



REPORT

# Low light intensity increased survival of coral spat in aquaculture

B. D. Ramsby<sup>1</sup> · F. Emonnot<sup>1</sup> · F. Flores<sup>1</sup> ·  
S. Schipper<sup>2</sup> · G. Diaz-Pulido<sup>2</sup> · M. A. Abdul Wahab<sup>1</sup> ·  
A. Severati<sup>1</sup> · A. P. Negri<sup>1</sup>

Received: 28 September 2023 / Accepted: 8 March 2024 / Published online: 20 April 2024  
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**Abstract** Coral reef ecosystems are declining and may not recover under future climate scenarios without intervention. Seeding reefs with corals bred in aquaculture is a promising restoration intervention; however, early coral recruits (spat) are vulnerable to overgrowth by benthic algae and maximizing their survival is essential for the feasibility of large-scale breeding operations. This study investigated the optimal light quality and intensity for spat survival and growth in the presence of algal communities typically used in coral aquaculture to induce larval settlement, but which might also outcompete spat and reduce survival during the grow-out period. Spat were exposed to two light spectra (blue and a full spectrum) at four light intensities (5–160  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) over 12-week post-settlement. Survival was reduced under the highest intensity by nearly 40% compared to the lowest intensity. Light spectrum only affected survival at 60  $\mu\text{mol m}^{-2} \text{s}^{-1}$ —where survival was higher under blue compared to full spectrum light. Light treatments did not affect final spat size but spat were 33% smaller at the highest light intensity in weeks 6 and 8 due to overgrowth by crustose coralline algae (CCA), which was most abundant under these conditions. Low light intensity, on the other hand, favored green and brown algae, potentially due to their respective physiologies or less competition

from crustose coralline algae. These results indicate that low light intensity presents several advantages for maintaining spat in coral aquaculture, including maximizing survival without significantly affecting growth, as well as minimizing husbandry and operating expenses.

**Keywords** Light spectrum · *Acropora kenti* · Competition · Crustose coralline algae · Recruit growth

## Introduction

Coral reefs are under increasing threat from many stressors, including more frequent heatwaves (Hughes et al. 2018), crown of thorns starfish outbreaks (Mellin et al. 2019), stronger cyclones (Cheal et al. 2017), and lethal diseases (Muller et al. 2020). The effects from these stressors can be devastating and widespread (De'ath et al. 2012) and reefs can take decades for reefs to recover to their pre-disturbance state (Robinson et al. 2019). There is a growing need to support the diversity and function of tropical reefs by developing interventions that assist coral recruitment and increase coral cover as the climate continues to change (Kleypas et al. 2021; Bay et al. 2023). While efforts to restore reefs have been successful at small scales (e.g., individual reef patches), the scale of reef restoration has failed to match the widespread and precipitous decline of coral reefs (Randall et al. 2020; Suggett and van Oppen 2022).

Reef restoration projects often transplant corals or split colonies into fragments to establish 'new' colonies on degraded reefs (Bayraktarov et al. 2019; Boström-Einarsson et al. 2020). Small coral fragments grow quickly and have relatively high survival (Edwards et al. 2015); however, the fragmentation method is labor intensive and sacrifices healthy corals for propagation (Randall et al. 2020). Seeding

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00338-024-02489-6>.

✉ B. D. Ramsby  
b.ramsby@aims.gov.au

<sup>1</sup> Australian Institute of Marine Science, Townsville, QLD 4810, Australia

<sup>2</sup> School of Environment and Science, Coastal and Marine Research Centre and Australian Rivers Institute, Griffith University, Brisbane, QLD 4111, Australia

reefs with coral larvae or early recruits (spat) can be a more efficient approach, as a few coral colonies can produce hundreds of thousands of individuals with comparable genetic diversity to the natural populations (Zayasu and Suzuki 2019). However, spat have a low chance of survival due to grazing, sediment smothering, and competition with benthic algae. It has been estimated that approximately fifty percent of spat settled on the reef die within days of settlement (Martinez and Abelson 2013; Cooper et al. 2014); therefore, methods to improve spat survival will increase the utility of sexually produced spat for reef restoration (Randall et al. 2020; Banaszak et al. 2023).

A number of environmental factors, including temperature, water flow, and light intensity, affect the performance of corals across their life history, with optimum conditions restricted to a narrow range (Leal et al. 2016; Barton et al. 2017). Light is particularly important due to the intracellular symbiosis between corals and Symbiodiniaceae, which provides corals with a large proportion of their energy budget through photosynthesis (Roth 2014). While higher light intensity can translate to greater photosynthesis and faster coral growth (Wijgerde 2013), excessive light also brings the additional costs of photosystem repair, bleaching, and potential damage to coral tissue (Gómez-Campo et al. 2022). The responses of corals to light can be influenced by species-specific and environmental factors, including morphology, its symbiont type, light acclimation history, the exposure intensity and duration, as well as the quantity and quality of the light spectrum (Roth 2014). Therefore, coral responses to different light exposures are variable, with some studies showing positive associations between light intensity and coral growth (Izumi et al. 2023), others showing a negative association (Wijgerde 2013), and some show no clear relationship (Forsman et al. 2012; Schutter et al. 2012; Wijgerde et al. 2012; Kuanui et al. 2020). For example, in a direct comparison, only three of 10 coral species had positive responses to increasing light intensities (Wijgerde 2013).

For spat, the response to light intensity may be even more complex than for adult corals. It can take 2–3 weeks for spat to establish symbioses (Koch et al. 2022), and during this period, spat rely on energetic reserves and heterotrophic feeding. Spat may be effectively asymbiotic, having only established a small population of symbionts, or may have partnered with a suboptimal symbiont; therefore, the light intensity required for growth and survival may change over the course of spat development (McMahon 2018; Kreh 2019; Brunner et al. 2022). As seen with adult corals, the response of spat to light intensity is mixed, with some evidence of faster growth and/or higher survival under low light intensity (McMahon 2018; e.g.,  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Kreh 2019; Rahnke et al. 2022) and other studies showing better performance under high light (Hancock et al. 2021; Koch et al. 2022). These studies and the range of light intensities that spat

experience, from  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$  for spat in a reef crevice (Doropoulos et al. 2016) to beyond  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  for adult corals on a reef flat (Carpenter 1985; Cooper et al. 2008), suggest that there is scope to optimize light conditions in aquaria to improve survival and growth of coral spat for restoration.

In addition to light intensity, the spectral properties of light can also affect coral growth and survival. Sunlight is relatively evenly distributed across the visible spectrum from 400 to 700 nm; however, the available light spectrum in marine ecosystems changes with depth and with the absorption characteristics of the water column (i.e., algal or particulate content; Jones et al. 2021). The spectra of LED light sources commonly used to grow corals often emphasize blue wavelengths (400–500 nm), which have been associated with more rapid growth in adult corals compared to individuals grown under natural (full) spectrum profiles (Kinzie et al. 1984; Rocha et al. 2013; Mendes et al. 2017). However, blue light does not accelerate coral growth at all light intensities or in all species (Wijgerde et al. 2012; Izumi et al. 2023). For instance, *Galaxea fascicularis* grew faster in a blue-dominated light but only at intensities  $\geq 125 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Wijgerde et al. 2012). Coral aquaculture, for the production of seeding units for reef restoration, can utilize either natural or artificial light sources and both can be manipulated in intensity and spectral quality, offering opportunities to optimize the growth and survival of spat prior to deployment on the reef.

Light can also indirectly affect corals by promoting the growth of other photosynthetic benthic competitors, including macroalgae (Chadwick and Morrow 2011). For example, crustose coralline algae (CCA) are commonly used to induce coral larval settlement (Heyward and Negri 1999; Abdul Wahab et al. 2023), but can subsequently compete with spat for space on settlement substratum (Harrington et al. 2004; Jorissen et al. 2020). Other macroalgae can exclude corals for space on the reef and algal removal leads to higher coral and spat survival (Birrell et al. 2008; Arnold et al. 2010; Smith et al. 2023). In addition, macroalgae (including CCA) have a different suite of photosynthetic pigments than Symbiodiniaceae which may lead to different responses to light intensity or spectra than corals (Barott et al. 2009; Cikoš et al. 2022). The success and feasibility of large-scale coral restoration programs that produce larvae will rely on careful consideration of light intensity and spectral quality to ensure that optimal conditions, and maximum benefits, are provided to spat prior to deployment on the reef (Randall et al. 2020; Banaszak et al. 2023).

This study assessed the effects of light intensity and spectral quality on the performance of coral spat over a 12-week period. *Acropora* sp. nov. aff. *kenti* larvae were settled onto conditioned substrate with a live benthic community typical of coral aquaculture facilities, including several species of

CCA, and exposed to combinations of light quantity (i.e., intensity) and quality (i.e., spectrum) to identify optimal light conditions for spat survival and growth.

