2020). In coral reef ecosystems, direct light and spectral quality are perceived as key influences to coral settlement patterns, with implications for depth-zonation in corals as well as changes in settlement preferences under poor water quality regimes (Mundy & Babcock 1998, Mundy & Babcock 2000, Fox 2004, Strader et al. 2015, Turner et al. 2018). In the shallows, the water column and benthos are exposed to high irradiance across a broad spectrum; but the spectral profile shifts left across the visible spectrum with increasing depth to become dominated by shorter (blue) wavelengths (Kirk 1994). Across sediment gradients, there is a competing right-shift towards the centre of the visible spectrum with green-yellow light becoming more dominant (Jones et al. 2016, Strydom et al. 2017, Cussioli et al. 2020). Under both gradients, these shifts in the spectral profile co-occur with decreasing light intensity.

For adult corals, there is a strong mechanistic basis for changes in the light environment influencing individual health. Adult corals are primarily autotrophic during their benthic lifecycle stage (Muscatine 1990), and coral photosynthesis and growth may be limited by decreases in light intensity and spectral shifts away from the maximally absorbance of

regions of chlorophyll *a* (blue and red wavelengths) termed 'photosynthetically usable radiation' (PUR) (Morel 1978, Dustan 1982). Consequently, benthic-light monitoring is suggested as a valuable metric to measure and manage water quality for inshore reefs (Gruber et al. 2019, Magno-Canto et al. 2019, Robson et al. 2019, Jones et al. 2020). But for coral early-life stages preceding the establishment of autotrophy (i.e. acquisition and utilisation of algal symbionts as the primary energetic pathway), the role direct light plays is an area of active research. Numerous studies have suggested light quality and quantity affects where larvae settle at depth and at which orientation (Mundy & Babcock 1998, Mundy & Babcock 2000). Indeed, sensory mechanisms to detect changes in light quality and intensity have been proposed with evidence of opsins and cryptochromes (a class of proteins involved in circadian rhythms) (Levy et al. 2007, Mason et al. 2012).

Despite plausible mechanisms to sense light in larvae, settlement responses to light often contradict, even within the same species. For example, *Acropora tenuis* settlement patterns purportedly increase (Mundy & Babcock 1998), decrease (Suzuki & Hayashibara 2006), or remain relatively unchanged (Yusuf et al. 2019) with light intensity. However, an issue is that many factors within the water column and on the benthos may simultaneously act on a settling larva, and that these are rarely controlled in experiments making interpretation of settlement patterns difficult. For example, grooves, edges and surface orientations of the substrate all influence the micro-light environment relevant to a larva. However, these physical characteristics can also affect thigmotactic behaviour in larvae, potentially creating unintended artefacts in settlement studies attempting to assess the influence of light. Therefore, even though light patterns at the time of settlement may correlate with settlement behaviour, it may not be a direct driver of observed patterns, as suggested for temperate invertebrate communities (Irving & Connell 2002). Further, light treatments common in laboratory experiments often do not match those that occur *in situ*. Most use narrow-band

(monochromatic) lighting or aquarium lights that exploit PUR by matching the profile to the absorption spectrum of the symbionts (Jones et al. 2020). While these systems are simple or optimized for photosynthesis and growth, the conditions do not effectively mimic the broader spectral patterns that are prevalent in the water column, nor the spectra that result from shifts in deeper water and in the presence of suspended sediments or plankton.

An alternate, but often overlooked, explanation of settlement patterns across depths and orientations is the potential influence of environmental conditions on the benthic substrate community in the weeks to months prior to settlement (Baird et al. 2003). Often the substrate in field recruitment tile surveys and laboratory experiments are conditioned in the same environments and configurations as those exposed to the larvae during settlement, making it challenging to disentangle long-term environmental and water-quality factors acting on the substrate from the acute light environment. For example, upwards-facing surfaces are exposed to sedimentation and higher light which in turn structures the substrate community. Autotrophs are common on these surfaces, whereas low-light specialists and heterotrophs often dominate undersides (Erwin et al. 2008, Doropoulos et al. 2020). Therefore, biotic factors that attract and repel larvae on these surfaces may impact settlement to a greater degree than the direct light environment present at the time of settlement. Conversely, field studies that attempt to link the substrate community with settlement patterns often ignore the water-quality conditions at the time of settlement, and can suffer from the known issues with identifying settlement cues and inhibitors visually (Erwin et al. 2008).

Recently, technological advancements in *in situ* spectroradiometers and aquarium light emitting diode (LED) technology have allowed for improved characterisation and simulation of a range of natural water column spectra and intensities. Here, we employ these technologies to address some of the limitations of prior light experiments by applying highly-controlled but realistic experimental approaches to investigate environmental influences on

settlement. We first measure *in situ* exposures with *in situ* spectroradiometers at scales relevant to settling larvae across depth, turbidity and within crevices. Next, we use these observations to inform the simulation of a range of natural water column spectra and intensities using a custom-built multispectral feedback LED lighting system for application in coral settlement experiments. These experiments are designed to eliminate variables such as three-dimensional shading and edge-effects that have confounded most previous experiments. We hypothesise that depth and water-quality light profiles at the time of settlement will lead to changes in settlement success. As an alternative hypothesis, we assess whether chronic (longer-term) water-quality conditions that impact the conditioning and quality (attraction or inhibition) of the settlement substrate is the primary driver of settlement success.

Methods

Methodological overview

To investigate the influence of light (quality and quantity) on coral settlement, coral larvae from the common Indo-Pacific corals *Acropora millepora* and *Acropora tenuis* were exposed to a number of different light treatments in a series of experiments. Light treatments included different intensity and spectra of narrow-band monochromatic light as well as spectra corresponding to clearer-water and naturally turbid coastal environments (see Settlement series 1; Table 1). Next, substrates conditioned at two sites of differing water quality were used to assess the impact of chronic effects of exposures on the substrate and the subsequent impact on coral settlement (see Settlement Series 2; Table 1).

122 Table 1. Experimental treatments used in each experiment. PAR = Photosynthetically Active Radiation (µmol
123 photons m^{-2} s^{-1}). DLI = Daily Light Integral (mol photons m^{-2} d^{-1}). 'Upwards' and 'downwards' refer to orientation
124 of the settlement discs during field conditioning. SS = suspended sediment. NTU = Nephelometric Turbidity
125 Units.

Design	**Exp.**	**Spectra**	**PAR**	**DLI**
Settlement series 1				
Monochromatic	Exp.1 & 5	Broad, blue, green, yellow, red	30	1.3
Simulated depth	Exp.2	Low broad, high broad, low blue, high blue	30, 320	1.3, 14
Simulated turbidity	Exp.3 and 5	~0.8, 1.5, 3, 9 NTU	30	1.3
Light intensity	Exp.4	Broad and SS-simulated (0.8 and ~9 NTU)	<1, 10, 30, 100, 300	<0.1, 0.3, 0.9, 3, 9
Experiment		**Treatment**	**PAR**	**DLI**
Settlement series 2				
Deposited sediment	Exp. 6	0.1, 0.3, 0.8, 2.5, 8, 25, 83, 250 mg cm^{-2}	30	1.3
Field conditioning	Exp. 7	Low-turbidity upwards, low-turbidity downwards, high-turbidity upwards, low-turbidity downwards	30	1.3

126 Coral collection, larval culturing and substrate conditioning

127 Coral collection and larval culturing followed Heyward and Negri (1999) and Ricardo et al.
128 (2018), and further details can be found in the Supplementary Material (Text S1). Artificial
129 substrates for settlement were created using 7-cm diameter polyvinyl chloride (PVC) discs.
130 PVC was used for the following reasons i) it presents a flat surfaces to ensure there is no
131 shading of downwelling light, ii) it can be manufactured to minimise edge-effects, and iii) is
132 successful at conditioning a number of settlement cues and thus frequently used in settlement
133 experiments (Lee et al. 2009, Fabricius et al. 2017, Kennedy et al. 2017, Ricardo et al. 2017).
134 For laboratory experiments, they were conditioned under layers of 70% block shade cloth
135 (maximum Photosynthetically Active Radiation (PAR) light intensity = ~250 µmol photons
136 m^{-2} s^{-1}) in flow-through outdoor SeaSim aquaria for ~3 months of the presence of crustose

137 coralline algae (CCA) *Porolithon onkodes* a common species known to induce settlement of
138 *Acropora* coral larvae (Heyward & Negri 1999). The discs were conditioned randomly within
139 the aquaria and CCA covered about 20–40% of the total disc area at the commencement of
140 each experiment.

141 Before settlement experiments commenced, larvae were assessed for their settlement
142 competency (*sensu* Guest et al. (2010)), and further details can be found in the
143 Supplementary Material (Text S1). For all settlement experiments excluding Exp. 6, each
144 disc was positioned at the base of a 500 mL black chamber containing 250 mL 0.5 µm-
145 filtered seawater (FSW). The outside of the disc was wrapped in thread seal Teflon tape
146 which effectively prevented larvae settling on the conditioned vertical edges of the disc.
147 Additionally, cleaned river sand was added to the bottom of the chambers up to prevent
148 larvae settling in the edges (Ricardo et al. 2017). At the commencement of the experiments,
149 larvae (n = 30) were added into the chambers to settle. A constant light intensity, as opposed
150 to a ramping light intensity, was used to prevent confounding across the light treatments, and
151 each treatment was programmed on a 12:12 light/dark cycle with the larvae censused after 12
152 hours of light exposure and then after a further 12 hours of darkness to assess any latency
153 effects. All experiments were conducted at 27˚C and measured using a Hobo Onset
154 Temperature logger in a reference chamber under each light.

155 In situ measures for laboratory light treatments

156 *In situ* light measurements of this study were conducted at inshore sites within Cleveland
157 Bay, Great Barrier Reef using a range of PAR light meters and spectroradiometers, with these
158 data used to justify the light treatment-levels used in experiments. Briefly, a light meter
159 connected to a diving pulse amplitude modulating fluorometer (PAM) (Walz, Germany) was
160 used to characterise the benthic substrate light intensity levels that coral larvae are likely to
161 settle (Table 2). We consequently selected 30 µmol photons m^{-2} s^{-1} for the 'control' light

intensity in experiments. To characterise long-term underwater light intensities and spectral changes with turbidity, two eight-wavelength multispectral radiometers (MS8, In Situ Marine Optics, Australia) were deployed in ~5-m depth at Florence Bay (lower turbidity; 19.121°S, 146.882°E) and Picnic Bay (higher turbidity; 19.186°S, 146.840°E) reefs. Additionally, to characterise more extreme light spectral profiles under turbidity and depth, instantaneous spectral profiles were measured using a USSIMO hyperspectral radiometer (In Situ Marine Optics, Australia) at a clear-water site (19.085°S, 146.947°E) at two depths (5 m and 21 m), and a highly turbid-water site at 5 m depth (19.169°S, 146.905°E). The light spectral profile at 5-m depth (~0.8 NTU) was then applied as the experimental control in all experiments. In addition to the *in situ* spectral measurements described above, individual light channels of the lighting systems (see below) were used to replicate more artificial monochromatic wavelengths commonly applied in spectral-light response studies. Further details can be found in the Supplementary Material (Text S2).

