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

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Abstract

Coral larval settlement patterns are influenced by a vast array of factors; 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 most 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 on 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

49 decreases in light intensity and spectral shifts away from the maximally absorbance of
50 regions of chlorophyll *a* (blue and red wavelengths) termed 'photosynthetically usable
51 radiation' (PUR) (Morel 1978, Dustan 1982). Consequently, benthic-light monitoring is
52 suggested as a valuable metric to measure and manage water quality for inshore reefs (Gruber
53 et al. 2019, Magno-Canto et al. 2019, Robson et al. 2019, Jones et al. 2020). But for coral
54 early-life stages preceding the establishment of autotrophy (i.e., acquisition and utilisation of
55 algal symbionts as the primary energetic pathway), the contribution of direct light influencing
56 recruitment patterns is an area of active research. Corals settle non-randomly, using a range
57 of cues which is thought to increase their chances of survival through the post-settlement
58 stage when mortality is high (Doropoulos et al. 2016, Brunner et al. 2020). Numerous studies
59 have suggested light quality and quantity affects where larvae settle at depth and at which
60 orientation (Mundy & Babcock 1998, Mundy & Babcock 2000). Indeed, sensory mechanisms
61 to detect changes in light quality and intensity have been proposed with evidence of opsins
62 and cryptochromes (a class of proteins involved in circadian rhythms) (Levy et al. 2007,
63 Mason et al. 2012).

64 Despite plausible mechanisms to sense light in larvae, settlement responses to light often
65 contradict, even within the same species. For example, *Acropora tenuis* settlement patterns
66 purportedly increase (Mundy & Babcock 1998), decrease (Suzuki & Hayashibara 2006), or
67 remain relatively unchanged (Yusuf et al. 2019) with light intensity. However, an issue is that
68 many factors within the water column and on the benthos may simultaneously act on a
69 settling larva, and that these are rarely controlled in experiments making interpretation of
70 settlement patterns difficult. For example, grooves, edges, and surface orientations of the
71 substrate all influence the micro-light environment relevant to a larva. However, these
72 physical characteristics can also affect thigmotactic behaviour in larvae, potentially creating
73 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 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 several 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

121 used to assess the impact of chronic effects of exposures on the substrate and the subsequent

122 impact on coral settlement (see Settlement Series 2; Table 1).

123

124

125

126 Table 1. Experimental treatments used in each experiment. PAR = Photosynthetically Active Radiation (µmol

127 photons m^{-2} s^{-1}). DLI = Daily Light Integral (mol photons m^{-2} d^{-1}). 'Upwards' and 'downwards' refer to orientation

128 of the settlement discs during field conditioning. SS = suspended sediment. NTU = Nephelometric Turbidity

129 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

130 Coral collection, larval culturing, and substrate conditioning

131 Coral collection and larval culturing followed Heyward and Negri (1999) and Ricardo et al.

132 (2018), and further details can be found in the Supplementary Material (Text S1). Artificial

133 substrates for settlement were created using 7-cm diameter polyvinyl chloride (PVC) discs.

134 PVC was used for the following reasons i) it presents a flat surfaces to ensure there is no

135 shading of downwelling light, ii) it can be manufactured to minimise edge-effects, and iii) is
136 successful at conditioning a number of settlement cues and thus frequently used in settlement
137 experiments (Lee et al. 2009, Fabricius et al. 2017, Kennedy et al. 2017, Ricardo et al. 2017).
138 For laboratory experiments, they were conditioned under layers of 70% block shade cloth
139 (maximum Photosynthetically Active Radiation (PAR) light intensity = ~250 µmol photons
140 m^{-2} s^{-1}) in flow-through outdoor SeaSim aquaria for ~3 months of the presence of crustose
141 coralline algae (CCA) *Porolithon onkodes* a common species known to induce settlement of
142 *Acropora* coral larvae (Heyward & Negri 1999). The discs were conditioned randomly within
143 the aquaria and CCA covered about 20–40% of the total disc area at the commencement of
144 each experiment.

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

In situ measurements for laboratory light treatments

In situ light measurements of this study were conducted at inshore sites within Cleveland Bay, Great Barrier Reef using a range of PAR light meters and spectroradiometers, with these data used to justify the light treatment-levels used in experiments. Briefly, a light meter connected to a diving pulse amplitude modulating fluorometer (PAM) (Walz, Germany) was used to characterise the benthic substrate light intensity levels that coral larvae are likely to 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

199 cm^{-2} nm^{-1}) were binned to the nearest nanometre and converted to photons (µmol photons m^{-2}

200 s^{-1} nm^{-1}) using the equation (Thimijan & Heins 1983):

201 $$\frac{nm \times irradiance\ (\mu W\ cm^{-2}\ nm^{-1})}{11962.15}$$

202 Settlement Series 1: Acute light exposure–experimental settlement trials

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

204 Five replicate chambers were positioned under each light treatment which included a realistic

205 broad-spectrum control and four narrow monochromatic bands. The width of the bands is

206 described using full-width at half maximum (FWHM). The median and FWHM correspond

207 to broad-spectrum: median λ = 535 nm; FWHM = ~172 nm; artificial blue light: λ = 441 nm;