## Materials and methods

### Coral collection, larval cultures, and settlement

Coral colonies were surveyed around Magnetic Island, QLD, Australia (19°07'43.2"S 146°52'38.5"E), and the Palm Island Group, QLD, Australia (18°45'54.8"S 146°31'36.1"E), between October 9 and 20, 2021. Gravid colonies of a species most similar to *Acropora kenti* (*A. sp. nov. aff. kenti* hereafter abbreviated as *A. kenti*) were identified via the presence of pigmented eggs. Until recently, this species was thought to be related to *A. tenuis* (Bridge et al. 2023). Gravid colonies (40–50 cm diameter) were collected using a hammer and chisel on SCUBA (1–9 m depth; Great Barrier Reef Marine Park Authority Permit G21/45348.1), transported to the Australian Institute of Marine Science National Sea Simulator (SeaSim; Townsville, QLD, Australia), and held in outdoor aquaria (2800 L; aquarium dimensions: 280 × 100 × 44 cm) for 5 days until spawning. The aquaria were maintained at reef temperature (~27.2 °C) and under natural sunlight (maximum photosynthetically active radiation (PAR): 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The holding aquaria were semi-recirculating systems that received three turnovers of filtered seawater per day (FSW; 0.1  $\mu\text{m}$  nominal).

When setting of gamete bundles was observed, indicating that spawning is imminent, colonies were individually isolated in six 60 L aquaria. Buoyant bundles were collected from 6 colonies that fully spawned within 1 h of release, gently agitated and filtered through a 106  $\mu\text{m}$  mesh to separate eggs and sperm, and then the eggs were washed thoroughly with FSW (> 4 × 300 mL). Similar volumes of eggs from the six colonies were pooled into 60 L FSW with ~1 × 10<sup>6</sup> sperm mL<sup>-1</sup> for fertilization. After 1 h under static conditions, embryos were gently rinsed in FSW to remove excess sperm and transferred to 500 L culture tanks at a density of 0.3 larvae mL<sup>-1</sup> (100 L h<sup>-1</sup> flow through; ~27.2 °C). Culture tanks were gently aerated to keep embryos suspended for 24 h after which point aeration was increased to promote water circulation.

Concrete tiles were used as a settlement substratum and were conditioned prior to larval settlement. Dunlop concrete resurfacer (Ardex Australia Pty Ltd.) was used to make 28 × 28 cm tiles following manufacturer instructions. Tiles were conditioned in a semi-recirculating indoor aquarium containing a mixed community of crustose coralline algae (CCA) to develop a biofilm (Supplementary Fig. 1; 2800 L; aquarium dimensions: 280 × 100 × 44 cm; semi-recirculating with 3 turnovers d<sup>-1</sup>). Custom LED aquarium lights

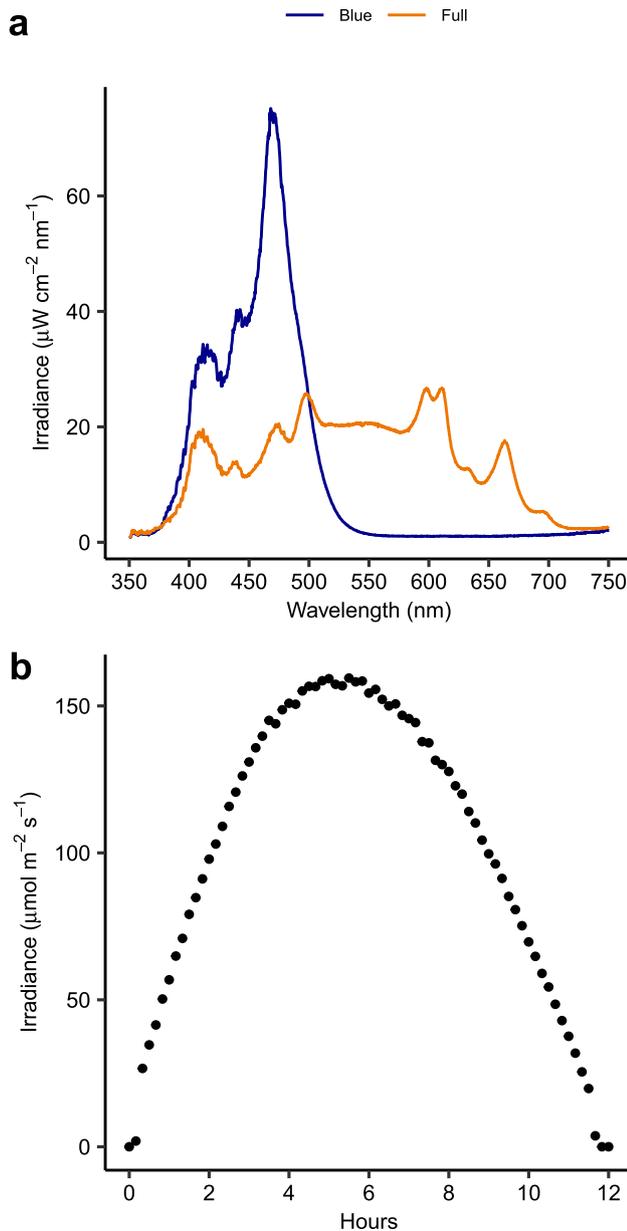
(blue and white dominated) and water temperature were controlled using a programmable logic controller (PLC, Siemens PCS7, Supervisory Control and Data Acquisition System (SCADA); max. PAR: 120  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; temp.: ~27.2 °C; Luter et al. 2021). After 6 weeks of conditioning, tiles were 43 ± 2% covered with a thin layer of CCA (Supplementary Fig. 2), which induces settlement of *Acropora* spp. (Harrington et al. 2004). Conditioned tiles were cut into smaller (4.2 × 4.2 cm) experimental tiles which were used for larval settlement ( $N=213$ ).

For larval settlement, experimental tiles were distributed between two 50 L aquaria with FSW. Approximately 2,000 9-d-old *A. kenti* larvae were added to each aquarium and allowed to settle on tiles overnight. Water quality parameters were within normal range during this period (27.5 ± 0.1 °C, 8.0 ± 0.1 mg O<sub>2</sub> L<sup>-1</sup>, 33.2 ± 0.1 PSU; HQ30D, Hach, USA). Tiles with more than five spat were transferred to a holding tank and larval settlement was repeated up to three times until all tiles had ≥ 5 spat to provide sufficient tile replication. Then, 10,000 cells mL<sup>-1</sup> of cultured *Cladocopium proliferum* (Butler et al. 2023), originally isolated in 2010 from coral *A. kenti* near Magnetic Island in Queensland, Australia (Australian Institute of Marine Science ID: SCF 055-01.10), were added to the settlement tanks overnight in order to induce uptake of Symbiodiniaceae (Quigley et al. 2020).

### Experimental setup and light treatments

Twenty-four hours after symbiont inoculation, tiles were distributed to 16 flow-through aquaria (50 L) where they were held for 12 weeks (0.8 L min<sup>-1</sup> FSW; 27.3 ± 0.1 °C SE). Each aquarium contained 8–9 tiles and had an internal pump for water circulation (Tunze turbelle, Penzberg, Germany).

To investigate the independent and combined effects of light spectrum and light intensity, we crossed two light spectra (blue or full spectrum) with four intensities (Fig. 1a, Table 1; midday max. nominally: 5, 15, 60, or 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), resulting in eight light treatments. Each light treatment was replicated in two aquaria with the highest intensity aquaria placed directly under the light source and lower intensity aquaria at increasing distance from the light source. Light was provided by LED panels developed by the National Sea Simulator and controlled by a SCADA system following a 12 h photoperiod with sinusoidal intensity profile (Fig. 1b). The blue spectrum was dominated by wavelengths of blue light and simulated artificial lighting common to some indoor aquarium systems and can be efficiently utilized by Symbiodiniaceae in coral (Wangpraseurt et al. 2014); the full spectrum simulated sunlight emission between 400 and 700 nm. Light intensities corresponded to 0.1–5.4 mol m<sup>-2</sup> d<sup>-1</sup> daily light integral (DLI; Table 1)



**Fig. 1** **a** Light spectra for the blue and full spectrum treatments ( $160 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). **b** Example diurnal cycle for the  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  treatment

which encompass light intensities in the reef habitats preferred by coral larvae (Doropoulos et al. 2016).

Each spectrum was measured using a Jaz spectrometer at  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  (JAZ-EL200, Ocean Insight, USA). Light intensity was measured continuously in the  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  treatment via the SCADA (LI-192 underwater quantum sensors, LI-COR Biosciences, USA) and weekly in all tanks manually (LI-192 with LI-250A light meter, LI-COR Biosciences, USA). The DLI for each treatment was calculated by scaling the continuous data

**Table 1** Summary of light intensity treatments. Maximum light intensity represents the average of 10 weekly measurements and estimated daily light integral (DLI)

Spectrum	Intensity	Max. intensity (SE) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	DLI (SE) ( $\text{mol m}^{-2} \text{d}^{-1}$ )
Blue	160	162.8 (2.1)	4.45 (0.06)
	60	61.4 (1.6)	1.68 (0.02)
	15	15.6 (0.7)	0.43 (<0.01)
	5	6.0 (0.2)	0.16 (<0.01)
Full	160	184.3 (3.3)	5.54 (0.08)
	60	58.6 (1.1)	1.87 (0.02)
	15	11.3 (0.5)	0.36 (<0.01)
	5	3.0 (0.1)	0.10 (<0.01)

from  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  to 60, 15, and  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$  treatments (Table 1).