Table 2. In situ measurements for design of the laboratory experiments. See text for further site details. PAR = Photosynthetically Active Radiation (µmol photons m^{-2} s^{-1}). DLI = Daily Light Integral (mol photons m^{-2} d^{-1}). FWHM = Full-width half-maximum.

Measurement	Instrument	Measurement	Details
Substrate light intensities	Diving PAM	15.56 PAR; ~0.5 DLI	Mean discrete measurements over a substrate during midday on a cloudless day.
Temporal light intensities	MS8 multispectral	342.89 midday PAR; 7.8 DLI	Mean intensities over a 3 mo. period at the low-turbidity site.
Spectral profiles	USSIMO hyperspectral	484 nm; 187 FWHM, 0.8 NTU (clear shallow) 484 nm; 126 FWHM, 1 NTU (clear deep) 559 nm; 124 FWHM, 5 NTU (turbid shallow)	Modal and full-width half maximum wavelength at clear shallow and deep water, and a shallow turbid-water site
Turbidity (NTU)	DL3 nephelometer	0.8 NTU, 1.5 NTU, 3.0 NTU, 9.4 NTU	NTU corresponding to the spectral profiles used. These values represent the 6th, 45th, 77th, and 88th percentile recorded at the turbid water site (Picnic Bay). NTU can be converted to

			suspended sediments using a conversion factor of 1.1.

*assumes a cosine approximation

Experimental lighting setup

Ten spectrally-tuneable LED-based light systems were designed in-house to simulate realistic light spectra found in marine environments. Each of the lights contained 840 individual LEDs controlled by 19 independent colour channels. The lighting system was integrated into a PLC system (Siemens PCS7, Supervisory Control and Data Acquisition System), with the channels adjusted through a feedback system to a user-defined light intensity level. Neutral density shade film was also added to each light to allow for greater control of the channels at lower light intensities. Light intensity was measured with a PAR Quantum sensor (Skye SKP 215). For Daily Light Integral calculations (DLIs), PAR measurements across a 24-hr period were summed. Irradiance in experiments were measured with a Jaz spectrometer (Ocean Optics) calibrated to a recently calibrated HL-2000 lamp. The spectrometer was connected to a 5-m long 400-µm diameter fibre optic with a 3.9 mm diameter in-water cosine corrector attached. Irradiance from spectrometers were interpreted as relative rather than absolute values because of the common issues associated with spectrometer calibrations, light flickering, and attenuation of light under cosine correctors (Johnsen 2012), and were therefore corrected against the PAR Quantum sensor. All absolute irradiance readings (in µW cm^{-2} nm^{-1}) were binned to the nearest nanometre and converted to photons (µmol photons m^{-2} s^{-1} nm^{-1}) using the equation (Thimijan & Heins 1983):

$$\frac{nm \times irradiance\ (\mu W\ cm^{-2}\ nm^{-1})}{11962.15}$$

Settlement Series 1: Acute light exposure–experimental settlement trials

Exp. 1. Artificial light spectra on A. millepora settlement

Five replicate chambers were positioned under each light treatment which included a realistic broad-spectrum control and four narrow monochromatic bands. The width of the bands are described using full-width at half maximum (FWHM). The median and FWHM correspond to broad-spectrum: median λ = 535 nm; FWHM = ~172 nm; artificial blue light: λ = 441 nm; ~17 nm, artificial green light: 499 nm; ~25 nm, artificial yellow light: 602 nm; ~28 nm, and artificial red light: 658 nm; ~20 nm) (Table 1). To demonstrate repeatability and to increase sensitivity to treatments, we repeated the experiment using a 'choice' design (more details in Supplementary Material, Text S3).

Exp. 2: Realistic depth-dependant light on A. millepora settlement

Settlement preferences in response to depth-derived light spectra and intensity is often cited in the literature to influence the zonation of corals (Mundy & Babcock 1998). Broad and artificial blue spectra were supplied at two light intensities (Table 1). The broad-light intensities used were based upon the USSIMO field data described above at 5-m depth and 21-m depth from the clear blue-water site and broadly matched spectral profiles used in Mundy and Babcock (1998). The light channels for the 'blue' treatment were used to reproduce more extreme artificial peaks.

Exp. 3: Realistic turbidity-dependant light spectra on A. millepora settlement

Five turbidity-dependent light spectral profiles were simulated using NTU percentiles in Jones et al. (2020), with light on a 12:12 h light/dark cycle and PAR held constant (~30 µmol photons m^{-2} s^{-1}; 1.3 DLI). The spectral patterns treatments were bracketed between NTU recorded at the clear-water site (site 47, ~0.8 NTU), and the 88th percentile at the turbid-water site (Picnic Bay, 9.4 NTU), which represented the best and worse-case turbidity scenarios

222 (Table 1 & 2). All spectral profiles used were at environmentally realistic light-intensity
223 combinations.

224 *Exp. 4: Light intensity in clear and turbid spectra on A. millepora settlement*

225 This experiment was designed to examine the combined effects of changes in light intensity
226 (5 levels) and quality (broad and shifted spectrums that would be associated with suspended
227 sediment concentrations equivalent to 0.8 NTU and ~9 NTU at 5-m depth). Five light
228 intensities were selected to cover the range of environmentally realistic values (<1, 10, 30,
229 100, 300 µmol photons m^{-2} s^{-1}, which equated to DLIs of <0.1, 0.3, 0.9, 3, 9 mol photons m^{-2}
230 d^{-1}), but more extreme combinations were also used to improve the model fit and assess the
231 strength of the response.

232 *Exp. 5. Artificial and realistic light spectra on A. tenuis settlement*

233 A reduced set of experiments were conducted on *A. tenuis* in 2018 and 2019. The 'realistic-
234 broad', 'artificial blue, 'artificial yellow, and 'artificial red' spectra (Experiment 1) were used
235 in the 2018 experiment. And subset of treatment levels 'realistic-broad', 'artificial red' were
236 conducted in 2019 to confirm results. Five simulated suspended sediment spectra (the same
237 as Experiment 3) were used to investigate realistic suspended-sediment spectral effects.

238 *Statistical analyses*

239 All acute-exposure settlement data were fit to Bayesian binomial generalised linear mixed
240 models, using a weakly informative prior (Cauchy; centre = 0, scale = 2.5) (Gelman et al.
241 2008) using the package *brms* (Bürkner 2017) in *R* (version 3.6.1). As hypotheses were
242 planned, we did not remove any factors of interest during model selection even if not
243 statistically significant, because all variables were of interest (Gelman & Hill 2006);
244 however, comparisons of WAICs (Watanabe–Akaike Information Criterions) were used to
245 assess if there were interactive effects. Standardised effect sizes and credible intervals of the

posterior distributions were used to interpret the effect. Effect concentrations (EC10s), which are common effect-size threshold metric used in ecotoxicology, were calculated when possible (Warne et al. 2018).

Settlement Series 2: Chronic exposure of water quality stressors to substrate quality

Exp. 6: Combined water quality stressors on substrate quality

To assess chronic exposure of water quality to the settlement cue, settlement discs were conditioned in the field under various light and sediment regimes. The discs were held in in PVC structures which orientated them either upwards facing or downwards facing. Each of the structures held 7 discs in different orientation and 3 structures were deployed at Florence Bay (relatively low turbidity; 19.121°S, 146.882°E) and Picnic Bay (relatively high turbidity; 19.186°S, 146.840°E) to condition for four months. Each structure was positioned randomly around a coral bombora to aid in retrieval in the turbid conditions. The upward facing surfaces are generally exposed to higher levels of light and accumulate deposited sediments, whereas downward facing surfaces are exposed to lower light intensities. One structure at each site included light meters (Hobo Onset, MX2202) at each orientation to monitor relative light, calibrated to the MS8 multispectral sensor described above. Only the first few days of data after deployment were used because of algal fouling of the light meter sensor.

Approximately 1 week before the anticipated coral spawning, the structures were collected and transferred to flow-through aquaria in the SeaSim. One structure from Florence Bay was lost in turbid water during retrieval. The majority of macroalgae and sediment were removed from the discs as their inclusion would have made a census impossible. Settlement of larvae on these discs occurred in chambers under identical conditions using the methods described above in Settlement series 1 to remove any light or thigmotactic effects, and therefore the settlement response only represented changes in the substrate ‘quality’. Thirty competent *A. millepora* larvae were added to each experimental chamber under a 12:12 light/dark cycle for

271 24 hrs (30 µmol photons m^{-2} s^{-1}; 1.3 DLI; broad-spectral profile) using the chamber set-up
272 described above. Settled larvae were carefully counted using a Leica stereoscope by
273 examining under all the remaining foliage. Discs were imaged with a Canon 90D camera
274 using an EF-S 18–55 lens.

275 Settlement success on the discs were analysed with binomial GLMMs with 'site' and
276 'orientation' as fixed effects and 'disc' as a random effect with the package *lme4* (Bates et al.
277 2015). Pairwise comparisons were estimated with the package *emmeans* (Lenth et al. 2018).
278 Community composition on the discs were analysed using photoQuad (v1.4) (Trygonis &
279 Sini 2012), by grouping identifiable taxonomic and abiotic groups (macroalgae, green
280 filamentous algae, red filamentous algae, CCA, cyanobacteria, tube worms, bryozoa, detritus,
281 empty space, epilithic algal matrix (EAM), coral recruit, and unidentified). Taxonomic data
282 was visually assessed using an nMDS (Bray-Curtis measure of dissimilarity) with the
283 package *vegan* (Oksanen et al. 2007) using square-root transformed data. Environmental
284 vectors and ellipses were subsequently added. To test differences in community structure
285 between sites and orientation, PERMANOVA based on 999 permutations was implemented
286 using the '*adonis'* function in *vegan*. Each distinct community was further examined to
287 explore potential associations of taxa with settlement. Multicollinearity was assessed using
288 variance inflation factors (VIF), pairs plots, and biological relevance (Zuur et al. 2010).
289 Indicator Species Analysis using the package *labdsv* (Roberts & Roberts 2016) was first used
290 to identify the most important taxa separating each group. Taxa with an indicator value >0.2
291 were used as a preliminary selection in a GLMM model. Corrected Akaike Information
292 Criterion (AICc) was used to select the most parsimonious model.

