



Effects of climate change and light limitation on coral recruits

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ABSTRACT: Climate change impacts and light attenuation from suspended sediments, due to runoff, natural resuspension or dredging, can both impede the replenishment of coral populations. Here we tested the independent and combined impacts of climate change (current temperature and dissolved CO₂, and 2 future climate scenarios) and a 1 mo long light attenuation period at 5 different light levels (0.1 to 4 mol photons m⁻² d⁻¹) on early *Acropora millepora* recruits. Additionally, we evaluated whether the effects were age dependent by comparing responses of recruits that were 1 mo old ('early attenuation') vs. 2 mo old ('late attenuation'). Recruit survival, size and Symbiodiniaceae densities increased slightly under moderate future climate conditions (current temperature +0.44°C, 692 ppm pCO₂), but decreased under a more severe climate scenario (+0.94°C, 985 ppm pCO₂). Light attenuation significantly decreased recruit survival, size and Symbiodiniaceae densities only for recruits exposed to the late attenuation, suggesting an increasing reliance on photosynthesis as recruits age. Under the more severe climate scenario tested, recruit survival was diminished by both climate change ($\leq 18 \pm 4\%$ [SE] in the early attenuation) and light limitation ($\leq 32 \pm 6\%$ in the late attenuation) compared with controls. However, there was no interaction between future climate scenarios and light attenuation, indicating that these effects were additive. This study demonstrates the potential effects of light limitation and future climate conditions on coral recruitment success and highlights the need to manage the timing of sediment-generating activities near reefs to optimise light availability for several months post settlement.

KEY WORDS: Water quality · Runoff · Sediment · Turbidity · Dredging

1. INTRODUCTION

Human-induced climate change, leading to ocean acidification and warming, can cause decreased calcification rates and bleaching in corals, which together represent the greatest threat to coral reef persistence over the coming centuries (Hughes et al. 2017a,b, Cornwall et al. 2021). The effects of these global stressors can be intensified by poor water quality (e.g. due to sediment runoff causing light attenuation), with additive and synergistic responses

common for tropical reef species (Ban et al. 2014, Uthicke et al. 2016, Castro-Sanguino et al. 2021). Thus, improvements in local water quality, coupled with reductions in atmospheric carbon dioxide emissions, could improve sustainable management and conservation of coral reefs (Carilli et al. 2010, Cornwall et al. 2021). However, despite many studies quantifying future ocean warming and acidification effects (Hoegh-Guldberg et al. 2007, Foster et al. 2015, van der Zande et al. 2020), the interactive effects of climate change with other common coral

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reef stressors are rarely investigated (Ban et al. 2014, Bruno et al. 2018), particularly for the early stages of the coral lifecycle (McLachlan et al. 2020). Consequently, the applicability of current coral ecosystem management regulations for future climate scenarios is uncertain (Bruno et al. 2018).

Elevated sediments and nutrients are considered among the most harmful anthropogenic stressors affecting nearshore coral reef ecosystems, with poor water quality driven by increasing concentrations of these contaminants estimated to threaten about 25% of the world's coral reefs (Burke et al. 2011). Activities within the catchments of rivers that flow into coastal waters can elevate sediments and nutrient runoff adjacent to reefs (Brodie et al. 2012, GBRMPA 2018). Sediments can also become elevated during natural resuspension events (Browne et al. 2012, Luter et al. 2021) and dredging operations (Erfte-meijer et al. 2012, Jones et al. 2016, Luter et al. 2021). Negative effects of sediments occur both when particles are suspended in the water column (i.e. disturbance of heterotrophic and autotrophic energy acquisition and tissue irritation) or when particles are deposited on the coral tissues (i.e. smothering and interfering with heterotrophic feeding) (Anthony & Fabricius 2000, Jones et al. 2015b, 2016, 2020a, Brunner et al. 2021). The impacts of sediments can occur throughout all coral life stages, including the pelagic larval and early recruit stages (Erfte-meijer et al. 2012, Jones et al. 2015b, 2016).

The potential for both suspended and deposited sediments to impact corals demands that experimental designs effectively separate these 2 effect pathways to understand their respective hazards (Jones et al. 2015b, 2016, Bessell-Browne et al. 2017a). For example, even thin sediment deposition layers ($>0.9 \text{ mg cm}^{-2}$; Ricardo et al. 2017) may have detrimental effects on processes such as coral larval settlement success, recruit survival and feeding responses (Weber et al. 2012, Jones et al. 2016, Ricardo et al. 2017, Brunner et al. 2021). In contrast, suspended sediment concentrations (e.g. up to 100 mg l^{-1} for 4 wk) observable in close proximity to capital dredging projects (Fisher et al. 2015, Jones et al. 2015a, 2016) show no significant effect on the survival of adult coral colonies in laboratory experiments, as long as their light requirements are met and in the absence of deposition (Bessell-Browne et al. 2017a). However, suspended sediments (0 to 100 mg l^{-1}) combined with light attenuation (down to $0 \text{ mol photons m}^{-2} \text{ d}^{-1}$) can cause bleaching and partial tissue mortality (up to $\sim 70\%$ after 4 to 7 wk) (Bessell-Browne et al. 2017a). Elevated suspended sediments

can also cause shifts in coral carbon acquisition, with shading reducing autotrophy but with heterotrophy potentially increasing due to increasing ingestion of suspended particles (Anthony & Fabricius 2000). However, as suspended sediment concentrations increase beyond species-specific thresholds, energy deficiencies such as reductions in storage lipids, calcification and growth can become evident (Anthony & Fabricius 2000, Anthony & Connolly 2004, Jones et al. 2020b, 2021, Luter et al. 2021).

Overall, light limitation is a major driver of decline in coral health associated with sediments in suspension (Bessell-Browne et al. 2017a), underscoring that consistent light availability is vital for the health and survival of coral colonies (Rogers 1979, Muscatine 1990, Anthony & Fabricius 2000, Jones et al. 2016). Despite the importance of a functioning coral-Symbiodiniaceae symbiosis, it is largely unknown at what age coral recruits begin to rely on autotrophic feeding (Muscatine 1990). Studies suggest that consistent light availability promotes the survival of symbiont-bearing coral larvae (Tomascik & Sander 1987, Rogers 1990, Isomura & Nishihira 2001) and coral recruits which are at least 4 mo old (Babcock & Mundy 1996). To better understand the potential vulnerability of coral recruits to light attenuation and climate change, it is important to identify whether there are differences in impacts on performance (i.e. survival and growth) between coral recruits shortly after settlement when they have only recently acquired Symbiodiniaceae, and older recruits with established symbioses that are potentially more reliant on autotrophic feeding.

The post-settlement life phase of corals is a bottleneck in the repopulation of reefs, with low survival success in comparison to other stages in the coral lifecycle (Loya 1976, Babcock 1985). However, only a few studies have quantified the effects of light attenuation on recently settled coral recruits that are just beginning to rely on autotrophic feeding through photosynthesis (e.g. Babcock & Mundy 1996, Abrego et al. 2012, Kuanui et al. 2020, Hancock et al. 2021, Noonan et al. 2022). Even fewer studies have investigated the combined effects of light attenuation and at least 1 climate stressor (ocean warming or ocean acidification) on coral recruits and juveniles (e.g. Abrego et al. 2012, Kuanui et al. 2020, Noonan et al. 2022). Understanding the ways in which light attenuation from elevated suspended sediments might combine with climate change to affect coral recruitment and population replenishment is important for managing and conserving coral reefs now and into the future.