Spat were supplied daily with a mixed live feed ( $2000 \text{ cells mL}^{-1}$  of a mix of *Tisochrysis lutea*, *Nannochloropsis oceanica*, *Pavlova lutheri*, *Dunaliella* sp.;  $0.5 \text{ nauplii mL}^{-1}$  of rotifers;  $0.5 \text{ nauplii mL}^{-1}$  of *Artemia salina*). All tile surfaces were uniformly cleaned on a weekly basis with a gentle brushing to remove superficial diatoms (but not green algae, brown algae or CCA). *Turbo* sp. snails ( $n=8-10$ , < 10 mm diameter) were added to each tank to help control diatom and non-coraline algal growth.

### Algal fouling

The benthic macroalgal community was monitored to assess the effects of light treatments on algal cover and determine whether the light treatments also affected spatial competition with coral spat. Each tile was photographed fortnightly with a Nikon D810 camera with a 60 mm lens and Nikon Speedlight SB-910 flash. The algal composition of 8 tiles per treatment was measured from images using ImageJ (Rasband 2018). Pixels on each tile that represented red (CCA)-, green- and brown-colored algae were manually selected and then used to sample the image for all pixels with matching hue, saturation, and brightness (Image > Adjust > Color threshold > Sample; Supplementary Fig. 2). Thus, the algal categories represent a color group rather than a taxonomic group of algae. Given the taxonomic diversity and difficulty in identifying morpho-anatomically CCA to species level, we have not attempted to quantify different CCA species. However, at the end of the experiment, thick CCA crusts were identified to genus level by microscopic examination. The area of the tile was measured by tracing the outline of the tile and the proportion of settlement tile area occupied by each component of the community was calculated.

## Spat survival and size

Spat survival was measured by calculating the proportion of living coral spat at each time point out of the number of spat initially settled on each tile ( $n = 18$  tiles per treatment). All living spat were counted; any clumps of spat where individuals could not be distinguished were counted as one spat. Spat growth ( $\text{mm}^2 \text{week}^{-1}$ ) was measured by tracing perimeters of spat in ImageJ and calculating the change in area from their initial size (Rasband 2018). Spat size can decrease through time due to tissue retraction or overgrowth by algae. Up to 26 spat (the median number per tile) were measured per tile and only spat that could be identified throughout the entire experiment were included, including chimeras established at settlement but excluding spat that fused during the experiment.

## Statistical analysis

All statistical analyses and graphical results were performed in R version 4.3.0 (R Core Team 2023). CCA, green, and brown algal cover were analyzed individually using generalized linear models. CCA cover was analyzed using a beta error distribution, logit link function, and a three-way interaction of spectrum, intensity, and time (including lower-order interactions and main effects). Brown algal cover was analyzed in the same way as CCA cover only using a tweedie error distribution to account for the absence of brown algae on some tiles. Green algal cover was also analyzed using a tweedie error distribution, however a model with a three-way interaction failed to converge, and two-way interactions of spectrum, intensity, and time were used instead. There was no significant difference between a model with a three-way interaction versus a model with three two-way interactions for green algal cover ( $\chi^2_{(1,18)} = 18.7, p = 0.41$ ).

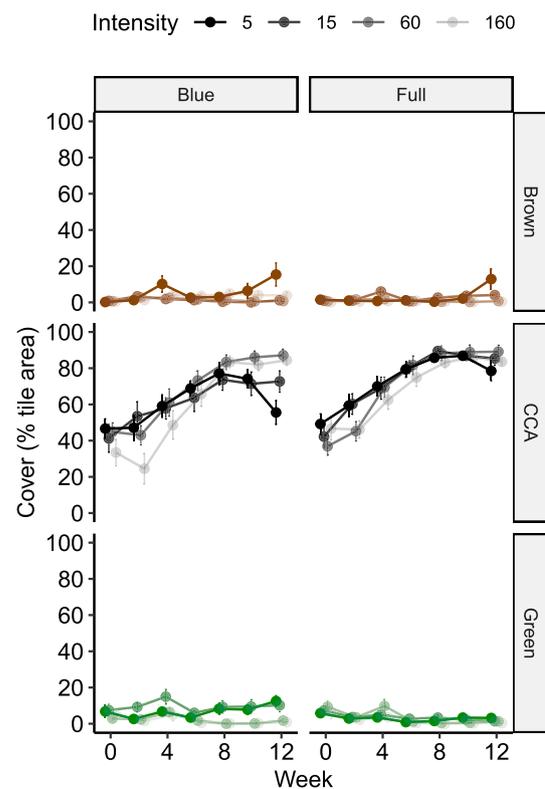
To determine whether spat survival differed among spectra, intensities, and over time, survival was analyzed using a generalized linear mixed model with a binomial error distribution and log link (Bates et al. 2015). Predictors included light spectrum, light intensity, and time and their higher-order interactions. In addition, Kaplan–Meier survival curves were used to determine final survival estimates and hazard ratios for each treatment (Kassambara et al. 2021; Therneau 2022). The survival as a function of CCA cover was compared between light treatments using 10 and 20% lethal concentrations (LC10, LC20), which is the % CCA cover required to reduce spat survival by 10 or 20%, respectively (Fisher et al. 2022). Spat size was analyzed using a linear mixed model with spectrum, intensity, and time as fixed predictors and aquarium and tile as random intercepts (Bates et al. 2015).

For all responses except LC10 and LC20, tank and tile were used as random effects to account for grouping and repeated measurements. Residuals from model predictions were used to check for uniformity and dispersion (Hartig 2022). Significant interactions (e.g., spectrum\*intensity\*time) were examined using pairwise comparisons of treatments within each timepoint (Kassambara et al. 2021; Therneau 2022; Lenth 2023). *P* values for pairwise comparisons were adjusted using the Tukey method (Lenth 2023).

## Results

### Algal fouling

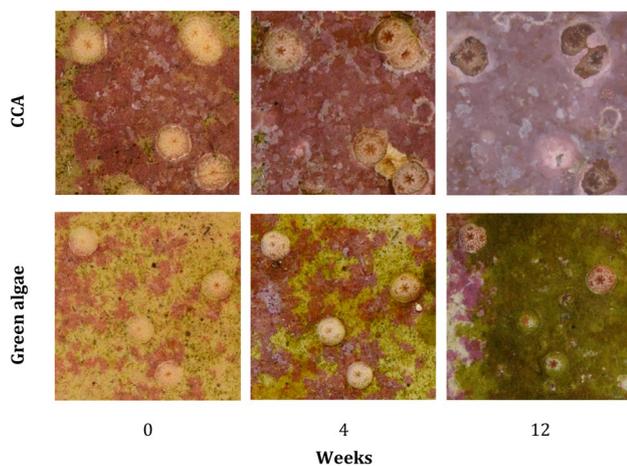
Initially, settlement tiles exhibited  $50 \pm 2\%$  (SE) total fouling including  $43 \pm 2\%$  crustose coralline algae (CCA),  $6 \pm 1\%$  green-colored algae, and  $1 \pm 0.2\%$  brown-colored algae (Fig. 2). At the end of the experiment, total fouling



**Fig. 2** Proportion of tile area occupied by brown algae, crustose coralline algae (CCA), and green algae. Rows distinguish components of the algal community while columns distinguish the two light spectra. Brown algae, CCA, and green algae are represented by brown, black, and green lines, respectively. Light intensities (5, 15, 60 and 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) are indicated using color shades, with darker shades representing lower intensities. Points represent means and error bars represent SE

had increased to  $88 \pm 2\%$  SE and consisted of  $80 \pm 2\%$  CCA,  $4 \pm 1\%$  green algae, and  $5 \pm 1\%$  brown-colored algae when averaged across all treatments (Fig. 2, Supplementary Fig. 2). Light treatments did not alter the general structure of the benthic macroalgal community (Fig. 2): CCA was 10 times more abundant than green or brown algae in every light treatment at the end of the experiment (Supplementary Fig. 3). The CCA included *Lithophyllum* sp., *Mesophyllum* sp., *Porolithon* sp., and *Titanoderma* sp.; however, these genera were not easily distinguished morphologically and were scored as a group (Fig. 3). By the end of the experiment, tiles exposed to high light intensity were almost completely covered by a thick, cream-colored *Lithophyllum* species while low-light tiles had CCA with thin, purple crusts (Supplementary Fig. 3).