293 *Exp. 7: Sediment smothering on substrate settlement cue*

294 While it was not feasible to investigate all water quality stressors on substrate quality, the
295 effect of temporary sediment deposition on the settlement cue was examined as a likely

296 mechanism (cause-effect pathway). Aragonite plugs (2-cm diameter) were conditioned for ~3
297 months in an outdoor aquarium system under 50% neutral density shade cloth (27 ˚ C;
298 maxima 200 µmol photons m^{-2} s^{-1}) and developed a thick covering of crustose algae
299 (*Titanoderma prototypum* and *Peyssonnelia* spp.). The experiment aimed to simulate a
300 sediment deposition and resuspension event and the plugs were exposed at various levels
301 (0.1, 0.3, 0.8, 2.5, 8, 25, 83, 250 mg cm^{-2}) of carbonate and siliciclastic deposited sediments
302 (see Ricardo et al. (2018) for sediment characterisation) in flow-through conditions under
303 ~30 µmol photons m^{-2} s^{-1} (PAR) linear-ramping lighting following Ricardo et al. (2017). The
304 sediments were then removed and each plug embedded in 60 mL glass chambers with
305 cleaned river sand to prevent settlement on vertical or under-surfaces. Ten competent larvae
306 were added to each chamber, and settlement on the sediment-free plugs was assessed at 24
307 hours. The plugs were then provided a recovery period of 3 days and then more larvae (n=10)
308 were added to each chamber and settlement assessed after a second 24 hours. Effective
309 quantum yields ($\Delta F/F_m$'), which estimates the photosystem II photosynthetic performance of
310 light-acclimated samples, were measured on the plugs after a 30 minute light-acclimation
311 period at 30 µmol photons m^{-2} s^{-1} with a mini-PAM (Waltz) using a red measuring light (6
312 mm fibre-optic probe) positioned ~ 3-mm away from the plug using a rubber spaces.
313 Measurements were taken before and after the exposure, and after the 3-day recovery period,
314 with 5 measurements per plug. The changes in settlement were analysed with a binomial
315 GLMM with 'plug' as random effect and the level of 'previously-deposited sediment' and
316 time (after exposure, recovery) as a fixed factor. The changes in yield at each time point was
317 measured with a four-parameter Weibull nonlinear model using the package *drc* (Ritz et al.
318 2016). The substrate composition was classified using Trainable Weka Segmentation in
319 ImageJ (Arganda-Carreras et al. 2017) on a Dell R820 256 GB High-performance Computer
320 System, and changes in proportion were predicted using a Dirichlet regression (Douma &

Weedon 2019) with 'previously-deposited sediment' and time (before exposure, after exposure, and recovery) as a fixed factor.

Results

Settlement Series 1: Acute light exposure–experimental settlement trials

Exp. 1: Artificial light spectra on A. millepora settlement

The spectral profiles of monochromatic light treatments were generally eight-fold narrower compared to the broad-spectrum "white" treatment (Fig. 1 a). During the light phase, settlement under monochromatic blue light was similar to the control, and while there was a ~16% decrease in settlement under red light and a ~27% decrease under green light, there was a no statistically detectable difference (the 95% credible intervals did not overlap zero) (Fig. 1 b-c). There was a clear difference yellow light from the broad-spectrum control (~35% decrease) (Fig. 1 b-c). These trends indicate that coral settlement may be suppressed by up to one-third with wavelengths between the 500 and 600 nm range. Although there was a small amount of additional settlement in the subsequent dark period from 12 to 24 hrs (~ 25%), settlement remained suppressed in the green and yellow treatments indicating potential latency effects. The variance explained by the model was 72%.

The light treatment wavelength in the choice experiment had generally wider spectral distributions than when each substrate was exposed independently because gel-filters were used instead of the multispectral lights (Fig. S1 a). There was no clear differences in settlement between the light treatments and broad-spectrum control, or over time (the 95% credible intervals did not overlap zero) (Fig S1 b-c). The variance explained by the model was 31%.

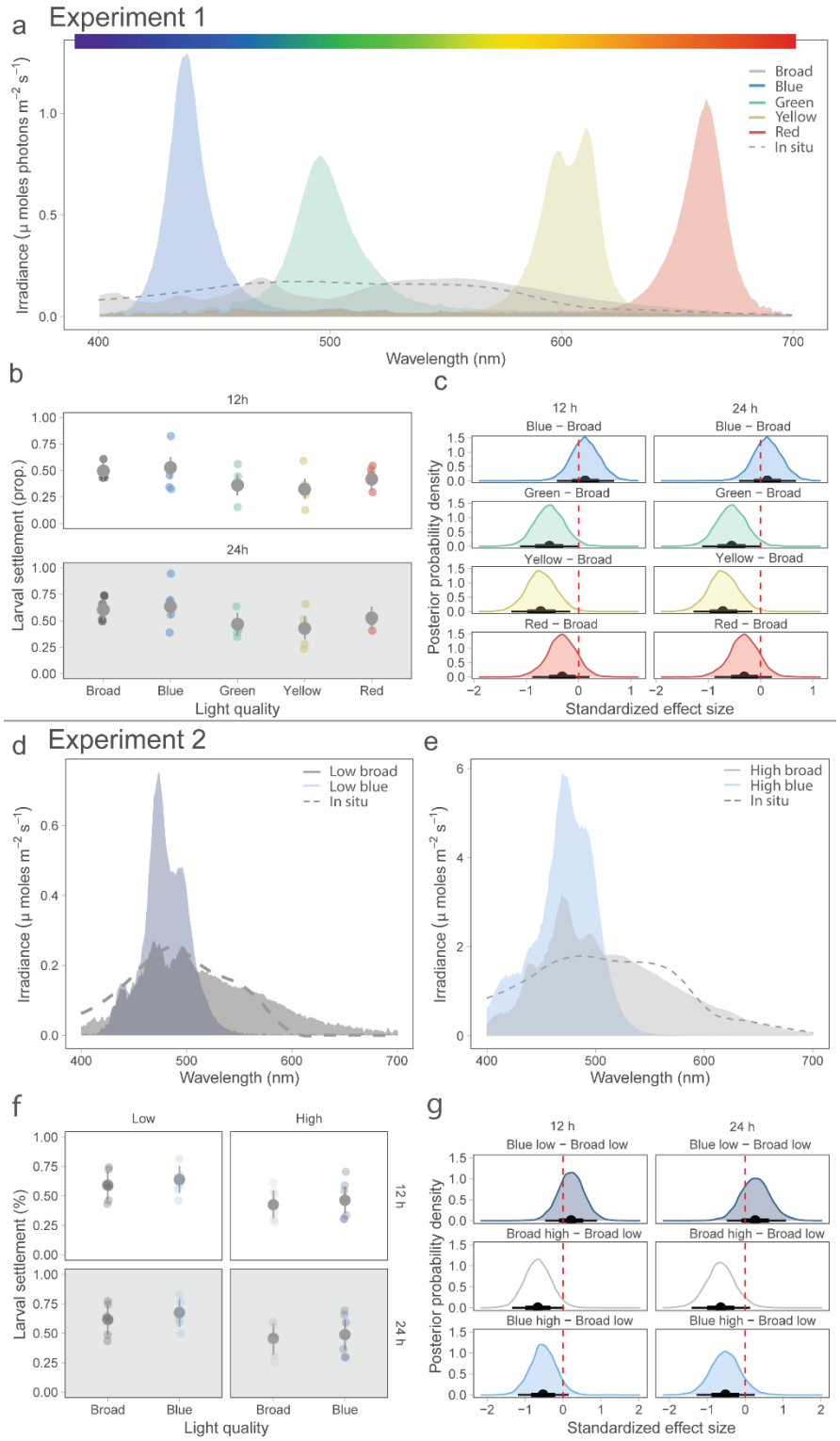


Fig. 1. Larval settlement of *Acropora millepora* under artificial monochromatic and depth-dependant light spectral profiles in Exp. 1 & 2. (a) Light spectral profiles used in Exp. 1. Grey dashed line = shallow clear-water site at 5-m depth and 0.8 NTU. (b) Exp. 1 larval settlement after 12 h (light) and 24 h (12 light + 12 h dark) (light grey), modelled means and 95% credible intervals (dark grey). (c) Exp. 1 Standardised Bayesian posterior half-densities