208 ~17 nm, artificial green light: 499 nm; ~25 nm, artificial yellow light: 602 nm; ~28 nm, and

209 artificial red light: 658 nm; ~20 nm) (Table 1). To demonstrate repeatability and to increase

210 sensitivity to treatments, we repeated the experiment using a 'choice' design (more details in

211 Supplementary Material, Text S3).

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

213 Settlement preferences in response to depth-derived light spectra and intensity is often cited

214 in the literature to influence the zonation of corals (Mundy & Babcock 1998). Broad and

215 artificial blue spectra were supplied at two light intensities (Table 1). The broad-light

216 intensities used were based upon the USSIMO field data described above at 5-m depth and

217 21-m depth from the clear blue-water site and broadly matched spectral profiles used in

218 Mundy and Babcock (1998). The light channels for the 'blue' treatment were used to

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

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

This experiment was designed to examine the combined effects of changes in light intensity (5 levels) and quality (broad and shifted spectrums that would be associated with suspended sediment concentrations equivalent to 0.8 NTU and ~9 NTU at 5-m depth). Five light intensities were selected to cover the range of environmentally realistic values (<1, 10, 30, 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} d^{-1}), but more extreme combinations were also used to improve the model fit and assess the strength of the response.

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

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

Statistical analyses

All acute-exposure settlement data were fit to Bayesian binomial generalised linear mixed models, using a weakly informative prior (Cauchy; centre = 0, scale = 2.5) (Gelman et al. 2008) using the package *brms* (Bürkner 2017) in *R* (version 3.6.1). As hypotheses were planned, we did not remove any factors of interest during model selection even if not statistically significant, because all variables were of interest (Gelman & Hill 2006); however, comparisons of WAICs (Watanabe–Akaike Information Criterions) were used to 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 loggers (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 logger sensor.

267 Approximately 1 week before the anticipated coral spawning, the structures were collected
268 and transferred to flow-through aquaria in the SeaSim. One structure from Florence Bay was
269 lost in turbid water during retrieval. The majority of macroalgae and sediment were removed
270 from the discs as their inclusion would have made a census impossible. Settlement of larvae
271 on these discs occurred in chambers under identical conditions using the methods described
272 above in Settlement series 1 to remove any light or thigmotactic effects, and therefore the
273 settlement response only represented changes in the substrate 'quality'. Thirty competent *A.*
274 *millepora* larvae were added to each experimental chamber under a 12:12 light/dark cycle for
275 24 hrs (30 µmol photons m^{-2} s^{-1}; 1.3 DLI; broad-spectral profile) using the chamber set-up
276 described above. Settled larvae were carefully counted using a Leica stereoscope by
277 examining under all the remaining foliage. Discs were imaged with a Canon 90D camera
278 using an EF-S 18–55 lens.

279 Settlement success on the discs were analysed with binomial GLMMs with 'site' and
280 'orientation' as fixed effects and 'disc' as a random effect with the package *lme4* (Bates et al.
281 2015). Pairwise comparisons were estimated with the package *emmeans* (Lenth et al. 2018).
282 Community composition on the discs were analysed using photoQuad (v1.4) (Trygonis &
283 Sini 2012), by grouping identifiable taxonomic and abiotic groups (macroalgae, green
284 filamentous algae, red filamentous algae, CCA, cyanobacteria, tube worms, bryozoa, detritus,
285 empty space, epilithic algal matrix (EAM), coral recruit, and unidentified). Taxonomic data
286 was visually assessed using an nMDS (Bray-Curtis measure of dissimilarity) with the
287 package *vegan* (Oksanen et al. 2007) using square-root transformed data. Environmental
288 vectors and ellipses were subsequently added. To test differences in community structure
289 between sites and orientation, PERMANOVA based on 999 permutations was implemented
290 using the '*adonis'* function in *vegan*. Each distinct community was further examined to
291 explore potential associations of taxa with settlement. Multicollinearity was assessed using

variance inflation factors (VIF), pairs plots, and biological relevance (Zuur et al. 2010). Indicator Species Analysis using the package *labdsv* (Roberts & Roberts 2016) was first used to identify the most important taxa separating each group. Taxa with an indicator value >0.2 were used as a preliminary selection in a GLMM model. Corrected Akaike Information Criterion (AICc) was used to select the most parsimonious model.

Exp. 7: Sediment smothering on substrate settlement cue

While it was not feasible to investigate all water quality stressors on substrate quality, the effect of temporary sediment deposition on the settlement cue was examined as a likely mechanism (cause-effect pathway). Aragonite plugs (2-cm diameter) were conditioned for ~3 months in an outdoor aquarium system under 50% neutral density shade cloth (27 ˚ C; maxima 200 µmol photons m^{-2} s^{-1}) and developed a thick covering of crustose algae (*Titanoderma prototypum* and *Peyssonnelia* spp.). The experiment aimed to simulate a sediment deposition and resuspension event and the plugs were exposed at various levels (0.1, 0.3, 0.8, 2.5, 8, 25, 83, 250 mg cm^{-2}) of carbonate and siliciclastic deposited sediments (see Ricardo et al. (2018) for sediment characterisation) in flow-through conditions under ~30 µmol photons m^{-2} s^{-1} (PAR) linear-ramping lighting following Ricardo et al. (2017). The sediments were then removed, and each plug embedded in 60 mL glass chambers with cleaned river sand to prevent settlement on vertical or under-surfaces. Ten competent larvae were added to each chamber, and settlement on the sediment-free plugs was assessed at 24 hours. The plugs were then provided a recovery period of 3 days and then more larvae (n=10) were added to each chamber and settlement assessed after a second 24 hours. Effective quantum yields ($\Delta F/F_m$'), which estimates the photosystem II photosynthetic performance of light-acclimated samples, were measured on the plugs after a 30-minute light-acclimation period at 30 µmol photons m^{-2} s^{-1} with a mini-PAM (Waltz) using a red measuring light (6 mm fibre-optic probe) positioned ~ 3-mm away from the plug using a rubber spacer.