CCA cover nearly doubled from 43 to 80% by week 12 (Fig. 2, Supplementary Fig. 2). The increase in CCA



**Fig. 3** Competition with CCA and green algae at 0, 4, and 12 weeks. The top row shows CCA (*Lithophyllum* sp.) which commonly overgrew coral spat. Note that the appearance of the same CCA changed over the course of the experiment. The bottom row shows overgrowth by green algae. Large patches of green algae were rare, but green algae often occurred around the margin of coral spat

cover depended on both the light intensity and spectrum (Table 2; spectrum\*intensity\*time). Post hoc comparisons of light treatments within each week indicate the main factor influencing CCA cover was light intensity (Supplementary Table 1). Initially, high light intensity had a negative effect on CCA cover, whereby CCA cover was significantly lower under blue  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  versus at 5 and  $15 \mu\text{mol m}^{-2} \text{s}^{-1}$  (both spectra). CCA cover was also significantly lower under blue  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  compared to full  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$ , suggesting an initial effect of light spectrum at the highest light intensity. However, there were no other differences in CCA cover between spectra for a given light intensity. In weeks 4, 6, and 8, there were no significant differences in CCA cover among light treatments. By week 12, light intensity had the opposite effect to that observed at week 2, where CCA cover was significantly lower at blue  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$  than in all other treatments.

Green algal cover, including *Bryopsis* sp. and *Pedobesia* sp., ranged from 2 to 6% and was recorded on 73% of the tiles by week 12 (Fig. 2). Light spectrum and light intensity had independent effects on the abundance of green algae, but the effects of each treatment varied over time (spectrum\*time, intensity\*time; Table 2). Almost no significant effects of light treatments were observed until week 6, after which point higher light intensities had a negative effect on green algal cover. Beginning at week 6, green algal cover was significantly lower at 60 and  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  compared to 5 and  $15 \mu\text{mol m}^{-2} \text{s}^{-1}$  at nearly all timepoints (Supplementary Table 2). To a lesser degree, light spectrum also affected green algal cover, which was significantly higher under blue versus full spectrum light in weeks 6 through 12 (Supplementary Table 2).

Brown algal cover, including *Colpomenia* sp., *Lobophora* sp., and chain-forming diatoms, ranged from 1–4% and was observed in 61% of tile photographs. While changes in brown algal cover depended on both light intensity and light spectrum, the major driver was a negative effect of high light intensity (Table 2; spectrum\*intensity\*time): in week 10, brown algal cover was significantly lower at 60

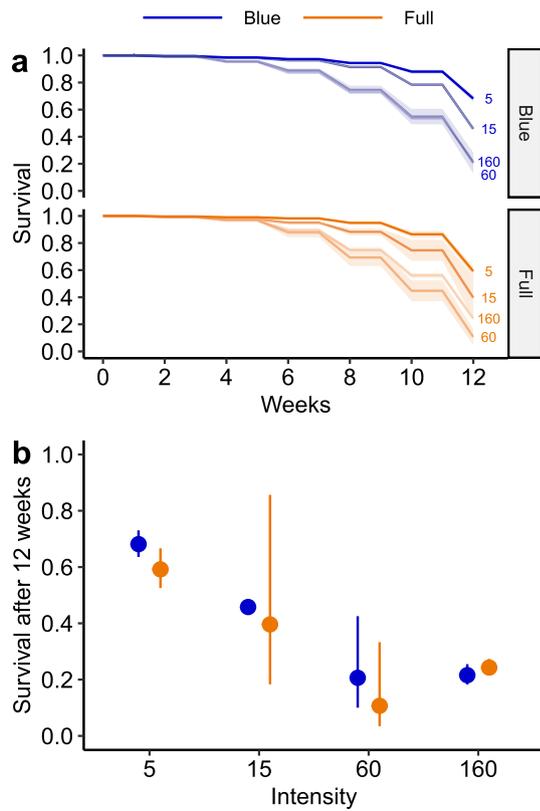
**Table 2** Algal fouling composition analysis using Wald chi-square tests of generalized linear models for the main effects of spectrum, intensity, and time and higher-order interactions while tank and tile were included as random effects

	Num df	CCA		Green		Brown	
		$X^2$	<i>P</i>	$X^2$	<i>P</i>	$X^2$	<i>P</i>
Spectrum	1	0.1	0.75	0.1	0.76	<0.1	0.97
Intensity	3	3.5	0.33	7.1	0.07	2.9	0.41
Time	6	93.4	<0.01	28.3	<0.01	57.0	<b>&lt;0.01</b>
Spectrum* Intensity	3	3.9	0.27	7.3	0.06	3.3	0.35
Spectrum*Time	6	14.7	0.02	28.9	<0.01	26.1	<b>&lt;0.01</b>
Intensity* Time	18	150.5	<0.01	114.2	<0.01	59.9	<b>&lt;0.01</b>
Spectrum* Intensity* Time	18	53.5	<0.01	–	–	40.5	<b>&lt;0.01</b>

The table includes the degrees of freedom (df), chi-square ( $X^2$ ), *P* values (*P*). *P* values less than or equal to 0.05 are indicated in bold

and  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  (full spectrum) than  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$  (blue spectrum; Supplementary Table 3). This negative effect of light intensity on brown algae was reinforced by week 12, when brown algal cover was significantly lower at 60 and  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  (full spectrum) compared to

$5 \mu\text{mol m}^{-2} \text{s}^{-1}$  (both spectra). In addition, in week 12, brown algal cover was significantly lower at  $60 \mu\text{mol m}^{-2} \text{s}^{-1}$  blue compared to  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$  full spectrum, further suggesting that intensity rather than spectrum is the primary driver of brown algal cover.



**Fig. 4** **a** Spat survival estimated from Kaplan–Meier survival curves over 12 weeks of exposure to each light treatment. Light spectra are indicated using different colors and light intensity as different shades, with darker shades corresponding to lower light intensities. Highlighted regions indicate  $\pm$ SE. **b** Mean survival and 95% confidence intervals after 12-week exposure to each light treatment

**Spat survival and size**

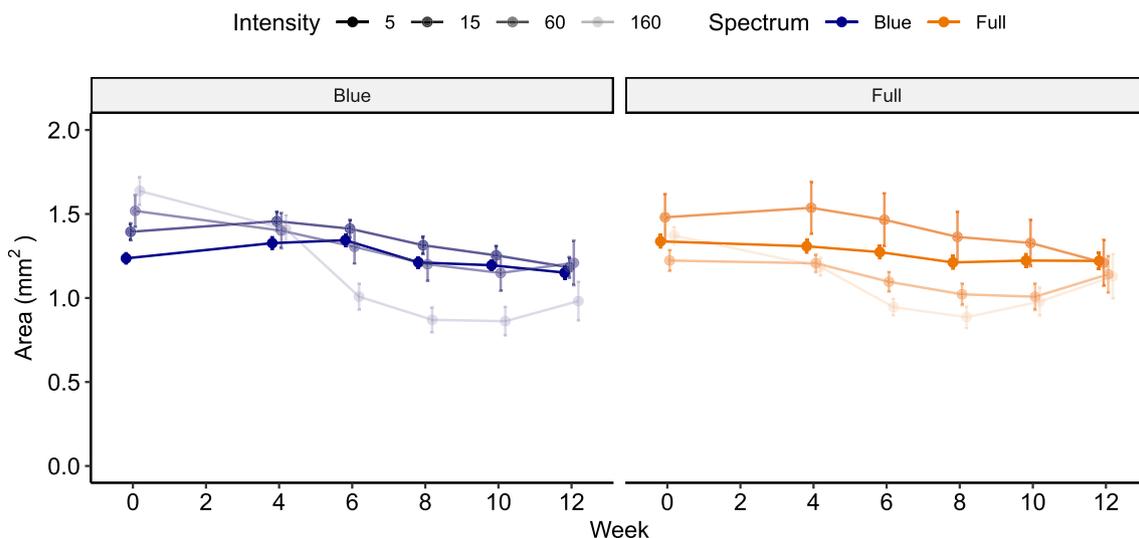
Spat survival gradually reduced over the 12-week experimental exposure period in all treatments but was strongly dependent on light treatment (Fig. 4). Higher light intensity had a strong negative effect on survival, but the effect was not apparent until after 6 weeks (intensity\*time; Fig. 4a, Table 3), when survival was higher at 5 and 15  $\mu\text{mol m}^{-2} \text{s}^{-1}$  compared to 60 or  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$ , regardless of light spectrum (Supplementary Table 4). Survival continued to be higher at low light intensity through week 12 (Fig. 4b, Supplementary Table 4). Hazard ratios also describe diminished survival with increasing light intensity: spat under 15, 60, and  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$  were 88, 346, and 285%, respectively, more likely to die than spat at  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In contrast to light intensity, light spectrum had little effect on mortality risk, as spat under full spectrum were 13% more likely to die than spat under blue spectrum light. In pairwise comparisons (spectrum\*intensity), the only significant effect of light spectrum was at  $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ , where average survival over the course of the experiment was 7.4% lower under full compared to blue spectrum light (Fig. 4a; Supplementary Table 4).