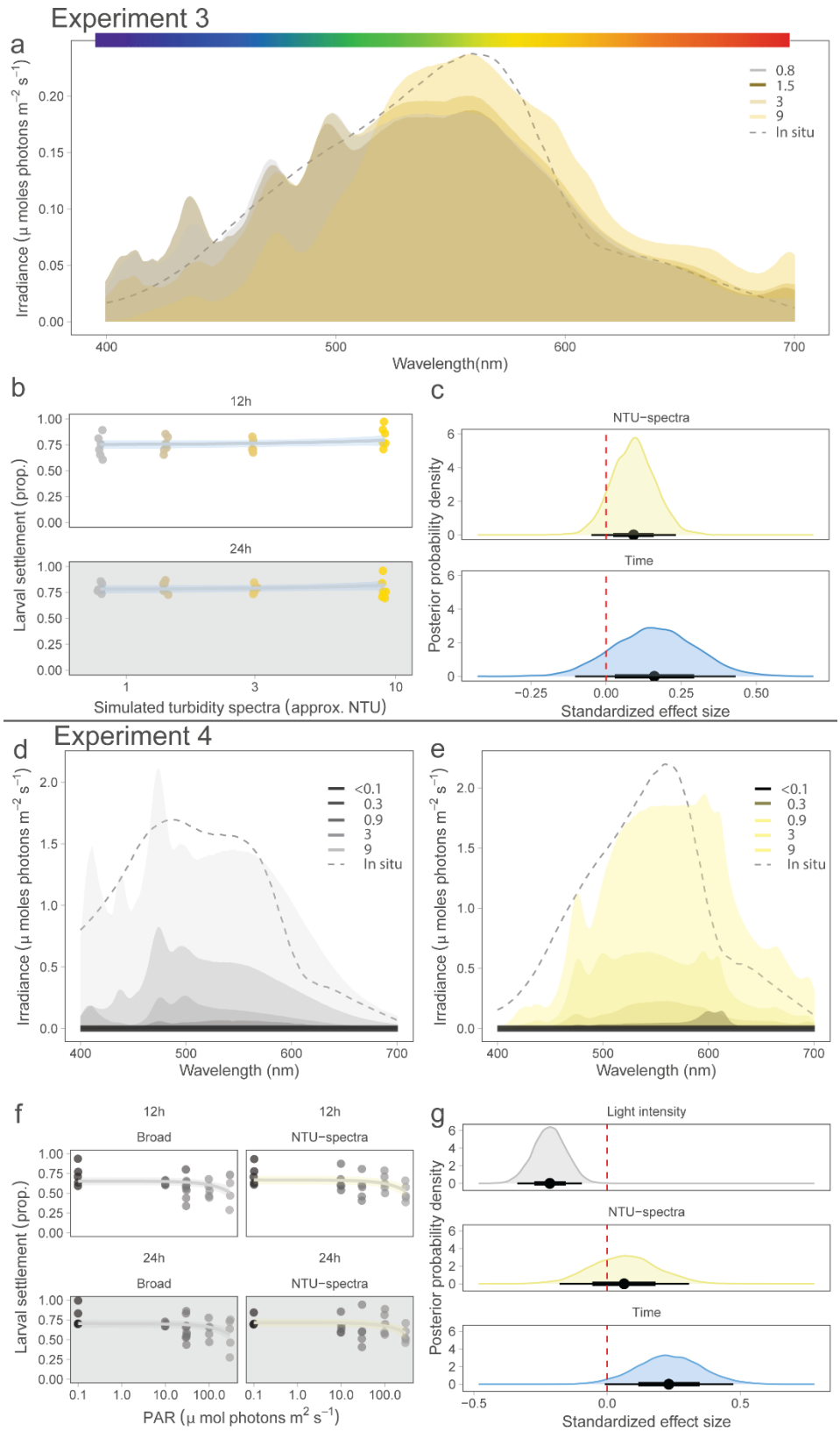
348 and credible intervals (thicker: 66%, thinner: 95%) of contrasts between each monochromatic light and the control
349 (broad spectra). The vertical dashed red line indicates the x-axis location of zero effect. (d) Lower-light spectral
350 profiles used in Exp. 2. Grey dashed line = deep clear-water site at 21 m depth and 1 NTU. (e) Higher-light spectral
351 profiles used in Exp. 2. Grey dashed line = shallow clear-water site at 5-m depth and 0.8 NTU. (f) Exp. 2 settlement
352 of larvae at two light intensities under broad-spectrum and artificial blue-light after 12 h (light) and 24 h (12 h
353 light + 12 h dark). (g) Standardised Bayesian posterior half-densities and credible intervals (thicker: 66%, thinner:
354 95%) of the contrasts between each light spectrum and the control (broad low). The vertical dashed red line
355 indicates the x-axis location of zero effect. Larval settlement competency was 90% for both experiments.

356 *Exp. 2: Realistic depth-dependant light on A. millepora settlement*

357 The low blue spectral profile had a narrower profile (FWHM = 39 nm) compared to the low
358 broad profile (FWHM = 118 nm) (Fig. 1d). Likewise, the high blue spectral profile had a
359 narrower profile (FWHM = 49 nm) compared to the low broad profile (FWHM = 81 nm)
360 (Fig. 1e). There was a moderate (although not significantly detectable) 28% decrease in
361 settlement under the higher light treatments (low: 0.62; 95% CI: 0.53–0.70); high: 0.44; 95%
362 CI: 0.35–0.54), and no evidence of an effect of the blue dominant spectra on settlement (Fig.
363 1f-g). A further 12 hr dark phase did not increase settlement indicating no latency effects
364 (Fig. 1f). The variance explained by the model was 78%.

365 *Exp. 3: Realistic turbidity-dependant light spectra on A. millepora settlement*

366 Low simulated-turbidity light treatments (~0.8–3 NTU) had similar spectral profiles whereas
367 the highest simulated-turbidity profile (~9 NTU) was narrower and peaked around ~550 nm
368 (Fig. 2a). The most parsimonious model only included 'time' as a predictor variable,
369 indicating no evidence of an influence on settlement between the low turbidity and high
370 turbidity-simulated spectra. Under the full model, there was no effect of the simulated
371 turbidity spectra (slope = 0.1; 95% CI = -0.05– 0.25), and there was a slight overall increase
372 of settlement between 12 hours (0.753, 95% CI: 0.721–0.783) and 24 hours (0.790, 95% CI:
373 0.761–0.819) (Fig. 2b,c). The variance explained by the full model was 25%.



374

375 Fig. 2. The relationship between light intensity and simulated turbidity spectra on larval settlement of *Acropora*
376 *millepora*. (a) Exp. 3 spectral profiles used to simulate in situ spectral patterns at various approximate turbidity
377 (NTU) levels (Jones et al. 2020). Grey dashed line = shallow clear-water site at 5-m depth and 0.8 NTU. (b) Exp.

3 larval settlement in the turbidity spectral treatments after 12 h (light) and 24 h (12 light + 12 h darkness). (c) Exp. 3 standardised Bayesian posterior half-densities and credible intervals (thicker: 66%, thinner: 95%) of contrasts. The vertical dashed red line indicates the x-axis location of zero effect. (d) Exp. 4 spectra used to simulate clear-water spectral patterns at five light intensities. Grey dashed line = shallow turbid-water site at 5-m depth and 5 NTU. (e) Exp. 4 spectra used to simulate high turbidity spectral patterns at five light intensities. (f) Exp. 4 larval settlement after 12 (light) and 24 hours (12 h light + 12 h dark) of the light exposure. (g) Exp. 4 standardised Bayesian posterior half-densities and credible intervals (thicker: 66%, thinner: 95%) of the contrasts. The vertical dashed red line indicates the x-axis location of zero effect. Larval settlement competency was 90% in both experiments.

Exp. 4: Light intensity in clear and turbid spectra on A. millepora settlement

The clear-water spectral profiles generally had a peak at in the blue wavelength (~480 nm) whereas the turbidity spectral profiles peaked in the green wavelengths (~550 nm) (Fig. 2d,e). There was no difference in settlement between the clear and turbid spectra treatments but a statistically detectable (the 95% credible intervals did not overlap zero) modest 22% decline in settlement at higher light intensities (12 hr: EC10 = 113 µmol photons m^{-2} s^{-1}; 95% CI: 11–214) (Fig. 2f,g). There was also a slight overall improvement in settlement of 8.4% following the dark-period, but there remained evidence of latency effects at higher light intensities (Fig. 2f-g). The variance explained by the model was 66%.

Exp. 5. Artificial and realistic light spectra on A. tenuis settlement

Settlement of *A. tenuis* in the broad spectra was low in both years (2018: ~20%; 2019: ~37%) compared with the settlement competency assays (>80%) indicating sub-optimal conditioning (CCA and biofilm) of the substrates for this species (Fig. 3a,c,e). In both years, the artificial red light increased settlement (2018: 2.2-fold greater, R^2 = 0.87; 2019: 1.4-fold greater, R^2 = 0.88) (Fig. 3a-d). There was no effect of the realistic dredge spectra (yellow-green dominant) on coral settlement (Fig. 3e,f), with 84% of the variance explained by the model.

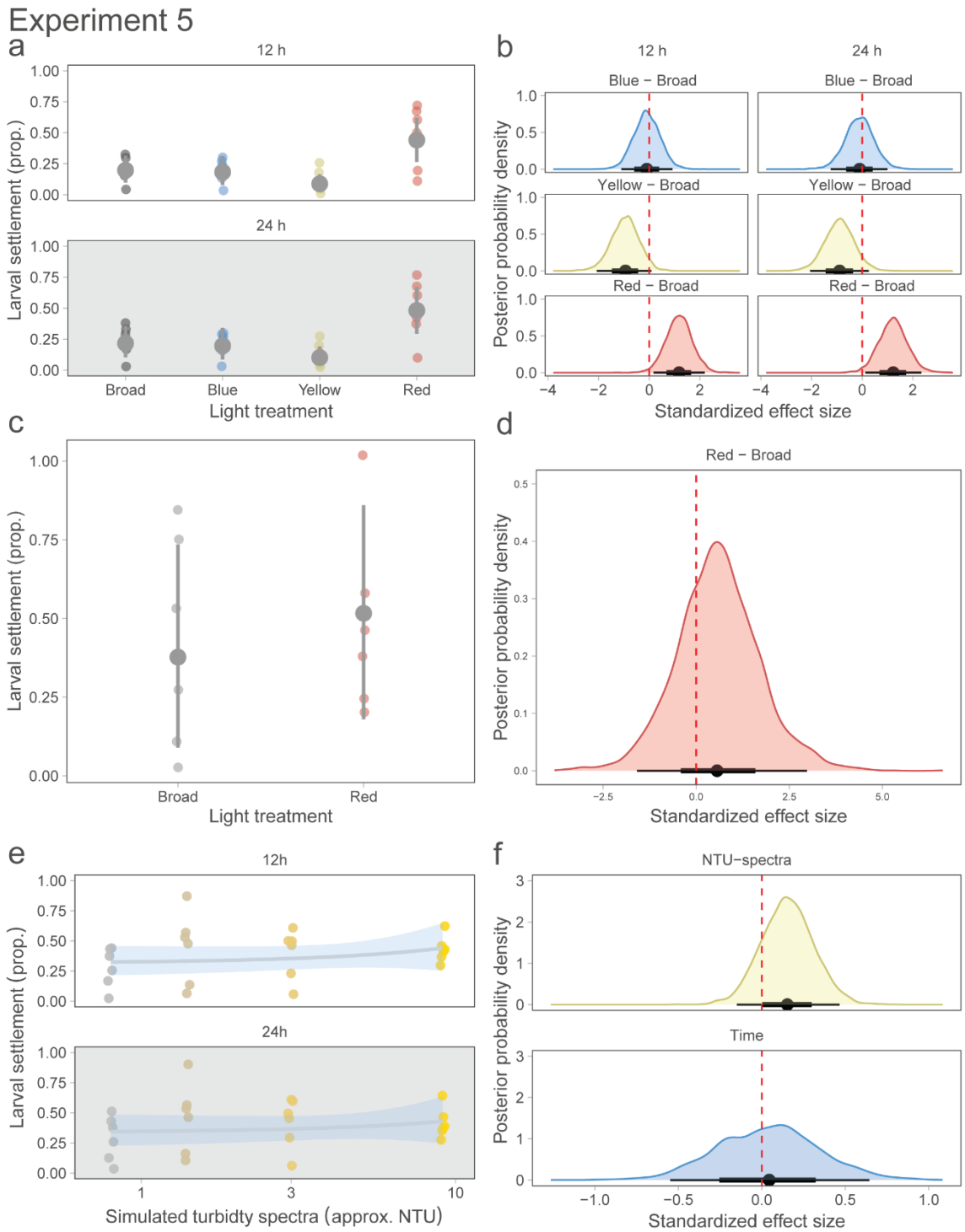


Fig. 3. Effects of artificial (monochromatic) and simulated turbidity spectral profiles on larval settlement of *Acropora tenuis* in Exp. 5. (a) Settlement after 12 and 24 hrs. Spectral profiles matched Exp. 1 (broad, artificial blue, artificial yellow, and artificial red). (b) Standardised Bayesian posterior half-densities and credible intervals (thicker: 66%, thinner: 95%) of contrasts between each monochromatic light and the control (broad spectra). The vertical dashed red line indicates the x-axis location of zero effect. (c) 2019 repeat experiment at only the broad