To test the hypothesis that the interacting effects of light attenuation and future climate stress are detrimental for coral recruits, we quantified the effects of 1 mo long light attenuation periods on the survival of coral recruits under 3 different climate scenarios. The light attenuation levels applied bracket those observed in response to sediment resuspension (Anthony et al. 2004, Cooper et al. 2008), input from land runoff (Cooper et al. 2008) and during capital and maintenance dredging activities (Fisher et al. 2015, Jones et al. 2015a, 2016). We also evaluated how recruit sizes, symbiont quantities and the photosynthetic activity of photosystem II in symbionts responded to these combined pressures. To test if light attenuation responses are dependent on the recruit age (Babcock & Mundy 1996), we attenuated the light 'early' (at 1–2 mo old) and 'late' (at 2–3 mo old) during the post-settlement development, as this information can inform the management of water quality (e.g. dredging or terrestrial runoff) to protect corals shortly after annual coral spawning events.

2. MATERIALS AND METHODS

2.1. Experiment timeline

We conducted manipulative tank-based experiments at the National Sea Simulator ('SeaSim') located at the Australian Institute of Marine Science (AIMS) in Townsville, Australia, to investigate the combined effects of climate change and light attenuation on the post-settlement survival of up to 4 mo old *Acropora millepora* (Ehrenberg, 1834) recruits ($\varnothing < 1$ mm, $n = 2998$), a corymbose coral species commonly found in shallow habitats on the Great Barrier Reef (GBR). The term 'recruit' was adopted to describe these early post-settlement corals < 40 mm in diameter (Doropoulos et al. 2016), although the term 'spat' is also commonly used to describe this early life stage. Throughout the entire experimental period, these early recruits were either exposed to 'current' or 2 future climate scenarios, which respectively consisted of elevated temperature and carbon dioxide partial pressure ($p\text{CO}_2$) treatments (detailed in Section 2.3; see also Table 1 and Fig. 1). The 'current' temperature was based on the daily 10 yr historic mean reef temperature at Davies Reef, a typical mid-shelf reef of the GBR, which increased from 26.2 to 28.7°C over the course of the experimental period between November and February. Temperatures of the 'medium' and 'high' stress treatments were designed to remain below the expected threshold for

thermal stress alone ($< 1^\circ\text{C}$ above current conditions; Liu et al. 2003, Kayanne 2017), given that 2 additional potential stressors were being applied. Yet, these temperature scenarios are consistent with the +1.5 and +2.0°C targets of the IPCC Paris Agreement (IPCC 2014, 2021) considering that water temperatures of the GBR have already increased by $\sim 0.9^\circ\text{C}$ since pre-industrial conditions (Lough et al. 2018): medium treatment of +1.3°C ($0.9 + 0.44^\circ\text{C}$) and high treatment of +1.8°C ($0.9 + 0.94^\circ\text{C}$) above pre-industrial temperatures. The $p\text{CO}_2$ was guided by the representative concentration pathway (RCP) model RCP8.5 that predicts $p\text{CO}_2$ levels of 680 and 940 ppm for the years 2050 and 2100, respectively (Meinhausen et al. 2011, IPCC 2014, 2021).

Commencing at 2 different coral recruit ages, 1 mo long light attenuation periods with 5 light intensities were simulated from: 1 to 2 mo after settlement ('early attenuation'), and 2 to 3 mo following settlement ('late attenuation') (detailed in Section 2.4; see also Table 1 and Fig. 1). Light intensities were based on conditions within habitats where coral larvae often settle on inshore reefs (e.g. control intensity of 4 mol photons $\text{m}^{-2} \text{d}^{-1}$; see Section 2.4). Light attenuation treatments bracketed conditions observed from sediment resuspension due to waves and storms (Anthony et al. 2004, Cooper et al. 2008, Luter et al. 2021) and land runoff (Cooper et al. 2008), as well as conditions observed during capital and maintenance dredging campaigns (Fisher et al. 2015, Jones et al. 2015a, 2016). Photosynthetic efficiencies were measured immediately prior to and after each light attenuation period (Fig. 1). Subsequently, the recruits were allowed to recover for 1 mo before the survival, size and symbiont quantities were measured (early attenuation: 3 mo after settlement, late attenuation: 4 mo after settlement) (Fig. 1).

2.2. Coral rearing and inoculation

In late October 2018, gravid *A. millepora* colonies were collected between 2 and 6 m water depth near Falcon Island in the central GBR ($18^\circ 45' 57.0'' \text{S}$, $146^\circ 31' 57.0'' \text{E}$) and transported to AIMS. Four days following the full moon (28 October 2018), egg-sperm bundles from 7 coral colonies were collected, cross-fertilised using approximately equivalent egg and sperm concentrations from each colony and then transferred (once $> 90\%$ of embryos showed cell cleavage) into 440 l flow-through tanks (1 μm filtered seawater) for larvae development following standard procedures (Pollock et al. 2017, Brunner et al. 2021).

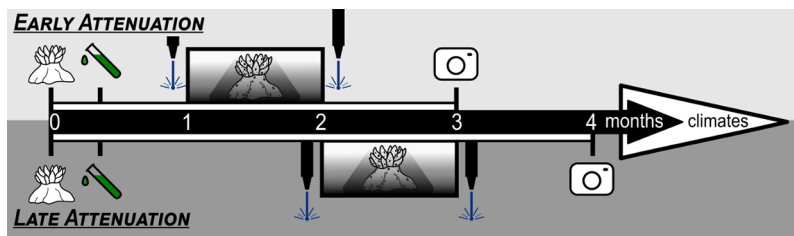


Fig. 1. Timeline for the 'early attenuation' and 'late attenuation' experiments. Newly settled *Acropora millepora* recruits (month 0) were grown in 4 mol photons $m^{-2} d^{-1}$ (except when the light was limited) and in 3 climate scenarios (3 replicate tanks per light-climate combination). One week after settlement, the recruits were inoculated with cultured Symbiodiniaceae (depicted by a vial). Once the recruits were either 1 or 2 mo old, depending on the attenuation experiment, the light was limited in 5 intensities (Table 1) for a period of 1 mo (coral in shaded box). Directly prior to and following the respective light attenuation periods, the maximum photosynthetic efficiency was measured (light pulse in months 1, 2 and 3). One month after the respective end of the light attenuation periods, the survival and size of the recruits were photographically documented, and they were then snap-frozen for later Symbiodiniaceae counts marking the end of each attenuation experiment in month 3 and 4

The average temperature in these 440 l flow-through tanks was $26.5 \pm 0.1^{\circ}C$ with an illumination of $2 \mu mol photons m^{-2} s^{-1}$ (12:12 h light:dark diurnal light cycle). Daily competency assays (Brunner et al. 2021) revealed settlement greater than 95% on the settlement-inducing crustose coralline alga (CCA) *Porolithon onkodes* 9 d following fertilisation, so the larvae were presented to disc-shaped experimental substrates made of polyvinyl chloride (PVC) (2 cm diameter \times 1 cm height, 120 discs per 50 l at approximately $2 larvae ml^{-1}$) on that day for mass-settlement. The discs were preconditioned for 2 mo with CCA rubble (including the CCAs *P. onkodes* and *Titanoderma tessellatum*) in outdoor flow-through tanks to allow the formation of a coral settlement-inducing biofilm (average daily light integral [DLI]: 4.0 mol

photons $m^{-2} d^{-1}$, achieved through an average maximum photosynthetic active radiation [PAR] of $120 \mu mol photons m^{-2} s^{-1}$).