Surviving spat exhibited slightly negative growth (due to tissue retraction or overgrowth, see following section) across all experimental treatments (Fig. 5). Changes in spat area depended on light spectrum and light intensity (spectrum\*intensity\*time), but no two light treatments were significantly different in post hoc comparisons in any given week (Table 3, Supplementary Table 5). The effect of light intensity on spat size also varied over the course of

**Table 3** Linear model results comparing spectrum\*intensity\*time for spat survival and growth

	Spat survival			Spat area		
	Num. df	$X^2$	<i>P</i>	Num. df	$X^2$	<i>P</i>
Spectrum	1	<0.1	0.85	1	0.4	0.56
Intensity	3	31.6	<0.01	3	5.3	0.15
Time	5	6.3	0.27	5	30.6	<0.01
Spectrum* Intensity	3	10.4	0.02	3	4.2	0.24
Spectrum*Time	5	1.41	0.92	5	8.7	0.12
Intensity* Time	15	78.4	<0.01	15	305.2	<0.01
Spectrum* Intensity* Time	15	21.3	0.13	15	61.5	<0.01

Spat survival was analyzed using a generalized linear mixed model with tank and tile were included as random effects and the degrees of freedom (df), chi-square statistic ( $X^2$ ), and *P* value (*P*) are reported. Spat area was analyzed using a linear mixed model and the df, F statistic (F), and *P* are reported. *P* values less than or equal to 0.05 are indicated in bold



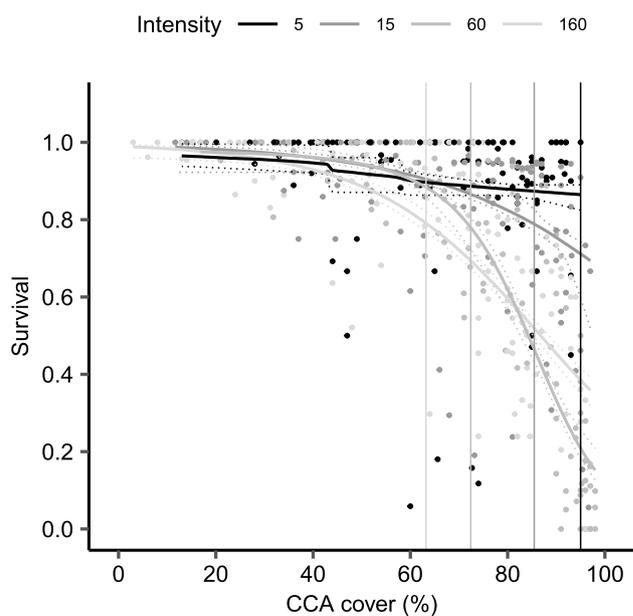
**Fig. 5** Spat area ( $\text{mm}^2$ ) over 12 weeks of exposure to each light treatment. Area represents the net outcome of growth and partial overgrowth, with only surviving spat included. Light spectra area indi-

cated using different colors and light intensities as different shades ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Points represent means and error bars represent SE

the experiment (intensity\*time): there were no significant differences in weeks 0–4, spat were significantly smaller at 160 compared to 15  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in weeks 6 and 8, but no significant differences in size were evident in weeks 10 or 12 (Supplementary Table 5).

### Relationship between CCA abundance and spat survival

High CCA cover was associated with low survival of *A. kenti* spat, which was exacerbated by high light intensity (Fig. 6). Under low light intensity, spat survival remained high despite high CCA cover; whereas under high light, spat survival decreased as CCA cover increased, suggesting more aggressive overgrowth by CCA (Fig. 6, Table 4). In comparison, the CCA cover associated with 20% spat mortality (LC20) decreased from >95% CCA cover at 5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  to 63% CCA cover at 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , suggesting that CCA was more detrimental to spat at higher light intensity (Fig. 6). In particular, *Lithophyllum* sp. completely covered tiles and was observed aggressively overgrowing spat, especially with thick crusts in the 60 and 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$  treatments (Fig. 6, Supplementary Fig. 3). Mortality at 5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  only reached 12% at the highest CCA cover recorded of 95%. CCA cover associated with 10% mortality (LC10) of coral spat did not show a clear association with light intensity (Table 4).



**Fig. 6** Spat survival was highest at low CCA cover but survival at CCA cover depended on the light intensity. Points represent the survival on each tile after 12 weeks. Curved lines and dotted regions represent the model-averaged predicted survival and 95% credible intervals, respectively. Vertical lines represent the lethal concentrations leading to 20% mortality (LC20)

### Discussion

To achieve ecologically meaningful scales of coral restoration, aquaculture programs engaging sexual propagation strategies need to produce a high yield of coral spat (Randall et al. 2020), requiring the optimization of larval settlement,

**Table 4** The lethal concentration of crustose coralline algae (CCA) resulting in 10 and 20% mortality (LC10 and LC20) for coral spat at each light intensity

Intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	LC10 (% cover CCA; 95% CI)	LC20 (% cover CCA; 95% CI)
5	44.3 (43.4, 95.0)	95 (47.8, 95.0)
15	67.4 (65.1, 84.1)	85.2 (82.6, 89.4)
60	64.1 (59.0, 66.6)	72.6 (67.9, 74.4)
160	49.5 (46.7, 56.8)	63.4 (60.8, 68.4)

For the 5  $\mu\text{mol}$  treatment, the LC10 and LC20 were poorly defined as survival was >90% for most of the experiment

and larval and spat survival (Pollock et al. 2017; Hancock et al. 2021; Rahnke et al. 2022). This study demonstrates that rearing spat under low light intensity maximizes their chance of survival on settlement surfaces with competitive algae, leading to a higher potential yield for coral restoration. The poor performance of spat grown at the higher light intensities tested was largely due to the presence of crustose coralline algae (CCA), which rapidly overgrew spat over a period of 12 weeks. In comparison to light intensity, light spectrum (full vs blue) had relatively minor effects on algal growth and spat survival. This study highlights the potential benefits of low-light conditions for rearing coral spat in aquaria and suggests minimal benefits of using full-spectrum light sources that mimic that of sunlight compared to blue-dominated LED lights (McMahon 2018; Kreh 2019; Rahnke et al. 2022).

The conditioning of substrates with biofilms, including CCA, is a common practice to induce settlement of coral larvae in experimental and aquaculture systems (Guest et al. 2010; Randall et al. 2020; Banaszak et al. 2023). In this study, coral larvae were presented with settlement surfaces that were half-covered with algae, the majority of which was CCA. This allowed for the assessment of the effects of light intensity and spectra (full vs blue) on algal growth, spat survival and the interaction between benthic macroalgae and spat in the first 12 weeks post-settlement. The total benthic algal cover increased from 52 to 88% over this period, with CCA dominating the algal community under all light intensity and spectrum treatments. In the first weeks, CCA cover was lowest under the highest intensity blue light, yet by week 12, the lowest CCA cover was evident in the lowest intensity blue light treatment, indicating dynamic responses of the algal community to light intensity as the experiment progressed. Similar but less extreme patterns in growth were also observed for CCA exposed to full spectrum light. After 12 weeks, there was 29 and 5% more CCA in high light than low light treatments in the blue and full spectrum exposures, respectively. High light intensity clearly favors rapid and potentially aggressive algal growth, yet light spectral quality

may be important to controlling selective algal growth under some conditions. Algae harvests visible light with a variety of photosynthetic pigments including chlorophyll *a* (all algae), chlorophyll *b* (green algae) and chlorophyll *c* (brown algae), primarily between 420 and 480 nm (blue spectrum) and between 630 and 670 nm (red) (Ke et al. 2021). However, CCA and cyanobacteria also contain the accessory photosynthetic pigments phycoerythrin and phycocyanin, which strongly absorb between 480 and 630 nm (green to red) (Kirk 2010). It is likely that the growth of each alga was at least subtly influenced by spectral quality in this experiment (Haxo and Blinks 1950). For example, CCA growth may be most inhibited by low intensity blue light due to the inability of phycoerythrin and phycocyanin to contribute to light harvesting for photosynthesis under these conditions, although chlorophyll *a* is also able to efficiently harvest light in the blue spectrum, potentially compensating light requirements under blue light.

Minor differences in cover of green and brown algae were observed among treatments, with both groups generally favored by low light conditions under both spectra. However, these results should not be assessed independently of the dominant CCA and any effects on the growth of the green and brown algal communities is likely to be influenced by both the direct effect of light conditions and competition for space with CCA. The direct effects of light intensity and spectra on each of the three groups of algae could only be assessed in the absence of competitors on the same substratum.