and artificial red treatments. (d) Standardised Bayesian posterior half-densities and credible intervals (thicker: 66%, thinner: 95%) of contrasts between each red light and the control (broad spectra). (e) Settlement in simulated-turbidity spectra reported in NTU after 12 h (light) and 24 h (12 light + 12 h darkness). (f) Standardised Bayesian posterior half-densities and credible intervals (thicker: 66%, thinner: 95%) of contrasts. Larval settlement competency for all assays were >80%.

Settlement Series 2: Chronic exposure of water quality stressors to substrate quality

Exp. 6: Combined water quality stressors on substrate quality

Water quality

The light environments of under surfaces were 8–9 fold lower than that of upwards facing surfaces of the field-deployed discs (Table 3). Light intensity was 30% and 20% lower at the higher turbidity Picnic Bay site compared with Florence Bay on upward and downward surfaces, respectively. Between sites, light on the downwards sides appeared only slightly lower, whereas the upward-facing surfaces were 1.44 fold higher at Florence Bay compared to Picnic Bay. Turbidity, which can be approximately converted to suspended sediment concentrations using a conversion factor of 1.1 (Jones et al. 2020), was greater at Picnic Bay (50th percentile = 1.62 NTU) compared to Florence Bay (50th percentile = 0.60 NTU).

Table 3. Water quality at each site and substrate orientation. Light was measured during the first 3 d of deployment. NTU was measured over for 1–2 mo. depending on the site.

Site	Orientation	DLI	NTU
Florence Bay	Upwards	18.5 (n=2)	0.6
Florence Bay	Downwards	2.07 (n=2)	
Picnic Bay	Upwards	12.9 (n = 2)	1.62
Picnic Bay	Downwards	1.65 (n = 1)	

Settlement

There was a clear difference in settlement on field conditioned discs at each orientation, with the effects more pronounced at the clearer water site (Florence Bay), compared with the more turbid-water site (Picnic Bay) (Fig. 4a,b). At Florence Bay there was a ~74% decrease (>99.99% probability of a negative effect) in settlement on the upwards-facing discs relative to the downward-facing discs. A similar although more modest trend occurred at Picnic Bay with a ~51% decrease (99.91% probability of a negative effect) in settlement on discs conditioned upwards. However, settlement on downwards-facing surfaces was lower at on discs conditioned at the more turbid Picnic Bay site by 36%. The variance explained by the model was 87%.

The community composition was different on discs at each site and orientation (Fig. 4c; PERMANOVA, $p = 0.002$), with clear separation between the upwards and downwards facing with discs. For Florence Bay downwards-facing discs, there was a negative correlation between crustose coralline algae and other red algae ($r = -0.74$, VIF = 2.78). Red algae was subsequently removed from the analysis. The exploratory analysis revealed CCA was associated with Florence Bay downwards-facing discs, tube worms with downwards-facing

surfaces at Picnic Bay, and empty space (uncolonised by macro-organisms) on Picnic Bay upwards-facing surfaces (Fig. S2).

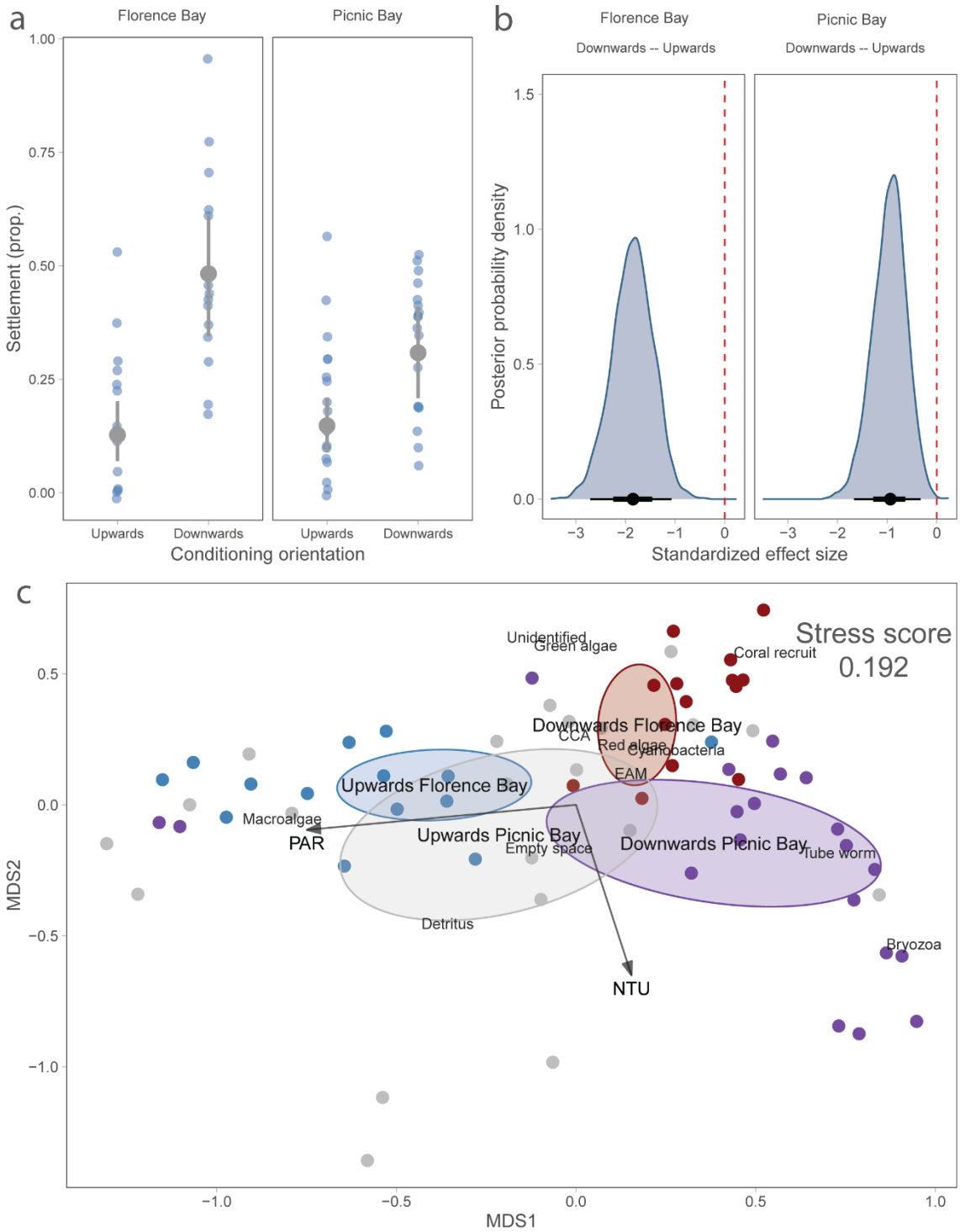


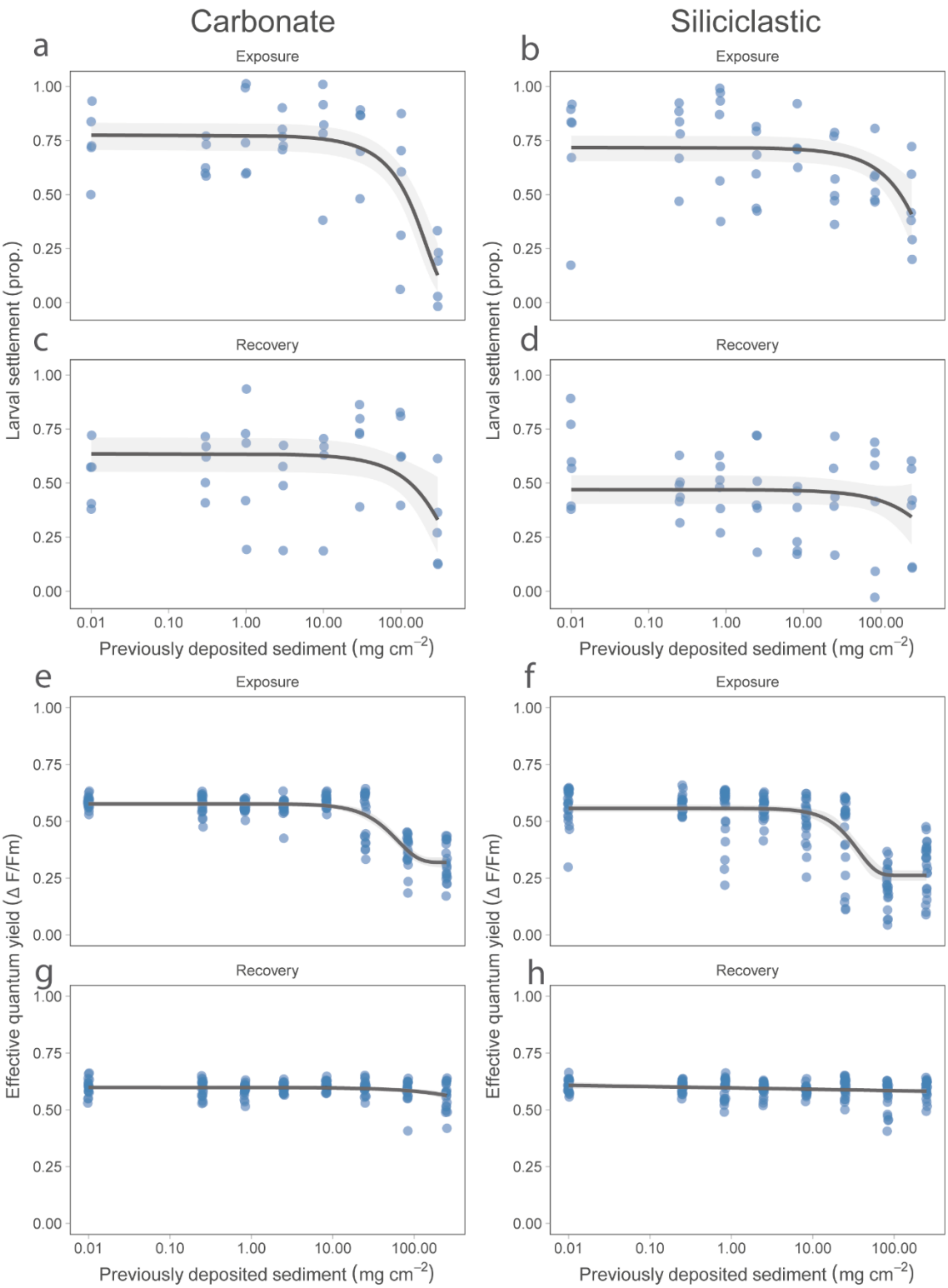
Fig. 4. Settlement and community composition of the settlement discs in Exp. 6. Settlement on the discs conditioned at (a) Florence Bay (clearer-water site) and (b) Picnic Bay (turbid-water site). All settlement occurred with discs facing upwards and under constant-light conditions. Larval competency was 80%. (c) An nMDS plot