Following settlement, discs with 1 to 12 uniformly settled coral recruits across the surface (i.e. no settlement close to other recruits or the disc rim) were haphazardly placed into 45 indoor flow-through 50 l tanks (a schematic diagram is provided in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m690p065.pdf) with 3 water turnovers per day and additional current in each tank provided by a Turbelle Nanostream 6015 pump (Tunze Aquarientechnik). The 100% flow-through tanks were supplied with temperature and pCO_2 manipulated water (0.04 μm filtered

seawater, details in Section 2.3; Table 1; Fig. S2) resulting in 3 climate scenarios, and were illuminated with 5 light intensities (details in Section 2.4; Table 1; Fig. S3) generated in 3 replicate tanks per light-climate combination (Fig. S1). All tanks were illuminated with the control intensity ($4.0 mol photons m^{-2} d^{-1}$) during the study apart from light attenuation periods. Prior to initiating the first light attenuation period, 30 or 31 discs in each flow-through tank were haphazardly transferred to either an 'early' or 'late' rack (1 tank $^{-1}$). During the 1 mo long light attenuation periods, the lighting was dimmed in 36 of the tanks (according to Fig. 1, Table 1; Fig. S3; see Section 2.4 for details) and the 9 control tanks remained at $4.0 mol photons m^{-2} d^{-1}$. To circumvent the need to set up 90 tanks, during the 'early' attenuation period, 'late'

Table 1. Climate and light treatments. The 'current' temperature was based on the daily 10 yr historic mean reef temperature at Davies Reef, which increased from 26.2 to $28.7^{\circ}C$ in the experimental period between November and February. The measured mean \pm SD temperature and carbon dioxide partial pressure (pCO_2) are provided, followed by the daily mean fluctuation (fluc.) in brackets. The daily temperature and pCO_2 profiles are graphically presented in Fig. S2. Daily light integral (DLI) and daily maximum photosynthetic active radiation (Max PAR) provided for all climates (repetition indicated by '**'). The coral recruits were kept in the 3 climate treatments, and in the highest (baseline) light intensity throughout the experiment. Only during the simulation of 1 mo long light attenuation periods were the light intensities attenuated in all 3 climate treatments

Climate	Temperature ($^{\circ}C$)		pCO_2 (ppm) Mean \pm SD (daily fluc.)	DLI (mol photons $m^{-2} d^{-1}$) Max PAR ($\mu mol photons m^{-2} s^{-1}$)				
	Range	Mean \pm SD (daily fluc.)		Baseline	Light attenuation			
Current	26.2 to 28.7	28.46 ± 0.52 (0.01)	428 ± 37 (2)	4.0	2.0	1.0	0.5	0.1
				123.5	61.8	31.0	15.5	3.0
Medium	Current + 0.44 (26.6–29.1)	28.95 ± 0.56 (0.01)	692 ± 7 (1)	*	*	*	*	*
High	Current + 0.94 (27.1–29.6)	29.56 ± 0.38 (0.01)	985 ± 34 (2)	*	*	*	*	*

racks were transferred to the control tank at 4.0 mol photons $\text{m}^{-2} \text{d}^{-1}$ and vice versa for the 'late' attenuation period. Coral recruits were fed daily with 10 ml newly hatched *Artemia* nauplii per 50 l tank (culture: approximately 4000 nauplii ml^{-1}) (Hii et al. 2009). Inoculation of the coral recruits with the Symbiodiniaceae species *Cladocopium goreaui* (ID: SCF055-01.10, isolated from *Acropora tenuis*), formerly known as *Symbiodinium* clade C1 (LaJeunesse et al. 2018), was performed daily by adding 100 ml *C. goreaui* culture ($\sim 200\,000$ cells ml^{-1} , reared in 27°C at 65 μmol photons $\text{m}^{-2} \text{s}^{-1}$ with a 14:10 h diurnal light cycle) per 50 l tank for the duration of 1 wk (Chakravarti et al. 2019) commencing once the recruits were 1 wk old (Fig. 1).

2.3. Climate treatments

In this study, coral recruits were subjected to 3 climate scenarios, a combination of adjusted temperature and carbon dioxide partial pressure (pCO_2), which are referred to as 'current', 'medium' and 'high' climate (Table 1). Daily temperatures of the current (present day) climate scenario were based on the historic daily mean reef temperature at a typical mid-shelf coral reef in the central GBR (Davies Reef: 18° 49' 53" S, 147° 38' 08" E) measured at 4 m water depth between 1991 and 2012 (AIMS 2020). Davies Reef and Falcon Island, the site of parental coral colony collection, have close to identical seawater temperatures (within 0.1°C) between November and February (2006–2018 data from Davies Reef and Pioneer Bay, <10 nautical miles from Falcon Island; Barneche et al. 2021). Selecting the Davies Reef temperature records facilitated daily automated adjustments in SeaSim to match the temperature profile on the reef over the experimental months (Fig. S2). The 10 yr historic daily mean temperature of 26.2°C was calculated for the typical spawning time of *A. millepora* in November (Harrison 2011), and the 10 yr historic daily mean temperature then increased to an annual maximum of 28.7°C at the end of the experiment in February. To ensure temperature stress alone did not cause mortality to a large proportion of recruits over the 3 and 4 mo exposure periods, the elevated temperatures applied here were relatively modest (Table 1). The cumulative thermal stress on corals can be estimated in degree heating weeks (DHWs, Liu et al. 2003), with 8 DHWs (e.g. 4 wk at 2°C above the annual maximum monthly temperature) often leading to coral bleaching and mortality (Hughes et al. 2017b, Kayanne 2017). By definition,

DHWs are only accumulated at 1°C above the annual maximum monthly temperature and therefore the maximum temperature applied in the high climate scenario was limited to <1°C above the monthly maximum at Davies Reef: +0.94°C above the control profile, which ranged between 26.2 and 28.7°C, resulting in a target temperature range of 27.1 to 29.6°C (Table 1; Fig. S2). The temperature profile of the medium climate scenario was set midway between the current and high values: +0.44°C above the control range (26.2 to 28.7°C), resulting in a target temperature range of 26.6 to 29.1°C (Table 1, Fig. S2). The applied temperature regimes roughly correspond with the +1.5 and +2.0°C targets of the IPCC Paris Agreement (IPCC 2014, 2021) given that the water temperature of the GBR has already increased by $\sim 0.9^\circ\text{C}$ since pre-industrial conditions (Lough et al. 2018): medium treatment of +1.3°C (0.9 + 0.44°C) and high treatment of +1.8°C (0.9 + 0.94°C) above pre-industrial temperatures.