Changes in cover only partially represent the influence of light on CCA, as the composition of CCA species also varied between light treatments over the duration of the exposure. However, identification of CCA to species (or even genera) was not practical due to limited morphological features that can be used for taxonomic purposes, and because CCA crusts changed in appearance with time (e.g. due to ontogenesis) and light treatment. Nevertheless, by 12 weeks, tiles in the high intensity treatments of both spectra were dominated by thick crusts (not measured but > 1 mm) of *Lithophyllum* sp., while tiles in low light treatments were not dominated by this species and CCA crusts were thinner (~0.5 mm) under both spectra. It is unclear, however, whether these thin CCA represent different species or are simply early life stages of the dominant CCA.

Low light intensity was associated with the highest spat survivorship by week 12, where spat survival was three times higher at 5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  compared to at 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (both spectra). This result could be due to a direct influence of light intensity on spat health or indirect influence via effects on algal communities that then alter competitive dynamics between spat and algae. Light intensity has the potential to influence coral spat health through the effects on symbiont autotrophy. Prior to the establishment of a

functional symbiosis, spat rely on lipid reserves and heterotrophy (Figueiredo et al. 2012; Toh et al. 2013a). The *A. kenti* spat were aposymbiotic until infection with *C. proliferum* within days of settlement and, although not measured, visual indications of symbiosis establishment (brown color of spat) were observed after 4 weeks. It is not clear in this experiment when autotrophy would provide a significant contribution to energetics of the spat. Other studies have reported that the optimal light intensity for spat growth can change over their early development. For example, 4-week-old spat grew faster at 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  compared to 240  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (McMahon 2018), while conversely a longer-term study found that 8-week-old species spat benefited from higher light intensity ( $> 120 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Kreh 2019). A previous study on *A. millepora* found that light attenuation had no influence on spat until 8 weeks, after which spat survival, size and symbiont density were all reduced (Brunner et al. 2022). While the timing of increased light requirements likely vary among coral species, these studies demonstrate that exposure to low light during early development appears to benefit a range of coral species.

The total CCA cover increased over 12 weeks across all light intensities; however, the LC20 for spat survival was reached at far lower % CCA cover under high light intensities than under the lower light intensities. While it could be argued that this indicates a direct negative effect of high intensity light on spat health, indirect effects likely play a role, as it was evident that the survival and growth of spat was strongly affected by competition with and overgrowth by macroalgae, particularly the CCA *Lithophyllum* sp. at higher light intensities. Although CCA is a favored inducer of coral larval settlement, the benefits of *Lithophyllum* sp. are less understood than for other CCA such as *Porolithon* or *Titanoderma* sp. (Heyward and Negri 1999; Harrington et al. 2004; Abdul Wahab et al. 2023). *Lithophyllum* sp. covered the surface of most settlement tiles by 12 weeks and it rapidly grew over spat in the process, especially at 60 and 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Supplementary Fig. 3). In addition, the dominance of CCA at high light intensity likely limit the abundance of other competitors, such as green and brown colored algae (Jorissen et al. 2020). Despite the visual evidence of overgrowth of spat by aggressive CCA at higher light intensities, further investigation is required to disentangle possible direct and indirect effects of light intensity on spat survival (Jorissen et al. 2020).

Spat size appeared to increase under 60 and 160  $\mu\text{mol m}^{-2} \text{s}^{-1}$  between weeks 8 and 12, suggesting that low light intensity may limit the growth of older spat as reported in other studies (McMahon 2018; Kreh 2019; Brunner et al. 2022). However, the survivors experienced little to no net growth over the course of the experiment, potentially due to space limitation. In the absence of competitors, spat growth would be an ideal whole organism response metric

to assess the direct effects of light intensity. However, low light intensity might also have promoted higher survival via reduced photoinhibition or photodamage in coral symbionts (Roth 2014; Nitschke et al. 2022). Future studies addressing the direct vs indirect effects of light intensity on spat growth and survival in aquaculture should include coral photophysiological and symbiont density measures and an experimental design pairing light exposures with and without spatial competition.

In contrast to intensity, light spectrum had only minor effects on spat or macroalgae after 12 weeks and did not seem to affect competition or overgrowth processes. Previous studies on the other hand found that light spectrum affects coral growth, although they disagree as to whether blue, white, or red light led to the fastest growth (Kinzie et al. 1984; Rocha et al. 2013; Mendes et al. 2017). Coral symbionts absorb light between 400 and 550 nm (blue) as well as between 650 and 700 nm (red) (Scheufen et al. 2017). In this study, the custom LED panels produced blue-dominated and full spectrum light, potentially producing a different response in comparison to other studies that applied a variety of spectra (LED, LEP, or fluorescent sources). Additionally, the intensity of high energy blue wavelengths here was up to 2.5 times higher in the blue spectrum than full spectrum due to the restricted spectral range of the former light source and required light intensities. On the one hand, this could benefit symbiotic spat through higher intensities of photosynthetically usable radiation, but excess energy may result in photoinhibition and the generation of harmful reactive oxygen species (Nitschke et al. 2022). Adult *A. kenti* generally occurs in shallow, relatively high-light intensity, full light spectrum, habitat such as upper reef slopes (Veron 2000), while spat survival is often highest in reef crevices with low light intensity ( $\sim 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Doropoulos et al. 2016), indicating that light requirements over the lifecycle of coral are likely to change dramatically (McMahon 2018; Kreh 2019; Brunner et al. 2022). In several studies, the benefits to coral growth from a full-spectrum light source are only reported at higher light intensity (e.g.,  $> 40 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Wijgerde 2013; Wijgerde et al. 2012), suggesting that the light spectrum (and potentially different light sources) may be of limited significance when rearing spat under low light.

Several studies that reported faster growth rates of spat at higher light intensities have linked this with the additional autotrophic energy acquisition from their symbiont (Hancock et al. 2021; Koch et al. 2022). Both feeding and provision of symbionts have long-term effects on spat development, as early access to both nutritional pathways can increase the survival of spat reared ex situ and transplanted in situ (Suzuki et al. 2013; Toh et al. 2014). Therefore, the energy requirements of spat should be carefully considered (and potentially supplemented further) if low light conditions are applied during rearing in aquaculture

to manage algal competition. *A. kenti* was provided with cultured symbionts in this study, but it is unclear as to when the photosymbiosis would contribute significant nutritional benefits to the coral; previous work suggest benefits are apparent > 8 weeks after settlement (McMahon 2018; Kreh 2019; Brunner et al. 2022). Spat are likely to feed on zooplankton within days following settlement (Cumbo et al. 2012; Toh et al. 2013a, b), and while it is unclear to what extent coral spat rely on autotrophy vs heterotrophy, it is clearly an important future consideration for coral aquaculture toward maximizing spat health and survival prior to deployment for reef restoration.

Ex situ restoration programs using sexually produced corals will require holding spat in aquarium systems prior to deployment (Lippmann et al. 2023), during which conditions can be adjusted to optimize the growth, condition, and survival of spat (Barton et al. 2017). This study demonstrated that low light conditions over the first 12 weeks can reduce mortality in spat by limiting overgrowth by CCA communities (used to induce larval settlement). The application of low light intensity for spat holding could also provide additional benefits for the production facility, including reducing power consumption (if conducted indoors) and minimizing husbandry (including the control of algal growth on tanks) required to maintain aquaria. As this study showed minimal effects of light spectra on algal growth or spat survival, costs could be further reduced by raising spat under shaded natural light prior to deployment, which may in turn facilitate increasing the scale of coral aquaculture for restoration.

While spat survival can be optimized through the control of light intensity ex situ, consideration should be given to the fate of spat following deployment under less controlled conditions. For example, there was very little mortality in spat maintained at  $\leq 15 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the first 10 weeks, but at 12 weeks, greater mortality was observed, likely due to overgrowth by slowly maturing CCA. This growth of CCA is likely to continue if spat were held longer and following in situ deployment. This ongoing hazard to spat could be reduced by excluding aggressive CCA such as *Lithophyllum* sp., and using a less competitive, thinner crust CCA species for settlement induction (Heyward and Negri 1999), the application of non-biocidal antifouling coatings (Tebben et al. 2014; Roepke et al. 2022), or by inducing settlement of coral larvae using dead (e.g. frozen or dried) CCA on settlement substrate. For a symbiotic organism that depends on photosynthesis, it is counterintuitive to maintain corals at low light intensity; while low light improves spat survival, it would be logical to increase light as the functional symbiosis with Symbiodiniaceae becomes established prior to deployment, which may help older spat survive through the first months following deployment in situ. This optimization

of aquarium and substrate conditions, along with efforts to optimize spat nutrition, and increase spat thermal tolerance have the potential to enable restoration programs to meet the pace and scale of coral decline for effective coral restoration (Barton et al. 2017; McLeod et al. 2022; Suggett and Madeleine J.H. van Oppen 2022; Banaszak et al. 2023).