showing community composition at each of the site and orientation combinations. Ellipses are represent 1 standard deviation around the centroids. Vectors represent the environmental factor fit. CCA = crustose coralline algae; EAM = Epilithic algal matrix, PAR = photosynthetically active radiation; NTU = Nephelometric Turbidity Units.

Exp. 7: Sediment smothering on the substrate settlement cue

Settlement

After the 3-day exposure to carbonate sediment, there was a clear decrease in settlement on the substrates exposed to the greatest levels of deposited sediment (Fig. 5a, EC10 = 38 mg cm^{-2}; 95% CI: 8.5–68). There was a slight improvement in larval settlement on the same substrate after the 3-day recovery period (Fig. 5c, EC10 = 63 mg cm^{-2}; 95% CI: 0–134). A similar yet less extreme response was observed following exposure to siliciclastic sediment (Fig. 5b, EC10 = 64 mg cm^{-2}; 95% CI: 16–112), with less influence on settlement after the recovery period (Fig. 5d, EC10 = 90 mg cm^{-2}; 95% CI: 0–217).



469

470 Fig. 5. Settlement of *Acropora millepora* larvae on CCA previously covered for 3-days in two types of deposited
471 sediment in Exp. 7. (a) Settlement following removal of carbonate sediment. (b) Settlement following removal of
472 siliciclastic sediment. (c, d) Settlement following a 3-day recovery period for each sediment type. (e) Effective
473 quantum yields ($\Delta F/F_m$') of CCA following removal of carbonate sediment (f) $\Delta F/F_m$' following removal of

474 siliciclastic sediment. (g, h) $\Delta F/F_m$' following a 3-day recovery period for each sediment type. Larval settlement
475 competency was 80%.

476 ### Sub-lethal indicators

477 Effective quantum yields ($\Delta F/F_m$') of the CCA on the settlement substrate decreased within
478 the same effect region (Fig. 5e,f; carbonate: EC10 = 28; siliciclastic: EC10 = 16 mg cm^{-2}) as
479 larval settlement success, and also recovered after a 3-day period (Fig. 5g,h; EC10s >250 mg
480 cm^{-2}). Before exposure, CCA of *Titanoderma protypum* covered ~61% of the plugs, and
481 *Peyssonnelia* spp. covered ~21% of the plugs. Bleaching (mostly driven by impacts on *T.*
482 *prototypum*) increased proportionally with sediment smothering (evident at > 30 mg cm^{-2}),
483 and did not regain pigment after the 3-day recovery period (Fig. S3a-c). This indicates that
484 changes in $\Delta F/F_m$' were a better predictor of settlement cue effectiveness than observed
485 bleaching.

486 ## General Discussion

487 Disentangling the various drivers affecting coral recruitment that occur sequentially and
488 simultaneously remains a challenge of marine ecology (Graham 2003, Houlahan et al. 2017).
489 While little can be done to control all co-occurring factors in observational studies (Graham
490 2003), manipulative studies offer unique opportunities to identify and quantify key drivers
491 that influence coral recruitment patterns and other biological processes (Chapman 2016,
492 Nosek & Errington 2020). For example, a number of correlating variables have been
493 described to predict coral spawning events, yet careful manipulation of only two (temperature
494 and light intensity) are required to reliably control the timing of spawning *ex situ* (Craggs et
495 al. 2017). Here we sought to test the relative importance of direct 'acute' light compared to
496 chronic water-quality factors impacting the substrate by applying highly controlled but
497 realistic experimental approaches. We first characterised the light environment at scales
498 relevant to settling larvae using spectroradiometers, and then used these data to inform a

499 selection of experimental treatment levels using a multispectral feedback LED lighting
500 system. In the case of *Acropora*, only unrealistic artificially narrow or high light-intensity
501 exposures led to settlement shifts in comparison to the lower broad-spectrum control light.
502 For example, monochromatic light of mid-range (green-yellow) wavelengths influenced
503 settlement negatively in some experiments; however, these effects were not observed under a
504 broader realistic spectra that occur in shallow waters, at depth and under high turbidity. To
505 improve the likelihood of detecting effects of light spectrum and intensity on settlement, we
506 opted for a sub-optimal conditioning to the discs in comparison to Ricardo et al. (2017) where
507 a more mature substrate community dominated by CCA may have overwhelmed light-
508 intensity effects. Nevertheless, the present study similarly indicated high light-intensity has
509 only a modest negative effect on settlement at levels typically found during midday on
510 exposed surfaces. It is not entirely surprising that larvae searching the benthos are relatively
511 insensitive to light intensity, as strong light gradients are only available for a few hours each
512 day. Interestingly, *A. tenuis* did show positive effects to artificial red light, especially in one
513 spawning year. In these experiments the larvae had high competency (ability to settle) but
514 low settlement success in the control treatments indicating sub-optimal conditioning, and this
515 supports the possibility that weaker settlement inducers/inhibitors (such as direct light) may
516 become more important in absence of strong settlement inducers such as mature CCA
517 colonies.

518 Several lines of evidence suggests that conditions the substrate are exposed to prior to
519 settlement may be critical for determining coral settlement outcomes (Baird et al. 2003,
520 Petersen et al. 2005, Kuffner et al. 2006, Szmant & Miller 2006, Suzuki & Hayashibara 2011,
521 Ricardo et al. 2017). Chronically altered light regimes and smothering by sediment led to
522 altered community assemblages on the substrate that evidently promote or prevent settlement
523 (Erwin et al. 2008, Arnold & Steneck 2011, Quimpo et al. 2020). Prior exposure of settlement

524 substrates to a variety of water quality conditions *in situ* elicited clear differences in the
525 settlement response, with larvae preferring the substrates that had been previously
526 conditioned under low light and not affected by sediment. While there remains some
527 limitations in characterising the community on settlement substrates visually and inferring
528 casual effects in absence of measuring possible confounders (Walker 2014), CCA colonised
529 downward-facing surfaces at the clear-water site was associated with high settlement,
530 whereas tubeworms were associated with decreasing settlement on the downwards-facing
531 surfaces conditioned at the turbid-water site. Empty space (possibly grazed clear by
532 gastropods observed at the time of retrieval) was associated with high settlement on the
533 upwards-facing surfaces. Known biological settlement inducers such as CCA are often
534 associated with specific light environments (Petersen et al. 2005, Bessell-Browne et al. 2017,
535 Briggs & Carpenter 2019) but are sensitive to sediment smothering (Harrington et al. 2005,
536 Ricardo et al. 2017), and searching larvae may favour these communities that could be
537 advantageous for post-settlement growth. However, optimal conditions and responses of
538 biological inducers for coral settlement (CCA and microbial biofilms) to stress remain
539 remarkably understudied (Webster et al. 2011, Webster et al. 2013), and derivation of water
540 quality and light thresholds for important algal and microbial inducers would improve
541 predictions for coral settlement.

542 In addition to the potential for chronic effects of light exposure on the benthic surfaces to
543 influence its structure and suitability for coral settlement, highly turbid conditions are also
544 associated with sediment deposition (Whinney et al. 2017), which can accumulate on
545 settlement surfaces directly affecting access by larvae (Hodgson 1990, Ricardo et al. 2017),
546 or indirectly affecting settlement by harming biological settlement inducers such as CCA
547 (Kendrick 1991, Harrington et al. 2005). Experiment 7 demonstrated strong associations
548 between sediment accumulation, declining quality of settlement cues and a subsequent

549 decrease in coral settlement. In the current study, even brief sediment exposures to the
550 substrate at levels that are common for inshore reefs (see Tebbett et al. (2018), and Jones et
551 al. (2020)) led to a decrease in settlement success, as well as physiological responses of the
552 substrate such as pigment loss (bleaching) and decreased $\Delta F/F_m$'. Sediment smothering can
553 reduce gas exchange, prevent waste removal, eliminate light, and change the surface
554 chemistry of the smothered organism (Weber et al. 2012, Jones et al. 2016). The settlement
555 response we observed was more pronounced with carbonate sediment, and the differences
556 between the two sediment types is possibly caused by seemingly rapid consolidation of these
557 sediments over the 3-day period, with the carbonate sediment bound more firmly to the
558 substrate at the time of removal. Following the subsequent 3-day recovery period, $\Delta F/F_m$' and
559 the dose-dependent settlement increased, whereas bleaching did not change, indicating photo-
560 physiological responses maybe more effective indicators of settlement success than bleaching
561 (loss of pigments). Although some recovery was observed following sediment removal,
562 turbid reefs are subject to ongoing sediment deposition and removal processes that likely
563 result in eventual loss or reduction of settlement inducers on upwards-facing surfaces over
564 longer durations (Kendrick 1991).