The pCO_2 applied in the current climate treatment (428 ± 37 ppm) was similar to the mean summer sea surface pCO_2 monitoring data (406 ppm, 2009–2019) from 2 GBR reef stations (Uthicke et al. 2014, Fabricius et al. 2020). For the medium and high climate scenarios, the pCO_2 levels were guided by RCP8.5 model (Meinshausen et al. 2011, IPCC 2014, 2021), which predicts pCO_2 levels of ~ 680 ppm by 2050 and ~ 940 ppm by 2100. The measured pCO_2 levels were therefore 692 ± 6 ppm (mean \pm SD) for the medium climate treatment and 985 ± 34 ppm for the high climate treatment (Table 1).

The 3 climate treatments in this study were automatically created by manipulating the temperatures and pCO_2 levels of the water passing through into the 50 l indoor flow-through tanks (more detail in Brunner et al. 2021). The temperature manipulation of the SeaSim facility is based on bringing heated water in close contact with the waterlines feeding the flow-through tanks, allowing greatest precision of the temperature control. Additionally, the flow-through tanks were respectively standing half submerged in heated water baths to minimise temperature fluctuations that may be caused by different positions within the climate-controlled room. The pCO_2 was manipulated by direct pCO_2 -injection and diffusion into water before it entered the flow-through tanks. Both the pCO_2 (Fig. S2a) and temperature manipulation were fully automatic and based on redundant feedback measurements automatically taken in 10 min intervals by a SIMATIC WinCC SCADA system (Siemens). Additionally, calibrated HOBO temperature loggers (UA-002-64, Onset Com-

puter) were placed haphazardly in the tanks to monitor the temperatures of the climate treatments ($n = 2$ loggers placed in individual tanks of each climate treatment) (Fig. S2b). For the determination of the total alkalinity (TA) and dissolved inorganic carbon (DIC), water samples were collected directly following the light attenuation periods, preserved with mercury chloride (0.04% in sample) and subsequently quantified with a Vindta 3C (Marianda; salinity reference material: CRM164 = 33.525). Using the R package 'Seacarb' version 3.2.16 (Gattuso et al. 2020) and temperature data measured during the water sample collection, the pH_T (arithmetic mean pH on the total scale based on the hydrogen ion concentration), pCO_2 and aragonite saturation state (Ω_{Arag}) were calculated precisely for each climate treatment ($n = 3$ tanks per climate treatment) (Table S1).

2.4. Light attenuation

The average light intensity of lower turbidity inshore reefs has been measured at 10–12 mol photons $\text{m}^{-2} \text{d}^{-1}$ at 2–4 m depth (Jones et al. 2020a, Luter et al. 2021) but can be far lower in cryptic habitats where coral larvae often settle (e.g. <0.5 mol photons $\text{m}^{-2} \text{d}^{-1}$; Doropoulos et al. 2016, Kenyon et al. 2020, Ricardo et al. 2021). The control light conditions had a maximum PAR of 124 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at solar noon, and this was extrapolated to a DLI of 4.0 mol photons $\text{m}^{-2} \text{d}^{-1}$ (Fig. S3b). This control intensity was chosen to resemble a partially shaded habitat in 4 m water depth, with light levels that were lower than exposed horizontal upward-facing surfaces but higher than in crevices or cryptic habitats (Doropoulos et al. 2016, Kenyon et al. 2020). The light was attenuated (see below) for periods of 1 mo, to intensities consistent with previous studies that quantified attenuation-response relationships in corals (Bessell-Browne et al. 2017a,b, Jones et al. 2020b, 2021, Luter et al. 2021). The light attenuation treatments were chosen to bracket the range of DLI that can be experienced by coral recruits during periods of increased turbidity from several causes. Monitoring studies near dredging projects (0.5 to 3 km from dredging site) have shown that DLI levels can be <0.1 mol photons $\text{m}^{-2} \text{d}^{-1}$ for up to 16 consecutive days (Jones et al. 2016), and can be, intermittently, as low as 0 mol photons $\text{m}^{-2} \text{d}^{-1}$ more than 20 d yr^{-1} , 0.5 mol photons $\text{m}^{-2} \text{d}^{-1}$ more than 120 d yr^{-1} or less than 2 mol photons $\text{m}^{-2} \text{d}^{-1}$ more than 340 d yr^{-1} (Fisher et al. 2015, Jones et al. 2015a). Light attenuation from sediment

resuspension can approach near-darkness for short periods but is not likely to be as extreme over long periods, with 28 d of continuous attenuation by approximately 60% from median conditions to ~ 4 mol photons $\text{m}^{-2} \text{d}^{-1}$, the most extreme attenuation period measured at Geoffrey Bay on Magnetic Island (GBR) for exposed upward-facing surfaces (Luter et al. 2021). However, these measurements recorded downwelling irradiance, and based on observations that corals often settle in cryptic areas with light levels $<10\%$ of that incident on upward-facing surfaces (Doropoulos et al. 2016, Kenyon et al. 2020, Ricardo et al. 2021), the likely 28 d attenuation would correspond to a DLI of <0.4 mol photons $\text{m}^{-2} \text{d}^{-1}$, consistent with the lower light treatments implemented here.

Standardised light periods were simulated in this experiment by applying a diurnal light cycle of 12:12 h with a linear ramping time of 3 h following sunrise and prior to sunset, using 1 Hydra FiftyTwo HD LED light (Aquaria Illumination) per tank (Fig. S3b). The 5 applied DLI levels (4, 2, 1, 0.5 and 0.1 mol photons $\text{m}^{-2} \text{d}^{-1}$) were created by using the controller of each LED light and digitally reducing its light output to a maximum PAR (measured in the centre of every tank at the height of the recruits) between the ramping times as listed in Table 1 and Fig. S3b. To avoid light pollution between adjacent tanks, shading-walls made of 5 mm thick black PVC were placed between them. The spectral profiles of the aquarium lights were adjusted (Fig. S3a) to better match inshore-reef light profiles at ~ 4 m depth using a JAZ spectrometer (Ocean Insight) by decreasing the blue channels and increasing the green and yellow channels (measured in the centre of every tank at the height of the recruits) (Jones et al. 2020a, 2021, Luter et al. 2021, Ricardo et al. 2021).