Measurements were taken before and after the exposure, and after the 3-day recovery period, with 5 measurements per plug. The changes in settlement were analysed with a binomial GLMM with 'plug' as random effect and the level of 'previously-deposited sediment' and time (after exposure, recovery) as a fixed factor. The changes in yield at each time point was measured with a four-parameter Weibull nonlinear model using the package *drc* (Ritz et al. 2016). The substrate composition was classified using Trainable Weka Segmentation in ImageJ (Arganda-Carreras et al. 2017) on a Dell R820 256 GB High-performance Computer 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.

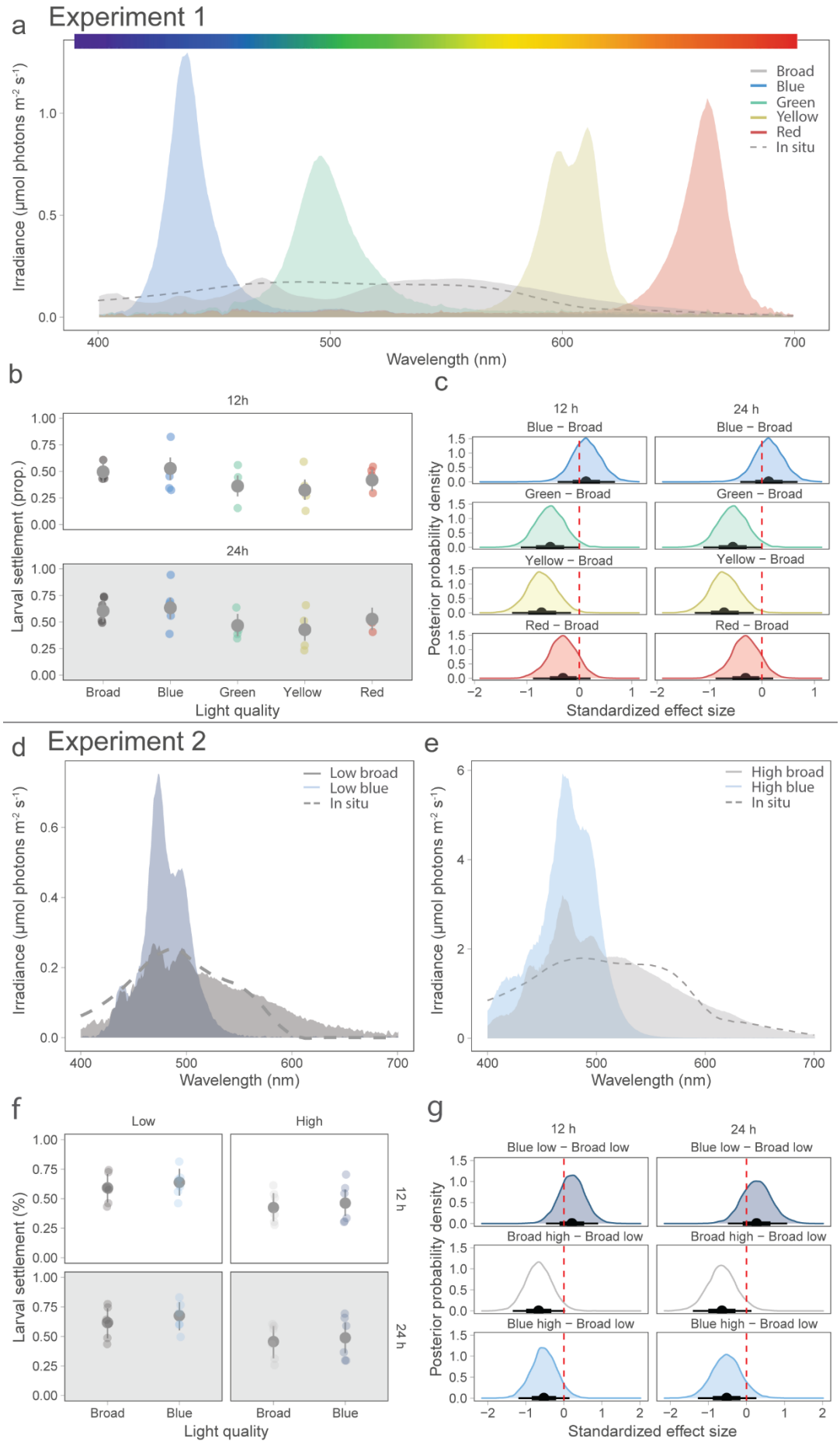
Results

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 were 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%.