565 It is often difficult to interpret studies assessing impacts of light or other water-quality factors
566 during coral settlement where substrates were not randomised immediately before settlement,
567 and where surfaces vary in sizes, roughness and aspects, introducing the possibility of edge
568 and orientational effects (Raimondi & Morse 2000). This is common in field settlement
569 assays where typically ~10 × 10 × 1 cm ceramic tiles are conditioned *in situ* for a few weeks
570 prior to the mass spawning events (Table S1), and there have been calls for greater
571 standardisation in settlement studies (Abelson & Gaines 2005, Davidson et al. 2019). Further,
572 larvae exhibit strong thigmotactic behaviour with an attraction to grooves, edges and aspects
573 in the absence of light (Nozawa et al. 2011, Whalan et al. 2015, Ricardo et al. 2017).

574 Edmunds et al. (2014) and Nozawa et al. (2011) suggests that a reduction in settlement on
575 horizontal surfaces of field-deployed settlement tiles may be due to a lack of micro-refuges at
576 small scales, and when these are present on natural substrates settlement occurs on upwards
577 surfaces. However for inshore reefs, deposited sediment and algal mats may infill these
578 refuges driving settlement to vertical and downwards-facing surfaces (Ricardo et al. 2017,
579 Tebbett & Bellwood 2019). Importantly, downwelling irradiance is confounded by
580 orientation and edge effects because of local shading, leading some authors to speculate that
581 direct light intensity is the driver of coral recruits settling near the edges of undersides (Morse
582 et al. 1988, Maida et al. 1994). The current study removed confounding thigmotactic and
583 orientation effects that are common on three-dimensional substrates and further crossed and
584 randomised designs are needed to conclusively separate light-intensity effects from possible
585 thigmotactic and substrate effects.

586 For the species tested here, and possibly many species in the genus *Acropora*, the influence
587 of light and physical challenges (such as sediment deposition and algal growth) on settlement
588 of the larvae is predominantly manifested indirectly by influencing the biology and quality of
589 settlement surfaces, rather than light as a direct cue influencing the settlement response.
590 However, in some species, there is greater 'weight of evidence' supporting the idea of light
591 sensitivity in settlement in other genera such as *Oxypora* (Babcock and Mundy, 1996; Mundy
592 and Babcock, 1998). Perhaps a more plausible explanation of settlement patterns under
593 various narrow-band spectra is a mistaken recognition of surface colour (i.e. spectral diffuse
594 reflection) from specular reflection. A number of studies have observed increased settlement
595 on orange-red surfaces and have suggested there is an attraction because CCA species
596 typically have a reflectance peak in the 600 nm region of the visible spectrum (Mason et al.
597 2011, Foster & Gilmour 2016). Alternatively, the attraction may be related to the loss of blue
598 light reflected from these surfaces, as reduced blue light is associated with temporary reduced

599 swimming speeds in larvae (Sakai et al. 2020). In our study, reduced settlement was observed
600 on CCA that had lost its red pigments (bleached), but after a recovery period improved
601 settlement correlated well with recovered photosystem activity, suggesting that physiological
602 processes (an indicator of healthy CCA) were a stronger driver of settlement than spectral
603 reflectance. Other studies have reported phototaxis of coral larvae in the water column (Lewis
604 1974, Szmant & Meadows 2006, Mulla et al. 2020, Sakai et al. 2020), although these
605 behaviours appear less consistent than observed in other marine invertebrates (Raimondi &
606 Morse 2000, Satheesh & Wesley 2010, Ricardo et al. 2014, Lillis et al. 2018, Abdul Wahab et
607 al. 2019).

608 The findings presented here suggest targeted management of water quality (e.g. sediment
609 plumes from dredging) in the weeks to months leading up to coral spawning events may be a
610 more meaningful area of focus for management rather than solely focussing on managing
611 water quality during the days of predicted settlement. Deposited sediments are known to
612 strongly repel coral settlers on upwards-facing surfaces (Ricardo et al. 2017), and while the
613 temporal dynamics (i.e. deposition vs resuspension) remains unresolved, evidence is building
614 that acute deposition events strongly tied to anthropogenic activities such as dredging can be
615 managed with a spatial separation area of a few kilometres (Jones et al. 2020). However little
616 evidence suggest that a short-term cessation of close-proximity dredging would improve
617 settlement outcomes, as the sediment would need time for resuspension, latent effects on the
618 substrate would remain for a number of days, and the chronic change in the water quality
619 environment would cause shifts in the substrate community. Likewise, improvements in
620 water quality and other factors that improve the substrate for settlement such as fish
621 herbivory (to control algal growth) would likely improve settlement success (Doropoulos et
622 al. 2016, Tebbett & Bellwood 2019).

Here we show for two common *Acropora* species that realistic light quality and quantity at the time of settlement plays a lesser role in determining settlement success in comparison to chronic water quality conditions impacting the settlement substrate over weeks to months prior to settlement – contrary to expectations. Teasing apart confounding factors inherent in settlement experiments will require innovative and creative experimental approaches, and with advancements in technology and better characterisation for the settlement environment, there are opportunities to further test, refine and reject old ideas. As researchers race to find ways to increase local reef resilience and scale-up restoration via seeding of coral larvae (Randall et al. 2020), it is crucially important to understand which factors primarily drive recruitment, and which act in a more subtle or infrequent manner.

Data accessibility

All raw data used in the figures can be accessed here https://github.com/gerard-ricardo/light-settlement.

Acknowledgements

This project was supported through government appropriation funding (AIMS) and from the Australian Government's National Environmental Science Program (NESP). We acknowledge In situ Marine Optics for their technical expertise with the light sensors. We acknowledge Eduardo Arias, Matt Salmon, Paul Boyd, Andrea Severati for design of the sediment dosing and lighting systems, and the AIMS SeaSim team for assistance for providing conditioning tanks, room set-up and animal husbandry requirements. We would also like to thank Lee Bastin, Florita Flores, Marie Thomas, Chris Brunner, Annika Lamb, Lonidas Koukoumaftsis and Christian Odea for assistance with coral spawning and image analyses.

References

Abdul Wahab MA, Maldonado M, Luter HM, Jones R, Ricardo G (2019) Effects of sediment resuspension on the larval stage of the model sponge Carteriospongia foliascens. Sci Total Environ:133837

Abelson A, Gaines S (2005) A call for a standardized protocol of coral recruitment research and outlines for its conception. Mar Pollut Bull 50:1745-1748

Arganda-Carreras I, Kaynig V, Rueden C, Eliceiri KW, Schindelin J, Cardona A, Sebastian Seung H (2017) Trainable Weka Segmentation: a machine learning tool for microscopy pixel classification. Bioinformatics 33:2424-2426

Arnold SN, Steneck RS (2011) Settling into an increasingly hostile world: the rapidly closing "Recruitment Window" for corals. PLoS ONE 6:e28681

Baird A, Babcock R, Mundy C (2003) Habitat selection by larvae influences the depth distribution of six common coral species. Mar Ecol Prog Ser 252:289-293

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G, Green P, Bolker MB (2015) Package 'lme4'. Convergence 12:2

Bessell-Browne P, Negri AP, Fisher R, Clode PL, Jones R (2017) Impacts of light limitation on corals and crustose coralline algae. Scientific Reports 7:11553

Briggs AA, Carpenter RC (2019) Contrasting responses of photosynthesis and photochemical efficiency to ocean acidification under different light environments in a calcifying alga. Scientific reports 9:1-10

Bürkner P-C (2017) brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80:1-28

Chapman P (2016) Ecological Risk and Weight of Evidence Assessments. In: Marine Ecotoxicology. Elsevier257-271

Craggs J, Guest JR, Davis M, Simmons J, Dashti E, Sweet M (2017) Inducing broadcast coral spawning ex situ: Closed system mesocosm design and husbandry protocol. Ecology and evolution 7:11066-11078

Cussioli MC, Seeger D, Pratt DR, Bryan KR, Bischof K, de Lange WP, Bornman JF, Pilditch CA (2020) Spectral differences in the underwater light regime caused by sediment types in New Zealand estuaries: implications for seagrass photosynthesis. Geo-Mar Lett:1-9

Davidson J, Thompson A, Logan M, Schaffelke B (2019) High spatio-temporal variability in Acroporidae settlement to inshore reefs of the Great Barrier Reef. PLOS ONE 14:e0209771

Doropoulos C, Roff G, Bozec YM, Zupan M, Werminghausen J, Mumby PJ (2016) Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. Ecol Monogr 86:20-44

Doropoulos C, Thomson DP, Trapon M, Cresswell AK, Turner JA, Babcock RC (2020) Depth gradients drive changes in early successional community composition and associated coral larvae settlement interactions. Mar Biol 167:1-9

Douma JC, Weedon JT (2019) Analyzing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. Methods in Ecology and Evolution

Dustan P (1982) Depth-dependent photoadaption by zooxanthellae of the reef coral Montastrea annularis. Mar Biol 68:253-264

Edmunds PJ, Nozawa Y, Villanueva RD (2014) Refuges modulate coral recruitment in the Caribbean and the Pacific. J Exp Mar Biol Ecol 454:78-84

Erwin P, Song B, Szmant A Settlement behavior of *Acropora palmata* planulae: Effects of biofilm age and crustose coralline algal cover. In. Proc Proceedings of the 11th international coral reef symposium Ft Lauderdale, Florida

Fabricius KE, Noonan SH, Abrego D, Harrington L, De'Ath G (2017) Low recruitment due to altered settlement substrata as primary constraint for coral communities under ocean acidification. Proceedings of the Royal Society B: Biological Sciences 284:20171536

Foster T, Gilmour J (2016) Seeing red: Coral larvae are attracted to healthy-looking reefs. Mar Ecol Prog Ser 559:65-71

Fox HE (2004) Coral recruitment in blasted and unblasted sites in Indonesia: assessing rehabilitation potential. Mar Ecol Prog Ser 269:131-139

Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models, Vol. Cambridge university press

Gelman A, Jakulin A, Pittau MG, Su Y-S (2008) A weakly informative default prior distribution for logistic and other regression models. The Annals of Applied Statistics 2:1360-1383

Giese AC (1959) Comparative physiology: annual reproductive cycles of marine invertebrates. Annu Rev Physiol 21:547-576

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809-2815

Gruber R, Waterhouse J, Logan M, Petus C, Howley C, Lewis S, Tracey D, Langlois L, Tonin H, Skuza M (2019) Marine Monitoring Program: Annual report for inshore water quality monitoring 2017-18.