2.5. Sampling

The recruit survival, size, symbiont density and photosynthetic efficiency (F_v/F_m) were quantified at different timepoints for the early and late light attenuation experiment, as described in Section 2.1 and in Fig. 1. For the survival (i.e. recruits featuring at least 1 living polyp) and size measurements (i.e. area of live tissue), the coral recruits were photographed (Fig. S4) using a Nikon D810 camera with a Nikon AF-S 60 mm f/2.8G ED macro lens and 4 Ikelite DS161 strobes. The resulting high-resolution images were analysed using the software ImageJ Fiji version 1.52u (Schindelin et al. 2012). Since variations of

CCA cover on the preconditioned discs were observed, which could potentially impact the post-settlement survival of coral recruits due to habitat competition (Harrington et al. 2004), photographs of the discs shortly after coral settlement were captured, and the total disc area covered by CCA was subsequently quantified in ImageJ Fiji. Coral recruits that fused with neighbouring recruits during the experiment were omitted from the dataset to avoid erroneous survival and size estimates (18 and 25% of recruits were omitted in the early and late attenuation experiments, respectively). This resulted in a dataset that tracked the fate of 2998 recruits on 1139 discs ($n = 5\text{--}63$ recruits per light–climate combination [$n = 15$] per replicate tank [$n = 3$] per experiment [$n = 2$]).

After the completion of the 1 mo recovery phases in each experiment (Fig. 1), all discs including the settled coral recruits were snap-frozen in liquid nitrogen and then stored at -80°C for later Symbiodiniaceae counts. The Symbiodiniaceae quantities were counted in a subset of recruits that were alive prior to freezing by scraping the recruits from discs using a scalpel, and then transferring them into individual 1.5 ml reaction tubes ($n = 329$, ranging between 1 and 16 recruits per light–climate combination across the replicate tanks and experiments). The coral skeletons were dissolved in 20 μl of 1% hydrochloric acid for 2 h and then diluted and homogenised with 20 μl filtered seawater using a vortex. Symbiont densities were counted with a Neubauer Improved Bright-Line haemocytometer (Blaubrand) and an Olympus light microscope (CX22LED), and normalised to symbiont cell quantities per polyp of each coral recruit.

The maximum photosynthetic efficiency of photosystem II of a subset of alive coral recruits ($n = \sim 4$ recruits per light–climate combination [$n = 15$] per replicate tank [$n = 3$] per experiment [$n = 2$]) directly prior to and following the respective light attenuation period (Fig. 1) was measured using an Imaging-PAM chlorophyll fluorometer (MAXI-Series, Walz). The coral recruits were dark-adapted by conducting the measurements at least 2 h after the simulated sunset by keeping them in a closed 15 l insulated cooler box filled with water of the corresponding climate treatment to ensure consistent water temperature during transport to the Imaging-PAM which was located in an adjacent laboratory. During the measurements, high-resolution photographs were used as reference to precisely select the detection area (around the entire alive recruit area), and the maximum quantum yield of photosystem II (F_v/F_m) was then calculated using standard formulae (Genty et al. 1989).

2.6. Statistical analyses

Statistical analyses were performed using R version 4.1.1 (R Core Team 2021). Following best practices to increase statistical power (Zuur et al. 2010), an initial data exploration was conducted and subsets of the data were created per experiment (early vs. later light attenuation). Each subset was separately analysed using generalised linear mixed-effects models with the package ‘glmmTMB’ (version 1.0.1) (Brooks et al. 2017). A binomial model was applied for the survivorship (survival in percentage), whereas for recruit sizes (mm^2) and the photosynthetic efficiency (F_v/F_m), Gaussian models were executed. For the symbiont counts (Symbiodiniaceae polyp $^{-1}$), a Poisson model was applied. The ‘climate scenario’ was incorporated as a categorical fixed factor, ‘light intensity’ as a continuous fixed factor and the ‘CCA area’ as a continuous covariate; furthermore, additional random factors for ‘tank ID’ ($n = 45$) and ‘settlement disc ID’ ($n = 1139$) were used. Non-significant interaction terms and covariates were removed from models by backwards deletion: this included the removal of non-significant light–climate interactions and of the covariate ‘CCA area’. The selection of these simpler models was validated using Akaike’s information criterion with the package ‘stats’ (version 3.6.2). The uneven numbers of recruits growing on each settlement disc was included in the models as offset to account for potential effects of interactions between recruits. Model assumptions such as homogeneity of variances, normal distribution of residuals, zero-inflation and assessment of overdispersion were tested and confirmed using simulation-based validation techniques presented as graphs (e.g. QQ-plot) and functions (e.g. Kolmogorov-Smirnov test) with the package ‘DHARMA’ (version 0.2.7) (Hartig 2020). Statistically significant differences between tested treatments were evaluated with an ANOVA (Type II), using the ‘Anova’ and ‘summary’ functions of the package ‘car’ (version 3.0.7) by deriving chi-squared values (Fox & Weisberg 2019).

3. RESULTS

We tested the effects of future climate conditions in conjunction with 1 mo long light attenuation periods applied at 2 different times after settlement of coral recruits. A 1 mo long light attenuation applied to younger recruits (1 mo old) had no effect on survival ($p = 0.638$; Table 2), while the same light attenuation

Table 2. Analysis of deviance results for *Acropora millepora* recruit survival, size of healthy coral tissue, quantity of Symbiodiniaceae polyp⁻¹ and maximum photochemical yield of photosystem II (F_v/F_m) following both light attenuation experiments (Expt). Age at sampling indicates whether data were obtained directly following the light attenuation periods or following a 1 mo long recovery phase. Significant results ($p < 0.05$) are in **bold**, and tested interactions are illustrated with '×'. L: light; C: climate. Age in **bold** is presented in Figs. 2–5. Age in *italics* is presented in Fig. S2

Test	Expt	Age at light attenuation (mo)	Age at sampling (mo)	p			df			χ^2 statistics		
				L	C	L×C	L	C	L×C	L	C	L×C
Survival	Early	1–2	2	0.113	0.710	0.845	1	2	2	2.501	0.683	0.335
	Early	1–2	3	0.638	<0.001	0.358	1	2	2	0.221	23.677	2.053
	Late	2–3	3	0.799	<0.001	0.909	1	2	2	0.064	15.546	0.188
	Late	2–3	4	<0.001	<0.001	0.796	1	2	2	23.146	19.219	0.454
Size	Early	1–2	3	0.811	0.001	0.321	1	2	2	0.056	17.197	2.269
	Late	2–3	4	0.013	0.005	0.529	1	2	2	6.129	10.552	1.272
Symbionts polyp ⁻¹	Early	1–2	3	0.261	0.014	0.428	1	2	2	1.258	8.442	1.696
	Late	2–3	4	0.001	0.003	0.430	1	2	2	11.450	11.560	1.686
F_v/F_m	Early	1–2	2	<0.001	0.290	0.823	1	2	2	24.984	2.473	0.388
	Late	2–3	3	<0.001	0.106	0.465	1	2	2	105.710	1.502	1.530

applied to older recruits (2 mo old) significantly decreased survival ($p < 0.001$). The medium future climate had a positive effect on the survival and size of recruits of both ages, but there was a net negative effect on both of these parameters under more intense future climate conditions. No statistically significant light–climate interactions were observed at either end of the light attenuation periods nor following the 1 mo recovery periods (all $p > 0.05$; see Table 2); therefore, the results for every response variable discussed in the following sections are for individual effects of light and climate only.