a
Experiment 1
Irradiance (µmol photons m-2 s-1)
Wavelength (nm)
Broad
Blue
Green
Yellow
Red
In situ
b
12h
24h
Larval settlement (prop.)
Broad
Blue
Green
Yellow
Red
Light quality
c
12 h
24 h
Blue − Broad
Green − Broad
Yellow − Broad
Red − Broad
Posterior probability density
Standardized effect size
d
Experiment 2
Low broad
Low blue
In situ
e
High broad
High blue
f
Low
High
12 h
24 h
Larval settlement (%)
g
Blue low − Broad low
Broad high − Broad low
Blue high − Broad low

347

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

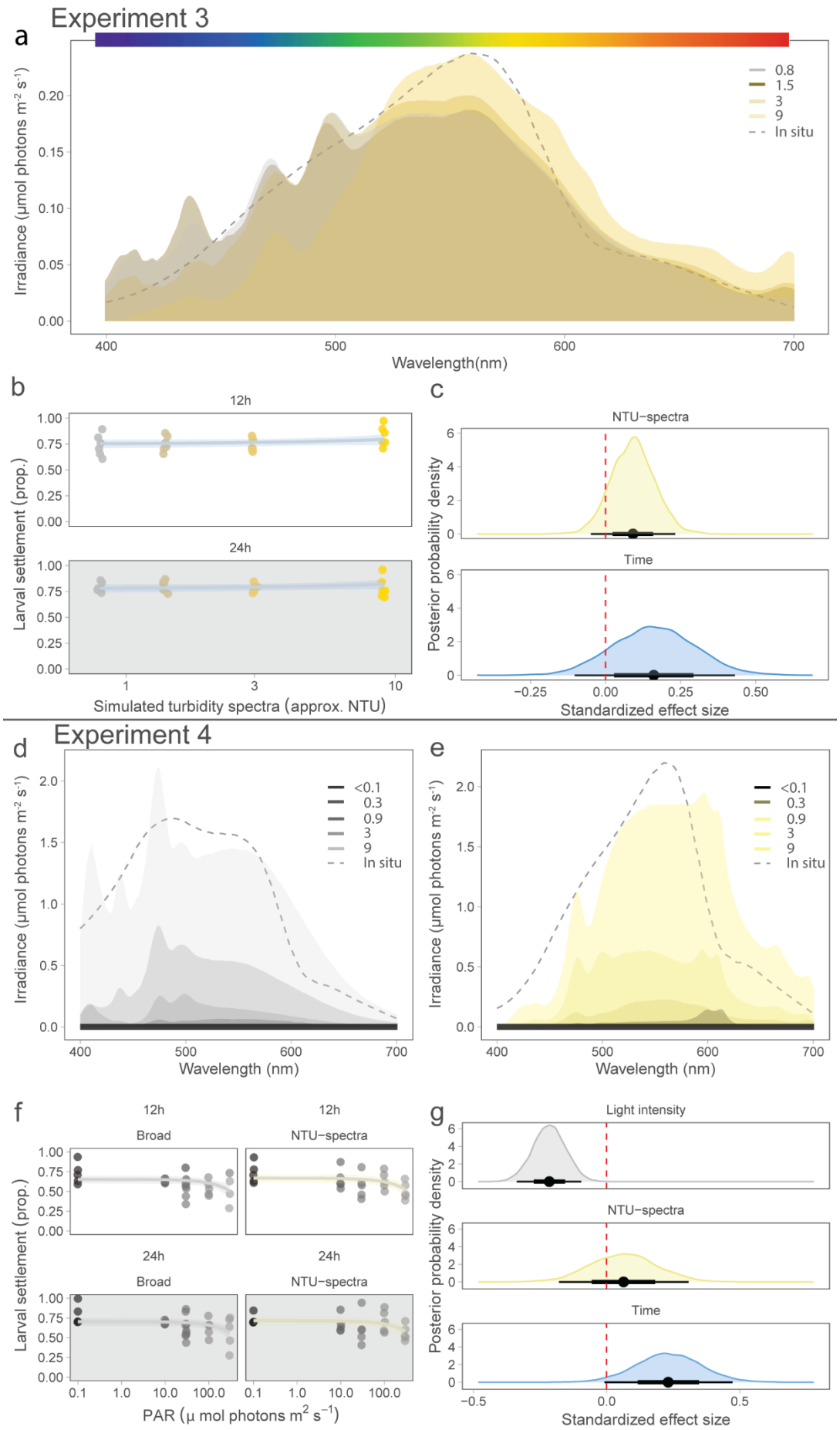
Exp. 2: Realistic depth-dependant light on A. millepora settlement

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

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

Low simulated-turbidity light treatments (~0.8–3 NTU) had similar spectral profiles whereas the highest simulated-turbidity profile (~9 NTU) was narrower and peaked around ~550 nm (Fig. 2a). The most parsimonious model only included ‘time’ as a predictor variable, indicating no evidence of an influence on settlement between the low turbidity and high turbidity-simulated spectra. Under the full model, there was no effect of the simulated

turbidity spectra (slope = 0.1; 95% CI = -0.05– 0.25), and there was a slight overall increase of settlement between 12 hours (0.753, 95% CI: 0.721–0.783) and 24 hours (0.790, 95% CI: 0.761–0.819) (Fig. 2b,c). The variance explained by the full model was 25%.