Guest J, Heyward A, Omori M, Iwao K, Morse A, Boch C (2010) Rearing coral larvae for reef rehabilitation. Reef rehabilitation manual:73-92

Harrington L, Fabricius K, Eaglesham G, Negri A (2005) Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. Mar Pollut Bull 51:415-427

Heyward A, Negri A (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18:273-279

Hodgson G (1990) Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. Coral Reefs 9:41-43

Houlahan JE, McKinney ST, Anderson TM, McGill BJ (2017) The priority of prediction in ecological understanding. Oikos 126:1-7

Irving AD, Connell SD (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. Mar Ecol Prog Ser 245:83-91

Johnsen S (2012) The optics of life: a biologist's guide to light in nature, Vol. Princeton University Press

Jones R, Fisher R, Francis D, Klonowski W, Luter H, Negri A, Pineda M-C, Ricardo G, Slivkoff M (2020) Risk assessing dredging activities in shallow-water mesophotic reefs. National Environmental Science Programme Project 2.1.9

Jones RJ, Bessel-Browne P, Fisher R, Klonowski W, Slivkoff M (2016) Assessing the impacts of sediments on corals. Mar Pollut Bull 102:9-29

Kendrick GA (1991) Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. J Exp Mar Biol Ecol 147:47-63

Kennedy EV, Ordoñez A, Lewis BE, Diaz-Pulido G (2017) Comparison of recruitment tile materials for monitoring coralline algae responses to a changing climate. Mar Ecol Prog Ser 569:129-144

Kirk JT (1994) Light and photosynthesis in aquatic ecosystems, Vol. Cambridge university press

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107-117

Lee C, Walford J, Goh B (2009) Adding coral rubble to substrata enhances settlement of Pocillopora damicornis larvae. Coral Reefs 28:529-533

Lenth R, Singmann H, Love J (2018) Emmeans: Estimated marginal means, aka least-squares means. R package version 1

Levy O, Appelbaum L, Leggat W, Gothlif Y, Hayward DC, Miller DJ, Hoegh-Guldberg O (2007) Light-responsive cryptochromes from a simple multicellular animal, the coral Acropora millepora. Science 318:467-470

Lewis JB (1974) Settlement behavior of planulae larvae of hermatypic coral *Favia-fragum* (Esper). J Exp Mar Biol Ecol 15:165-172

Lillis A, Apprill A, Suca JJ, Becker C, Llopiz JK, Mooney TA (2018) Soundscapes influence the settlement of the common Caribbean coral Porites astreoides irrespective of light conditions. Royal Society Open Science 5:181358

Magno-Canto MM, McKinna LI, Robson BJ, Fabricius KE (2019) Model for deriving benthic irradiance in the Great Barrier Reef from MODIS satellite imagery. Optics express 27:A1350-A1371

Maida M, Coll J, Sammarco P (1994) Shedding new light on scleractinian coral recruitment. J Exp Mar Biol Ecol 180:189-202

Mason B, Beard M, Miller MW (2011) Coral larvae settle at a higher frequency on red surfaces. Coral Reefs 30:667-676

Mason B, Schmale M, Gibbs P, Miller MW, Wang Q, Levay K, Shestopalov V, Slepak VZ (2012) Evidence for multiple phototransduction pathways in a reef-building coral. PLoS ONE 7:e50371

Morel A (1978) Available, usable, and stored radiant energy in relation to marine photosynthesis. Deep Sea Research 25:673-688

Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. J Exp Mar Biol Ecol 116:193-217

Mulla AJ, Lin C-H, Takahashi S, Nozawa Y (2020) Species-specific phototaxis of coral larvae causes variation in vertical positioning during dispersal. bioRxiv:2020.2007.2031.230235

Mundy C, Babcock R (1998) Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? J Exp Mar Biol Ecol 223:235-255

Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre-or post-settlement processes? A case study of three contrasting species. Mar Ecol Prog Ser 198:109-119

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. Coral Reefs 25:1-29

Nosek BA, Errington TM (2020) What is replication? PLoS Biol 18:e3000691

Nozawa Y, Tanaka K, Reimer JD (2011) Reconsideration of the surface structure of settlement plates used in coral recruitment studies. Zool Stud 50:53-60

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ, Suggests M (2007) The vegan package. Community ecology package 10:631-637

Petersen D, Laterveer M, Schuhmacher H (2005) Spatial and temporal variation in larval settlement of reefbuilding corals in mariculture. Aquaculture 249:317-327

Quimpo TJR, Ligson CA, Manogan DP, Requilme JNC, Albelda RL, Conaco C, Cabaitan PC (2020) Fish farm effluents alter reef benthic assemblages and reduce coral settlement. Mar Pollut Bull 153:111025

Raimondi PT, Morse AN (2000) The consequences of complex larval behavior in a coral. Ecology 81:3193-3211

Randall CJ, Negri AP, Quigley KM, Foster T, Ricardo GF, Webster NS, Bay LK, Harrison PL, Babcock RC, Heyward AJ (2020) Sexual reproduction of corals for reef restoration in the Anthropocene. Mar Ecol Prog Ser 635:203-232

Ricardo GF, Davis AR, Knott NA, Minchinton TE (2014) Diel and tidal cycles regulate larval dynamics in salt marshes and mangrove forests. Mar Biol 161:769-784

Ricardo GF, Jones RJ, Clode PL, Humanes A, Giofre N, Negri AP (2018) Sediment characteristics influence the fertilisation success of the corals *Acropora tenuis* and *Acropora millepora*. Mar Pollut Bull 135:941-953

Ricardo GF, Jones RJ, Nordborg M, Negri AP (2017) Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces. Sci Total Environ 609:277-288

Ritz C, Strebig JC, Ritz MC (2016) Package 'drc'. In:

Roberts DW, Roberts MDW (2016) Package 'labdsv'. Ordination and Multivariate

Robson B, Canto M, Collier C, di Perna S, Logan M, Patricia Menendez, Lachlan McKinna, Sam Noonan, Fabricius K (2019) Benthic light as ecologically-validated GBR-wide indicator for water quality. Final Technical Report National Environmental Science Programme

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241:1460-1466

Sakai Y, Kato K, Koyama H, Kuba A, Takahashi H, Fujimori T, Hatta M, Negri AP, Baird AH, Ueno N (2020) A step-down photophobic response in coral larvae: implications for the light-dependent distribution of the common reef coral, *Acropora tenuis*. Scientific Reports

Satheesh S, Wesley SG (2010) Influence of substratum colour on the recruitment of macrofouling communities. J Mar Biol Assoc UK 90:941-946

Strader ME, Davies SW, Matz MV (2015) Differential responses of coral larvae to the colour of ambient light guide them to suitable settlement microhabitat. Royal Society open science 2:150358

Strydom S, McMahon K, Lavery PS (2017) Response of the seagrass Halophila ovalis to altered light quality in a simulated dredge plume. Mar Pollut Bull 121:323-330

Suzuki G, Hayashibara T Inhibition of settlement and metamorphosis in Acropora (Anthozoa, Scleractinia) larvae by high-intensity light. In. Proc Proc 10th Int Coral Reef Symp

Suzuki G, Hayashibara T (2011) Do epibenthic algae induce species-specific settlement of coral larvae? J Mar Biol Assoc UK 91:677-683

Szmant AM, Meadows MG (2006) Developmental changes in coral larval buoyancy and vertical swimming behavior: implications for dispersal and connectivity. Proc 10th Int Coral Reef Symp 1:431-437

Szmant AM, Miller MW Settlement preferences and post-settlement mortality of laboratory cultured and settled larvae of the Caribbean hermatypic corals Montastraea faveolata and Acropora palmata in the Florida Keys, USA. In. Proc Proceedings of the 10th international coral reef symposium. Okinawa

Tebbett SB, Bellwood DR (2019) Algal turf sediments on coral reefs: what's known and what's next. Mar Pollut Bull 149:110542

Tebbett SB, Goatley CH, Bellwood DR (2018) Algal turf sediments across the Great Barrier Reef: Putting coastal reefs in perspective. Mar Pollut Bull 137:518-525

Thimijan RW, Heins RD (1983) Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. HortScience 18:818-822

Trygonis V, Sini M (2012) photoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. J Exp Mar Biol Ecol 424:99-108

Turner JA, Thomson DP, Cresswell AK, Trapon M, Babcock RC (2018) Depth-related patterns in coral recruitment across a shallow to mesophotic gradient. Coral Reefs 37:711-722

Vanderklift M, Doropoulos CA, Gorman D, Leal IAV, Minne AJ, Statton J, Steven AD, Wernberg T (2020) Using propagules to restore coastal marine ecosystems. Frontiers in Marine Science 7:724

Walker JA (2014) The effect of unmeasured confounders on the ability to estimate a true performance or selection gradient (and other partial regression coefficients). Evolution 68:2128-2136

Warne M, Batley G, Van Dam R, Chapman J, Fox D, Hickey C, Stauber J (2018) Revised Method for Deriving Australian and New Zealand Water Quality Guideline Values for Toxicants. Prepared for the revision of the Australian and New Zealand Guidelines for Fresh and Marine Water Quality. Australian and New Zealand Governments and Australian state and territory governments, Canberra. In:

Weber M, de Beer D, Lott C, Polerecky L, Kohls K, Abed RM, Ferdelman TG, Fabricius KE (2012) Mechanisms of damage to corals exposed to sedimentation. Proceedings of the National Academy of Sciences 109:E1558-E1567

Webster NS, Soo R, Cobb R, Negri AP (2011) Elevated seawater temperature causes a microbial shift on crustose coralline algae with implications for the recruitment of coral larvae. ISME Journal 5:759-770

Webster NS, Uthicke S, Botté ES, Flores F, Negri AP (2013) Ocean acidification reduces induction of coral settlement by crustose coralline algae. Global Change Biol 19:303-315

Whalan S, Abdul Wahab MA, Sprungala S, Poole AJ, de Nys R (2015) Larval settlement: the role of surface topography for sessile coral reef invertebrates. PLoS ONE 10:e0117675

Whinney J, Jones R, Duckworth A, Ridd P (2017) Continuous in situ monitoring of sediment deposition in shallow benthic environments. Coral Reefs:1-13

Yusuf S, Zamani N, Jompa J, Junior M Larvae of the Coral Acropora tenuis (Dana 1846) Settle Under Controlled Light Intensity. In. Proc IOP Conference Series: Earth and Environmental Science. IOP Publishing

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14