**Acknowledgements** We thank J. Montalvo Proano and S. Ferguson for their assistance with the experiment. The AIMS National Sea Simulator staff, especially M. Salmon and E. Arias for their assistance with lighting. T. Barker maintained the algal cultures and rotifers. This research was supported by the Reef Restoration and Adaptation Program (RRAP), which is funded by a partnership between the Australian Government's Reef Trust and the Great Barrier Reef Foundation. We acknowledge the Bindal, Manbarra, and Wulgurukaba Peoples as the Traditional Owners where this work took place. We pay our respects to their Elders past, present and emerging and we acknowledge their continuing spiritual connection to their land and sea country.

**Author contributions** A.P.N., A.S., M.A.A.W., and G.D.-P. designed the study. B.D.R., F.E., and F.F. performed the study. S.S. and G.D.-P. described the crustose coralline algae. B.D.R. and F.E. collected the data. B.D.R. analyzed the data and drafted the manuscript with F.F. and A.P.N. All authors revised the manuscript and approved the final draft.

#### Declarations

**Conflict of interests** The authors have no competing interests to declare that are relevant to the content of this article. This research was supported by the Reef Restoration and Adaptation Program (RRAP), which is funded by a partnership between the Australian Government's Reef Trust and the Great Barrier Reef Foundation.

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#### References

- Abdul Wahab MA, Ferguson S, Snekkevik VK, McCutchan G, Jeong S, Severati A, Randall CJ, Negri AP, Diaz-Pulido GA (2023) Hierarchical settlement behaviours of coral larvae to common coralline algae. *Sci Rep* 13:5795

- Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Mar Ecol Prog Ser* 414:91–105
- Banaszak AT, Marhaver KL, Miller MW, Hartmann AC, Albright R, Hagedorn M, Harrison PL, Latijnhouwers KRW, Mendoza-Quiroz S, Pizarro V, Chamberland VF (2023) Applying coral breeding to reef restoration: best practices, knowledge gaps, and priority actions in a rapidly evolving field. *Restor Ecol*, pe13913
- Barott K, Smith J, Dinsdale E, Hatay M, Sandin S, Rohwer F (2009) Hyperspectral and physiological analyses of coral-algal interactions. *PLoS ONE* 4:e8043
- Barton JA, Willis BL, Hutson KS (2017) Coral propagation: a review of techniques for ornamental trade and reef restoration. *Rev Aquac* 9:238–256
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Bay LK, Gilmour JP, Muir B, Hardisty PE (2023) Management approaches to conserve Australia's marine ecosystem under climate change. *Science* 381(80-):631–636
- Bayraktarov E, Stewart-Sinclair PJ, Brisbane S, Boström-Einarsson L, Saunders MI, Lovelock CE, Possingham HP, Mumby PJ, Wilson KA (2019) Motivations, success, and cost of coral reef restoration. *Restor Ecol* 27:981–991
- Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. In: Gibson RN, Atkinson RJA, Gordon JDM (eds) *Oceanography and marine biology: an annual review*. Taylor and Francis, pp 25–63
- Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli DM, Cook N, Ferse SCA, Ancock B, Harrison PL, Hein MY, Shaver E, Smith A, Suggett DJ, Stewart-Sinclair PJ, Vardi T, McLeod IM (2020) Coral restoration—a systematic review of current methods, successes, failures and future directions. *PLoS ONE* 15:e0226631
- Bridge TCL, Cowman PF, Quattrini AM, Bonito VE, Sinniger F, Harii S, Head CEI, Hung JY, Halafih T, Rongo T, Baird AH (2023) A *tenuis* relationship: traditional taxonomy obscures systematics and biogeography of the “*Acropora tenuis*” (Scleractinia: Acroporidae) species complex. *Zool J Linn Soc*, zlad062
- Brunner CA, Ricardo GF, Uthicke S, Negri AP, Hoogenboom MO (2022) Effects of climate change and light limitation on coral recruits. *Mar Ecol Prog Ser* 690:65–82
- Butler CC, Turnham KE, Lewis AM, Nitschke MR, Kemp D, Hoegh-Guldberg O, Fitt WK, van Oppen MJH, LaJeunesse TC (2023) Formal recognition of host-generalist species of dinoflagellate (*Cladocopium*, Symbiodiniaceae) mutualistic with Indo-Pacific reef corals. *J Phycol* 59:698–711
- Carpenter RC (1985) Relationships between primary production and irradiance in coral reef algal communities. *Limnol Oceanogr* 30:784–793
- Chadwick NE, Morrow KM (2011) Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N (eds) *Coral reefs: an ecosystem in transition*. Springer, Cham, pp 347–371
- Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. *Glob Chang Biol* 23:1511–1524
- Cikoš AM, Šubarić D, Roje M, Babić J, Jerković I, Jokić S (2022) Recent advances on macroalgal pigments and their biological activities (2016–2021). *Algal Res* 65:102748
- Cooper TF, Ridd PV, Ulstrup KE, Humphrey CA, Slivkoff M, Fabricius KE (2008) Temporal dynamics in coral bioindicators for water quality on coastal coral reefs of the Great Barrier Reef. *Mar Freshw Res* 59:703–716
- Cooper WT, Lirman D, Vangroningen MP, Parkinson JE, Herlan J, McManus JW (2014) Assessing techniques to enhance early post-settlement survival of corals in situ for reef restoration. *Bull Mar Sci* 90:651–664
- Cumbo VR, Edmunds PJ, Fan TY (2012) Scleractinian corals capture zooplankton within days of settlement and metamorphosis. *Coral Reefs* 31:1155
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci* 109:17995–17999
- Doropoulos C, Roff G, Bozec Y, Zupan M, Werninghausen J, Mumby PJ (2016) Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. *Ecol Monogr* 86:20–44
- Edwards AJ, Guest JR, Heyward AJ, Villanueva RD, Baria MV, Bollozos ISF, Golbuu Y (2015) Direct seeding of mass-cultured coral larvae is not an effective option for reef rehabilitation. *Mar Ecol Prog Ser* 525:105–116
- Figueiredo J, Baird AH, Cohen MF, Flot JF, Kamiki T, Meziane T, Tsuchiya M, Yamasaki H (2012) Ontogenetic change in the lipid and fatty acid composition of scleractinian coral larvae. *Coral Reefs* 31:613–619
- Fisher R, Barneche D, Ricardo GF, Fox D (2022) bayessec: a Bayesian no-effect-concentration (NEC) Algorithm. R package version 2.1.0.3
- Forsman ZH, Kimokeo BK, Bird CE, Hunter CL, Toonen RJ (2012) Coral farming: effects of light, water motion and artificial foods. *J Mar Biol Assoc United Kingdom* 92:721–729
- Gómez-Campo K, Enríquez S, Iglesias-Prieto R (2022) A road map for the development of the bleached coral phenotype. *Front Mar Sci* 9:806491
- Guest JR, Heyward AJ, Omori M, Iwao K, Morse ANC, Boch C (2010) Rearing coral larvae for reef rehabilitation. In: Edwards A.J. (eds) *Reef rehabilitation manual. Coral Reef Targeted Research & Capacity Building for Management Program*. St. Lucia, Australia, pp 73–98
- Hancock JR, Barrows AR, Roome TC, Huffmyer AS, Matsuda SB, Munk NJ, Rahnke SA, Drury C (2021) Coral husbandry for ocean futures: leveraging abiotic factors to increase survivorship, growth, and resilience in juvenile *Montipora capitata*. *Mar Ecol Prog Ser* 657:123–133
- Harrington L, Fabricius KE, De'ath G, Negri AP (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428–3437
- Hartig F (2022) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.5
- Haxo FT, Blinks LR (1950) Photosynthetic action spectra of marine algae. *J Gen Physiol* 33:389–422
- Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 18:273–279
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TCL, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison HB, Hobbs JPA, Hoey AS, Hoogenboom MO, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett MS, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* (80-)359:80–83
- Izumi R, Tan ES, Higa H, Shi Z, Takeuchi Y, Isomura N, Takemura A (2023) Effects of light intensity and spectral composition on the growth and physiological adaptation of Acroporid corals. *Coral Reefs* 42:385–398
- Jones R, Pineda MC, Luter HM, Fisher R, Francis D, Klonowski W, Slivkoff M (2021) Underwater light characteristics of turbid coral reefs of the inner central great barrier reef. *Front Mar Sci* 8:727206
- Jorissen H, Baumgartner C, Steneck RS, Nugues MM (2020) Contrasting effects of crustose coralline algae from exposed and subcryptic habitats on coral recruits. *Coral Reefs* 39:1767–1778