Experiment 3
a
Irradiance (µmol photons m-2 s-1)
0.8
1.5
3
9
In situ
Wavelength(nm)
b
12h
24h
Larval settlement (prop.)
Simulated turbidity spectra (approx. NTU)
c
NTU−spectra
Time
Posterior probability density
Standardized effect size
Experiment 4
d
e
<0.1
0.3
0.9
3
9
In situ
Irradiance (µmol photons m-2 s-1)
Wavelength (nm)
f
12h
24h
Broad
NTU−spectra
Larval settlement (prop.)
PAR (µ mol photons m2 s−1)
g
Light intensity
NTU−spectra
Time
Posterior probability density
Standardized effect size

378

Fig. 2. The relationship between light intensity and simulated turbidity spectra on larval settlement of *Acropora millepora*. (a) Exp. 3 spectral profiles used to simulate in situ spectral patterns at various approximate turbidity (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). PAR measurements at the clearer-water site (Florence Bay) exceeded this threshold 21.2% of the time. 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.

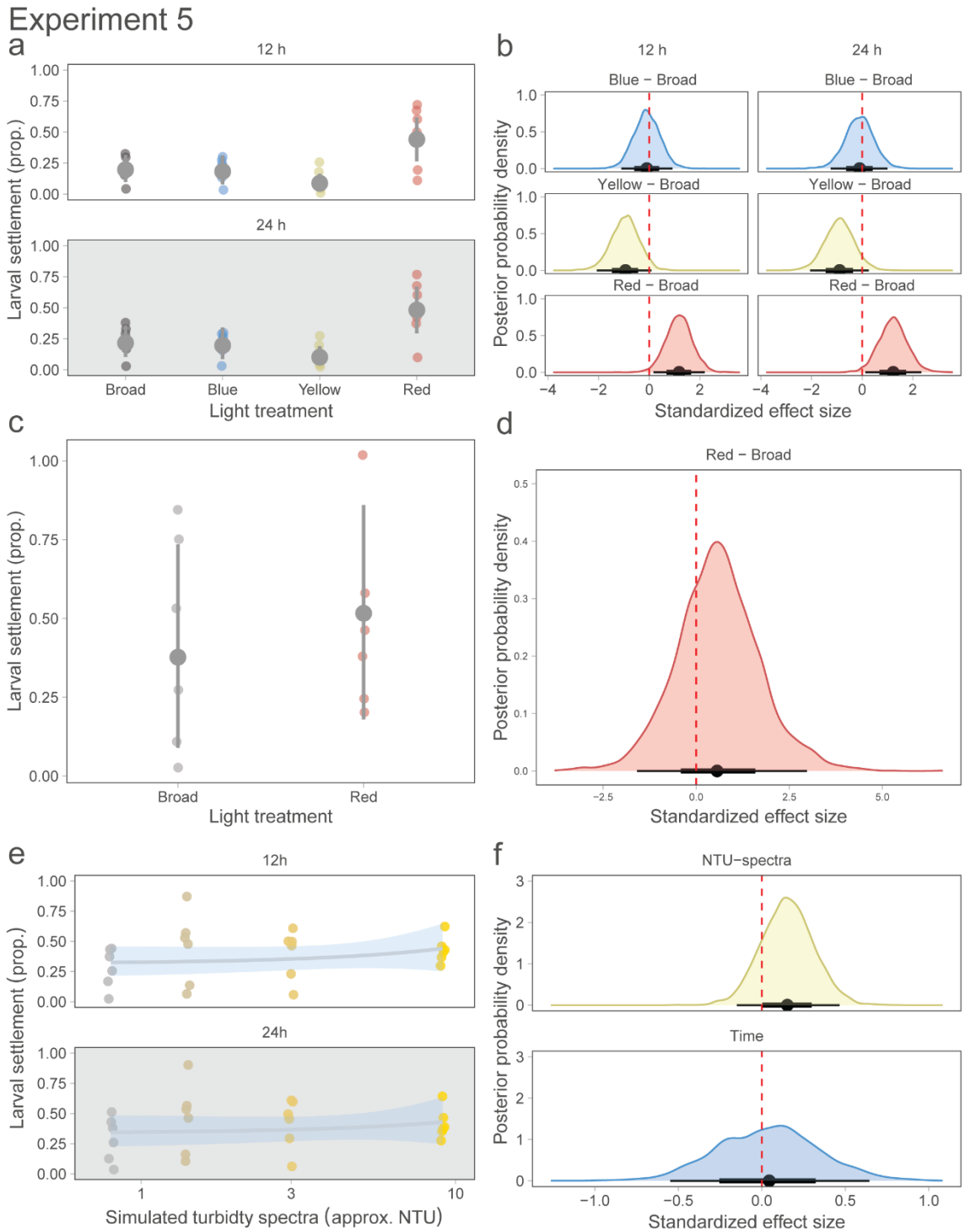


Fig. 3. Effects of artificial (monochromatic) and simulated turbidity spectral profiles on larval settlement of *Acropora tenuis* in Exp. 5. (a) Settlement after 12 and 24 hrs. Spectral profiles matched Exp. 1 (broad, artificial blue, artificial yellow, and artificial red). (b) Standardised Bayesian 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 downwards-facing surfaces were 8–9 fold lower than that of upwards-facing surfaces on the field-deployed discs (Table 3). Light intensity was 30% lower on the upward-facing surfaces at the clearer-water site (Florence Bay) compared with the higher-turbidity site (Picnic Bay), and 20% lower on the downward-facing surfaces. 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).