3.1. Coral recruit survival

Immediately following the light attenuation periods, the survival of recruits in the early attenuation experiment (2 mo old) was very high ($99 \pm 0\%$ [SE]) and did not differ among climate treatments ($p = 0.710$; Table 2; Fig. S5). Recruits in the later attenuation experiment (3 mo old) also survived well in the current climate ($63 \pm 5\%$) and fared substantially better under the medium climate scenario ($81 \pm 4\%$) but suffered greater, yet non-significant ($p = 0.617$), mortality in the high climate scenario ($53 \pm 6\%$ survival) (Table 2; Fig. S5). By the end of the respective 1 mo recovery phases, the mean survival of coral recruits in the control light scenario (4 mol photons $m^{-2} d^{-1}$) averaged across climate treatments was reduced to $50 \pm 6\%$ following the early attenuation (3 mo old) and $42 \pm 9\%$ following the late attenuation (4 mo old) (Fig. 2; Table S2) indicating post-settlement mortality independent of the

tested treatments. Subsequent comparisons of survival and size of recruits were therefore made 1 mo after the end of the light attenuation periods when recruits were 3 and 4 mo old (Fig. 1), to capture the immediate effect of light attenuation, and the latent effects of stress that resulted in mortality for up to 1 mo following exposure. Statistically significant effects of light attenuation on survival were only observed 1 mo following the late treatment period when the corals were 4 mo old ($p < 0.001$; Table 2). Between the highest (4 mol photons $m^{-2} d^{-1}$) and lowest light treatments (0.1 mol photons $m^{-2} d^{-1}$), survival decreased by $34 \pm 7\%$, $48 \pm 8\%$ and $18 \pm 7\%$ for the current, medium and high climate treatments, respectively (Fig. 2; Table S2 shows averages across climates). Because in the high climate treatment the survival was already lowest at 4 mol photons $m^{-2} d^{-1}$, the decrease in survival between 4 and 0.1 mol photons $m^{-2} d^{-1}$ was not as great as for the other climate treatments. Throughout the entire experiment, the total recruit survival was the lowest for recruits grown in the high climate scenario for both attenuation times and across light intensities (early attenuation: average $35 \pm 4\%$ in high climate, $52 \pm 4\%$ in current climate; late attenuation: $10 \pm 4\%$ in high climate, $15 \pm 4\%$ in current climate) (Table S2). However, the greatest survival in this study was observed for recruits grown in the medium climate (early attenuation: $66 \pm 4\%$, late attenuation: $34 \pm 7\%$; Table S2). The lack of interactions between climate and light limitation indicates that all responses from the combined pressures were likely additive rather than synergistic (Table 2).

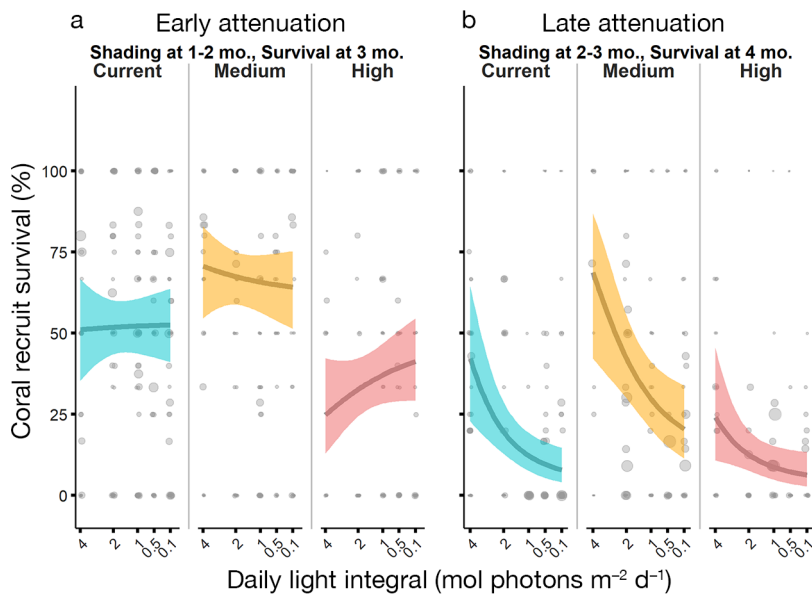


Fig. 2. Survival (%) of *Acropora millepora* recruits continuously exposed to 3 climate treatments, as well as 1 mo long light attenuation periods with 5 light intensities at 2 different ages. (a) Early attenuation: Coral recruits exposed to a 1 mo light attenuation period at 1–2 mo old and survival shown 1 mo later at 3 mo old. (b) Late attenuation: Light attenuation at 2–3 mo old and survival shown at the age of 4 mo. Ribbons illustrate 95% confidence intervals of predicted mean light effects in each climate treatment. Grey bubbles are % survival per settlement disc, and their size is proportional to the number of recruits settled on an individual disc, ranging from 1 to 12 (total of 2998 recruits on 1139 discs)

3.2. Coral recruit size

The mean size (\pm SE) of the coral recruits (area of healthy coral tissue) in the baseline scenario ($4 \text{ mol photons m}^{-2} \text{ d}^{-1}$) was $0.96 \pm 0.03 \text{ mm}^2$ 1 mo after the early light attenuation (3 mo old recruits), and the mean recruit size 1 mo following the later light attenuation was slightly greater ($1.09 \pm 0.07 \text{ mm}^2$, 4 mo old recruits) (Table S2). Following the recovery periods, recruit sizes were not significantly affected by light attenuation when exposed early (light attenuation at 1–2 mo of age, measured at 3 mo of age) ($p = 0.811$; Table 2). However, recruits exposed to light attenuation later (2–3 mo old, measured at 4 mo of age) showed a significant decrease in size across the light treatments ($p = 0.013$), with sizes of $1.09 \pm 0.07 \text{ mm}^2$ at $4 \text{ mol photons m}^{-2} \text{ d}^{-1}$ decreasing to 0.92 ± 0.05 at $0.1 \text{ mol photons m}^{-2} \text{ d}^{-1}$ averaged across the climate treatments (Fig. 3; Table S2). Recruits grown in the high climate treatments were significantly smaller in both light attenuation experiments (early: $0.88 \pm 0.02 \text{ mm}^2$; late: $0.86 \pm 0.07 \text{ mm}^2$) compared to recruits grown in the medium climate scenario (early: $p =$

0.002 , $0.97 \pm 0.01 \text{ mm}^2$; late: $p = 0.011$, $1.10 \pm 0.05 \text{ mm}^2$) and the current climate scenario (early: $p < 0.001$, $0.98 \pm 0.02 \text{ mm}^2$; late: $p = 0.046$, $0.96 \pm 0.06 \text{ mm}^2$) (Table S2). The statistical analyses of effects on recruit size were consistent regardless of whether growth was measured as change in size over time, change proportional to initial size, or absolute size at the end of the experiment (given that all recruits have approximately the same size following larvae settlement; results not shown).