- Kassambara A, Kosinski M, Biecek P (2021) survminer: Drawing Survival Curves using “ggplot2.” R package version 0.4.9
- Ke W, Yin Y, Chen X, Qiu B (2021) Chlorophylls. In: Gao K, Hutchins DA, Beardall J (eds) Research methods of environmental physiology in aquatic sciences. Springer, pp 95–106
- Kinzie RA, Jokiel PL, York R (1984) Effects of light of altered spectral composition on coral zooxanthellae associations and on zooxanthellae in vitro. *Mar Biol* 78:239–248
- Kirk JTO (2010) The photosynthetic apparatus of aquatic plants. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, pp 265–307
- Kleypas J, Allemand D, Anthony KRN, Baker AC, Beck MW, Zeitlin L, Hilmi N, Hoegh-Guldberg O, Hughes TP, Kaufman L, Kayanne H, Magnan AK, Mcleod E, Mumby PJ, Palumbi S, Richmond RH, Rinkevich B, Steneck RS, Woolstra CR, Wachenfeld DR, Gattuso J (2021) Designing a blueprint for coral reef survival. *Biol Conserv* 257:109107
- Koch HR, Matthews B, Leto C, Engelsma C, Bartels E (2022) Assisted sexual reproduction of *Acropora cervicornis* for active restoration on Florida’s Coral Reef. *Front Mar Sci* 9:959520
- Kreh P (2019) Optimizing lighting regimes for rearing *Orbicella faveolata* and *Acropora cervicornis* recruits. Nova Southeastern University
- Kuanui P, Chavanich S, Viyakarn V, Omori M, Fujita T, Lin C (2020) Effect of light intensity on survival and photosynthetic efficiency of cultured corals of different ages. *Estuar Coast Shelf Sci* 235:106515
- Leal MC, Ferrier-Pagès C, Petersen D, Osinga R (2016) Coral aquaculture: applying scientific knowledge to ex situ production. *Rev Aquac* 8:136–153
- Lenth R V (2023) emmeans: estimated marginal means, aka least-squares means. R package version 1.8.7
- Lippmann RB, Helmstedt KJ, Gibbs MT, Corry P (2023) Optimizing facility location, sizing, and growth time for a cultivated resource: a case study in coral aquaculture. *PLoS ONE* 18:e0282668
- Luter HM, Pineda MC, Ricardo GF, Francis DS, Fisher R, Jones R (2021) Assessing the risk of light reduction from natural sediment resuspension events and dredging activities in an inshore turbid reef environment. *Mar Pollut Bull* 170:112536
- Martinez S, Abelson A (2013) Coral recruitment: the critical role of early post-settlement survival. *ICES J Mar Sci* 70:1294–1298
- McLeod IM, Hein MY, Babcock RC, Bay LK, Bourne DG, Cook N, Doropoulos C, Gibbs MT, Harrison PL, Lockie S, van Oppen MJH, Mattocks N, Page CA, Randall CJ, Smith A, Smith HA, Suggett DJ, Taylor B, Vella KJ, Wachenfeld DR, Boström-Einarsson L (2022) Coral restoration and adaptation in Australia: the first five years. *PLoS ONE* 17:e0273325
- McMahon NJ (2018) Optimization of light Irradiance during the early life of sexually-produced porites astreoides and Agaricia agaricites Recruits. Nova Southeastern University
- Mellin C, Matthews S, Anthony KRN, Brown SC, Caley MJ, Johns KA, Osborne K, Puotinen M, Thompson A, Wolff NH, Fordham DA, MacNeil MA (2019) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. *Glob Chang Biol* 25:2431–2445
- Mendes C, Fernandes C, Moreira A, Chambel J, Maranhao P, Leandro S (2017) Effect of LEDs light spectrum on success of fragmentation and growth of leather coral *Sarcophyton* spp. *Int J Aquac* 7:57–63
- Muller EM, Sartor C, Alcaraz NI, van Woesik R (2020) Spatial epidemiology of the stony-coral-tissue-loss disease in Florida. *Front Mar Sci*, 7.
- Nitschke MR, Rosset SL, Oakley CA, Gardner SG, Camp EF, Suggett DJ, Davy SK (2022) The diversity and ecology of Symbiodiniaceae: a traits-based review. *Adv Mar Biol*, pp 55–127
- Pollock FJ, Katz SM, Water JAJM Van De, Davies SW, Hein MY, Torda G, Matz M V., Beltran VH, Buerger P, Puill-Stephan E, Abrego D, Bourne DG, Willis BL (2017) Coral larvae for restoration and research: a large-scale method for rearing *Acropora millepora* larvae, inducing settlement, and establishing symbiosis. *PeerJ* 5:e3732
- Quigley K, Randall CJ, van Oppen MJH, Bay LK (2020) Assessing the role of historical temperature regime and algal symbionts on the heat tolerance of coral juveniles. *Biol Open* 9:bio047316
- R Core Team (2023) R: a language and environment for statistical computing.
- Rahnke SA, Hancock JR, Munk NJ, Caruso C, Drury C (2022) Optimizing sexual reproduction of *Montipora capitata* for restoration: effects of abiotic conditions and light acclimation on juvenile survival and growth. *Mar Ecol Prog Ser* 691:41–54
- Randall CJ, Negri AP, Quigley K, Foster T, Ricardo GF, Webster NS, Bay LK, Harrison PL, Babcock RC, Heyward AJ (2020) Sexual production of corals for reef restoration in the Anthropocene. *Mar Ecol Prog Ser* 635:203–232
- Rasband WS (2018) ImageJ.
- Robinson JPW, Wilson SK, Graham NAJ (2019) Abiotic and biotic controls on coral recovery 16 years after mass bleaching. *Coral Reefs* 38:1255–1265
- Rocha RJM, Pimentel T, Seródio J, Rosa R, Calado R (2013) Comparative performance of light emitting plasma (LEP) and light emitting diode (LED) in ex situ aquaculture of scleractinian corals. *Aquaculture* 402–403:38–45
- Roepke LK, Brefeld D, Soltmann U, Randall CJ, Negri AP, Kunzmann A (2022) Antifouling coatings can reduce algal growth while preserving coral settlement. *Sci Rep* 12:15935
- Roth MS (2014) The engine of the reef: photobiology of the coral-algal symbiosis. *Front Microbiol* 5:422
- Scheufen T, Iglesias-Prieto R, Enriquez S (2017) Changes in the number of symbionts and *Symbiodinium* cell pigmentation modulate differentially coral light absorption and photosynthetic performance. *Front Mar Sci* 4:1–16
- Schutter M, Van Der Ven RM, Janse M, Verreth JAJ, Wijffels RH, Osinga R (2012) Light intensity, photoperiod duration, daily light flux and coral growth of *Galaxea fascicularis* in an aquarium setting: a matter of photons? *J Mar Biol Assoc United Kingdom* 92:703–712
- Smith HA, Fulton SE, McLeod IM, Page CA, Bourne DG (2023) Seaweeding: manual removal of macroalgae facilitates rapid coral recovery. *J Appl Ecol* 30:e13624
- Suggett DJ, van Oppen MJH (2022) Horizon scan of rapidly advancing coral restoration approaches for 21st century reef management. *Emerg Top Life Sci* 6:125–136
- Suzuki G, Yamashita H, Kai S, Hayashibara T, Suzuki K, Iehisa Y, Okada W, Ando W, Komori T (2013) Early uptake of specific symbionts enhances the post-settlement survival of *Acropora* corals. *Mar Ecol Prog Ser* 494:149–158
- Tebben J, Guest JR, Sin TM, Steinberg PD, Harder T (2014) Corals like it waxed: paraffin-based antifouling technology enhances coral spat survival. *PLoS ONE* 9:1–8
- Therneau TM (2022) A Package for Survival Analysis in R.
- Toh TC, Peh JWK, Chou LM (2013a) Heterotrophy in recruits of the scleractinian coral *Pocillopora damicornis*. *Mar Freshw Behav Physiol* 46:313–320
- Toh TC, Peh JWK, Chou LM (2013b) Early onset of zooplanktivory in equatorial reef coral recruits. *Mar Biodivers* 43:177–178
- Toh TC, Ng CSL, Peh JWK, Ben TK, Chou LM (2014) Augmenting the post-transplantation growth and survivorship of juvenile scleractinian corals via nutritional enhancement. *PLoS ONE* 9:e98529
- Veron J (2000) Corals of the World. Australian Institute of Marine Science, Townsville, QLD, Australia

- Wangpraseurt D, Tamburic B, Szabó MN, Suggett DJ, Ralph PJ, Kü HI M (2014) Spectral effects on *Symbiodinium* photobiology studied with a programmable light engine. PLoS ONE 9:e112809
- Wijgerde T, Henkemans P, Osinga R (2012) Effects of irradiance and light spectrum on growth of the scleractinian coral *Galaxea fascicularis* - applicability of LEP and LED lighting to coral aquaculture. Aquaculture 344–349:188–193
- Wijgerde T (2013) Coral growth under light emitting diode and light emitting plasma: a cross-family comparison. Adv Aquar Online Mag, pp 1–31
- Zayasu Y, Suzuki G (2019) Comparisons of population density and genetic diversity in artificial and wild populations of an arborescent coral, *Acropora yongei*: implications for the efficacy of “artificial spawning hotspots.” Restor Ecol 27:440–446

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