436 Table 3. Water quality at the clearer (Florence Bay) and turbid (Picnic Bay) water sites and each substrate
437 orientation. Light was measured during the first 3 d of deployment. NTU was measured for 1–2 mo. depending
438 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)	
Picnic Bay	Downwards	1.65 (n = 1)	1.62

439

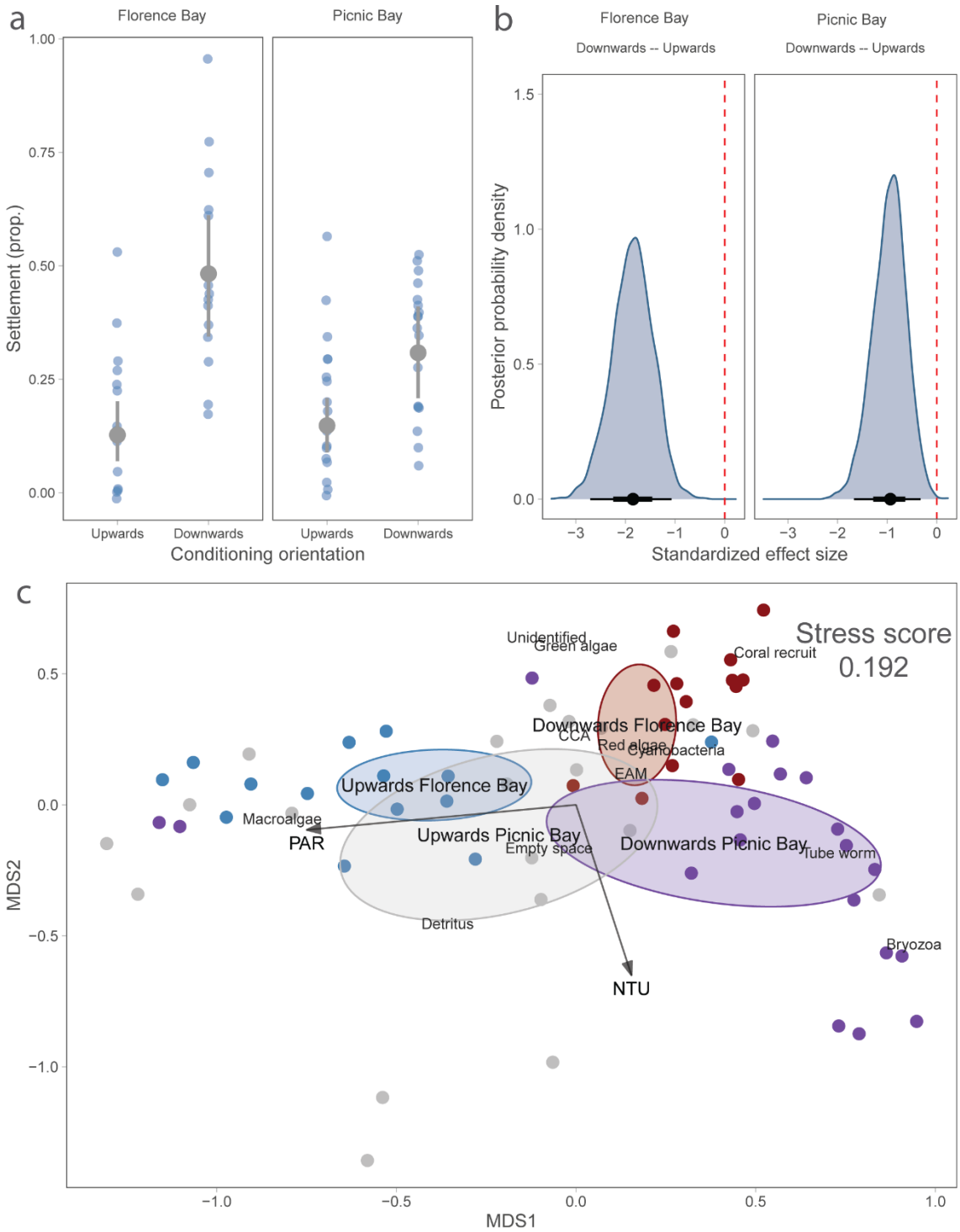
440 Settlement

441 There was a clear difference in settlement on field conditioned discs at each orientation, with
442 the effects more pronounced at the clearer-water site (Florence Bay), compared with the more
443 turbid-water site (Picnic Bay) (Fig. 4a,b). At Florence Bay there was a ~74% decrease
444 (>99.99% probability of a negative effect) in settlement on the upwards-facing discs relative
445 to the downward-facing discs. A similar although more modest trend occurred at Picnic Bay
446 with a ~51% decrease (99.91% probability of a negative effect) in settlement on discs
447 conditioned upwards. However, settlement on downwards-facing surfaces was lower at on
448 discs conditioned at the more turbid Picnic Bay site by 36%. The variance explained by the
449 model was 87%.