3.3. Symbiodiniaceae quantities

Mean (\pm SE) Symbiodiniaceae quantities per coral polyp in the baseline conditions ($4 \text{ mol photons m}^{-2} \text{ d}^{-1}$) were very similar in both light attenuation experiments, ranging between $230 \pm 60 \text{ cells polyp}^{-1}$ (early attenuation) and $225 \pm 53 \text{ cells polyp}^{-1}$ (late attenuation) following the respective recovery periods (Table S2). Consistent with the results for recruit survival, the symbiont populations were significantly affected ($p = 0.014$) by climate stress for recruits exposed early to light attenuation (light attenuation at 1–2 mo of age, measured at 3 mo of age), and by both light attenuation ($p = 0.001$) and climate stress ($p = 0.003$) for recruits exposed later in their development (light attenuation at 2–3 mo of age, measured at 4 mo of age) (Table 2, Fig. 4). In the medium climate, approximately 1.5 to 2 times greater symbiont populations were observed (early attenuation: $365 \pm 66 \text{ cells polyp}^{-1}$; late attenuation: $171 \pm 39 \text{ cells polyp}^{-1}$), which was higher than symbiont populations within recruits grown in the current climate (early: $256 \pm 55 \text{ cells polyp}^{-1}$; late: $111 \pm 28 \text{ cells polyp}^{-1}$) and the high climate scenario (early: $174 \pm 42 \text{ cells polyp}^{-1}$; late: $114 \pm 37 \text{ cells polyp}^{-1}$) (Table S2). However, recruits exposed to light attenuation later showed a significant decrease in symbiont density with decreasing light intensity ($p = 0.001$), declining from $225 \pm 53 \text{ cells polyp}^{-1}$ at $4 \text{ mol photons m}^{-2} \text{ d}^{-1}$ to $93 \pm 18 \text{ cells polyp}^{-1}$ at $0.1 \text{ mol photons m}^{-2} \text{ d}^{-1}$, and this trend was consistent across all climate scenarios (Table 2, Fig. 4).

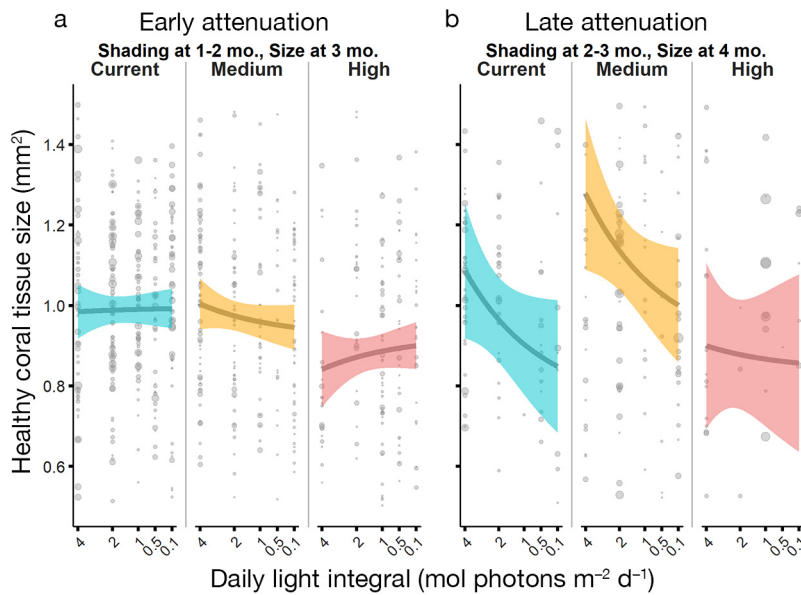


Fig. 3. Area of healthy coral tissue (mm^2) of living *Acropora millepora* recruits (≥ 1 polyp) continuously exposed to 3 climate treatments and 1 mo long light attenuation periods with 5 light intensities at 2 different ages. (a) Early attenuation: Coral recruits exposed to a 1 mo light attenuation period at 1–2 mo old and size shown 1 mo later at 3 mo old. (b) Late attenuation: Light attenuation at 2–3 mo old and size shown at the age of 4 mo. Ribbons illustrate 95% confidence intervals of predicted mean light effects in each climate treatment. Grey bubbles are raw data, and their size is proportional to the number of recruits settled on an individual settlement disc, ranging from 1 to 7 (total of 945 living recruits)

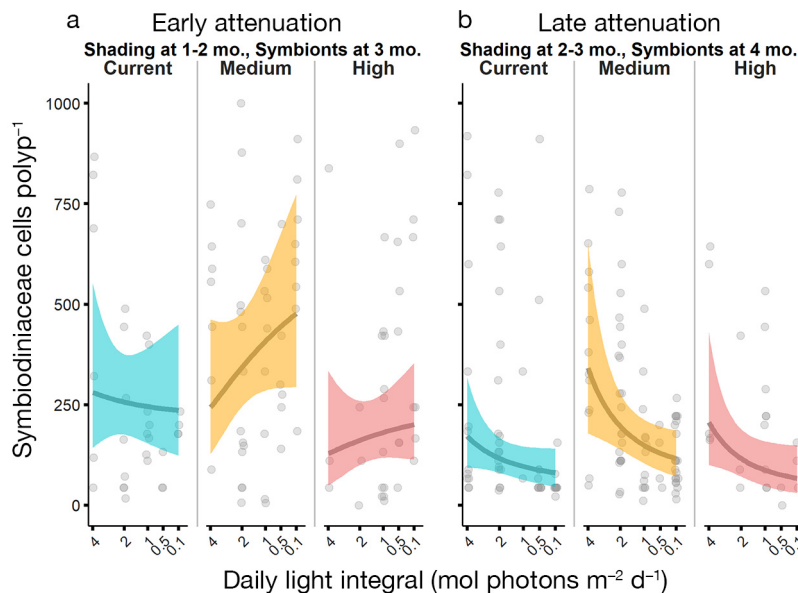


Fig. 4. Quantity of Symbiodiniaceae per polyp in living *Acropora millepora* recruits (≥ 1 polyp) continuously exposed to 3 climate treatments and 1 mo long light attenuation periods with 5 light intensities at 2 different ages. (a) Early attenuation: Coral recruits exposed to a 1 mo light attenuation period at 1–2 mo old and symbiont quantities shown 1 mo later at 3 mo old. (b) Late attenuation: Light attenuation at 2–3 mo old and symbiont quantities shown at the age of 4 mo. Ribbons illustrate 95% confidence intervals of predicted mean light effects in each climate treatment. Grey dots are raw data (total of 329 recruits, randomly subsampled from a total of 1193 live recruits)

3.4. Photosynthetic activity

The maximum quantum yield of photosystem II (F_v/F_m) measured prior to both early (2 mo old recruits, $p = 0.290$) and late (3 mo old recruits, $p = 0.106$) light attenuation periods were not affected by climate treatments and averaged 0.37 ± 0.01 and 0.38 ± 0.01 , respectively. However, when measured directly following the end of the light attenuation periods (Fig. 1), F_v/F_m was significantly affected by the light attenuation in both the early ($p < 0.001$) and late experiment ($p < 0.001$) (Table 2, Fig. 5;

Table S2). Between the highest light intensity ($4 \text{ mol photons m}^{-2} \text{ d}^{-1}$, early attenuation: 0.29 ± 0.02 , late attenuation: 0.22 ± 0.01) and the lowest light intensity ($0.1 \text{ mol photons m}^{-2} \text{ d}^{-1}$, early attenuation: 0.50 ± 0.02 , late attenuation: 0.35 ± 0.01), F_v/F_m increased by a factor of ~ 1.5 averaged across climate treatments (Table S2). Yet, no significant light–climate interactions, nor any individual climate effects (averaged across the 3 climates: early attenuation: 0.45 ± 0.02 , late attenuation: 0.36 ± 0.01) were identified in either light attenuation experiment (Table 2, Fig. 5).