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

456 downwards-facing surfaces at Picnic Bay, and empty space (uncolonized by macro-

457 organisms) on Picnic Bay upwards-facing surfaces (Fig. S2).



458

459 Fig. 4. Settlement and community composition of the settlement discs in Exp. 6. Settlement on the discs

460 conditioned at (a) Florence Bay (clearer-water site) and (b) Picnic Bay (turbid-water site). All settlement occurred

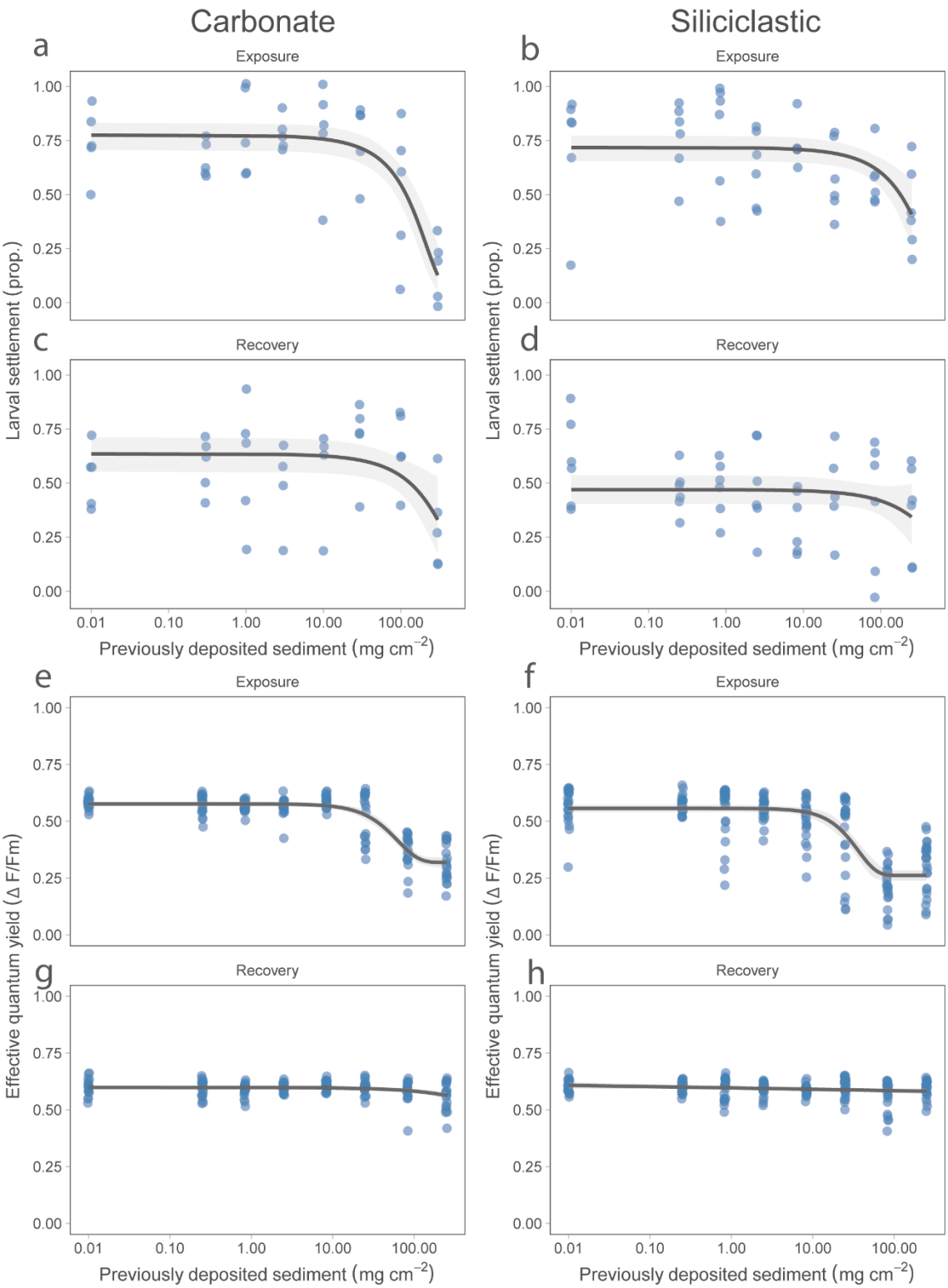
461 with discs facing upwards and under constant-light conditions. Larval competency was 80%. (c) An nMDS plot

showing community composition at each of the site and orientation combinations. Ellipses 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).



474

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

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

481 ### Sub-lethal indicators

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

491 ## General Discussion

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

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

523 Several lines of evidence suggest that water-quality conditions acting on the substrate prior to
524 settlement may be critical for determining coral settlement outcomes (Baird et al. 2003,
525 Petersen et al. 2005, Kuffner et al. 2006, Szmant & Miller 2006, Suzuki & Hayashibara 2011,
526 Ricardo et al. 2017). Chronically altered light regimes and smothering by sediment lead to
527 altered community assemblages on the substrate that evidently promote or prevent settlement
528 (Erwin et al. 2008, Arnold & Steneck 2011, Quimpo et al. 2020). In this study, prior exposure

529 of the settlement substrates to a variety of water quality conditions *in situ* elicited clear
530 differences in the settlement response, with larvae preferring the substrates that had been
531 previously conditioned under low light and not affected by sediment. While there remains
532 some limitations in characterising the community on settlement substrates visually and
533 inferring casual effects in absence of measuring possible confounders (Walker 2014), CCA
534 colonised downward-facing surfaces at the clear-water site was associated with high
535 settlement, whereas tubeworms were associated with decreasing settlement on the
536 downwards-facing surfaces conditioned at the turbid-water site. Empty space (possibly
537 grazed clear by gastropods observed at the time of retrieval) was associated with high
538 settlement on the upwards-facing surfaces. Known biological settlement inducers such as
539 CCA are often associated with specific light environments (Petersen et al. 2005, Bessell-
540 Browne et al. 2017, Briggs & Carpenter 2019) but are sensitive to sediment smothering
541 (Harrington et al. 2005, Ricardo et al. 2017), and searching larvae may favour these
542 communities that could be advantageous for post-settlement growth. However, optimal
543 conditions and responses of biological inducers for coral settlement (CCA and microbial
544 biofilms) to stress remain remarkably understudied (Webster et al. 2011, Webster et al.
545 2013), and derivation of water quality and light thresholds for important algal and microbial
546 inducers would improve predictions for coral settlement.

547 In addition to the potential for chronic effects of light exposure on the benthic surfaces to
548 influence its structure and suitability for coral settlement, highly turbid conditions are also
549 associated with sediment deposition (Whinney et al. 2017), which can accumulate on
550 settlement surfaces directly affecting access by larvae (Hodgson 1990, Ricardo et al. 2017),
551 or indirectly affecting settlement by harming biological settlement inducers such as CCA
552 (Kendrick 1991, Harrington et al. 2005). In the current study, there were strong impacts of
553 sediment accumulation and declining quality of settlement cues, resulting in a subsequent

554 decrease in coral settlement. Even brief sediment exposures to the substrate at levels that are
555 common for inshore reefs (see Tebbett et al. (2018), and Jones et al. (2020)) led to a decrease
556 in settlement success, as well as physiological responses of the substrate such as pigment loss
557 (bleaching) and decreased $\Delta F/F_m$'. Sediment smothering can reduce gas exchange, prevent
558 waste removal, eliminate light, and change the surface chemistry of the smothered organism
559 (Weber et al. 2012, Jones et al. 2016). The settlement response we observed was more
560 pronounced with carbonate sediment, and the differences between the two sediment types is
561 possibly caused by seemingly rapid consolidation of these sediments over the 3-day period,
562 with the carbonate sediment bound more firmly to the substrate at the time of removal.
563 Following the subsequent 3-day recovery period, $\Delta F/F_m$' and the dose-dependent settlement
564 increased, whereas bleaching did not change, indicating photo-physiological responses
565 maybe more effective indicators of settlement success than bleaching (loss of pigments).
566 Although some recovery was observed following sediment removal, turbid reefs are subject
567 to ongoing sediment deposition and removal processes that likely result in eventual loss or
568 reduction of settlement inducers on upwards-facing surfaces over longer durations (Kendrick
569 1991).

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

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

590 For the species tested here, and possibly many species in the genus *Acropora*, the influence
591 of light and physical challenges (such as sediment deposition and algal growth) on settlement
592 of the larvae is predominantly manifested indirectly by influencing the biology and quality of
593 settlement surfaces, rather than light as a direct cue influencing the settlement response.
594 However, in some species, there is greater 'weight of evidence' supporting the idea of light
595 sensitivity in settlement in other genera such as *Oxypora* (Babcock and Mundy, 1996; Mundy
596 and Babcock, 1998). Perhaps a more plausible explanation of settlement patterns under
597 various narrow-band spectra is a mistaken recognition of surface colour (i.e., spectral diffuse
598 reflection) from specular reflection. Several studies have observed increased settlement on
599 orange-red surfaces and have suggested there is an attraction because CCA species typically
600 have a reflectance peak in the 600 nm region of the visible spectrum (Mason et al. 2011,
601 Foster & Gilmour 2016). Alternatively, the attraction may be related to the loss of blue light
602 reflected from these surfaces, as reduced blue light is associated with temporary reduced
603 swimming speeds in larvae (Sakai et al. 2020). In our study, reduced settlement was observed

604 on CCA that had lost its red pigments (bleached), but after a recovery period improved
605 settlement correlated well with recovered photosystem activity, suggesting that physiological
606 processes (an indicator of healthy CCA) were a stronger driver of settlement than spectral
607 reflectance. Other studies have reported phototaxis of coral larvae in the water column (Lewis
608 1974, Szmant & Meadows 2006, Mulla et al. 2020, Sakai et al. 2020), although these
609 behaviours appear less consistent than observed in other marine invertebrates (Raimondi &
610 Morse 2000, Satheesh & Wesley 2010, Ricardo et al. 2014, Lillis et al. 2018, Abdul Wahab et
611 al. 2019).

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

627 Here we show for two common *Acropora* species that realistic light quality and quantity at the
628 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.

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