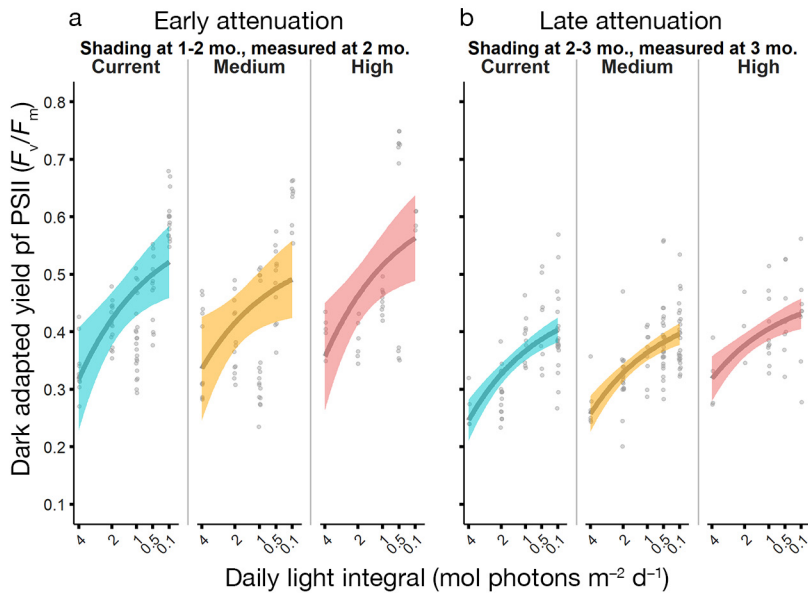


Fig. 5. Maximum quantum yield of photosystem II (PSII) (F_v/F_m) of dark-adapted living *Acropora millepora* recruits (≥ 1 polyp) continuously exposed to 3 climate treatments and 1 mo long exposure to 5 light intensities at 2 different ages. (a) Early attenuation: Coral recruits exposed to a 1 mo light attenuation at 1–2 mo old with F_v/F_m measured directly after the attenuation period. (b) Late attenuation: Light attenuation at 2–3 mo old with F_v/F_m measured directly after the attenuation period. Ribbons illustrate 95% confidence intervals of predicted mean light effects in each climate treatment. Grey dots are raw data of the subsampled living coral recruits ($n = 1\text{--}4$ recruits per light–climate combination [$n = 15$] per replicate tank [$n = 3$] per experiment [$n = 2$])

4. DISCUSSION

Future climate scenarios and light attenuation both affected the performance (survival, size, symbiont quantities and photosynthetic efficiency) of coral recruits, but these effects changed substantially during the first few months after settlement. For example, light attenuation did not negatively affect the performance of recruits shaded early (at 1–2 mo old) in any climate treatments following a 1 mo recovery, for any performance metric; however, recruits shaded later (at 2–3 mo old) were negatively affected by light attenuation in all climate scenarios following a 1 mo recovery. Compared to the current climate treatment, positive climate effects were observed under modest $+0.44^\circ\text{C}$, 692 ppm pCO_2 conditions (up to $19 \pm 6\%$ greater survival, and $13 \pm 5\%$ greater sizes), whereas more severe climate conditions ($+0.94^\circ\text{C}$, 985 ppm) impeded survival and sizes by up to 18 ± 4 and $9 \pm 7\%$, respectively.

There was no evidence that simultaneous effects of ocean warming and ocean acidification in combination with light attenuation were synergistic following the applied treatments, because no statistical inter-

actions in any of the 2-factor analyses were present. However, the significant negative effects on the survival, size and symbiont density of older recruits suggests that the effects of climate and light limitation are additive. This is consistent with the results of other studies showing that adult corals can suffer from additive (non-interactive) effects when 2 stressors are present. For example, combined high pCO_2 and light attenuation led to decreases in calcification rates of adult corals, followed by bleaching and mortality (Vogel et al. 2015, van der Zande et al. 2020, Noonan et al. 2022). Similar or more intense negative responses of adult corals can also be observed due to additive effects of increased temperatures and light attenuation (Noonan & Fabricius 2016, van der Zande et al. 2020). The present study is the first to demonstrate the combined effects of 3 stressors on coral recruits: light attenuation, ocean warming and ocean acidification. Furthermore, we demonstrate that light attenuation only negatively affects *Acropora millepora* recruits after at least 2 mo post-settle-

ment, which informs regulators on the appropriate timing for activities that can affect benthic light availability, such as dredging operations (Jones et al. 2016) or cloud brightening (Latham et al. 2013).

4.1. Effects of future climate scenarios on recruits

Elevated temperatures and pCO_2 are well-known stressors affecting corals and coral reef ecosystems (Hoegh-Guldberg et al. 2007). Contrary to expectation, the performance of the *A. millepora* recruits in the medium climate change scenario of this study (Control $+0.44^\circ\text{C}$, 692 ppm) was equivalent to, or slightly enhanced above the performance of recruits within the current climate treatment ($26.2\text{--}28.7^\circ\text{C}$, 428 ppm). In contrast, the more severe (albeit modest, $+0.94^\circ\text{C}$, 985 ppm) climate scenario had detrimental effects on coral recruit survival, size and symbiont quantities (Table 1, Figs. 2–4). In another study with 2 wk old *A. tenuis* recruits, a similar trend of slightly elevated performance at medium temperatures ($+1^\circ\text{C}$) and reduced survival and symbiont quantities at high temperatures ($+3^\circ\text{C}$) compared to

current temperatures (28°C) was observed, particularly where light levels were very high (~12 mol photons m⁻² d⁻¹) (Abrego et al. 2012). These results support the interpretation that small increases in temperature can drive increases in metabolic rates, growth rates and pigment concentrations (Noonan & Fabricius 2016, Jurriaans & Hoogenboom 2020, Mason et al. 2020).

In high light environments, the availability of inorganic carbon can limit carbon fixation (Muscatine et al. 1989, MacKenzie et al. 2005), and small increases in pCO₂ (~800 ppm) under these conditions can have positive effects on photosynthetic organisms (Noonan & Fabricius 2016), including, for example, a ~3% increase in F_v/F_m for adult *A. hyacinthus* (Noonan et al. 2022). Our observed trend of increased symbiont density within coral recruits under the medium climate scenario is also consistent with a release of carbon-limitation enhancing photosynthesis and promoting symbiont cell division (e.g. Davy et al. 2012). However, for the late experiment, recruits were larger in the medium climate scenario, suggesting more rapid growth (calcification) rates under these conditions despite the decline in aragonite saturation state from 3.8 (control) to 2.6 (medium climate), which was expected to result in a decrease in recruit calcification (e.g. Langdon et al. 2000). Species-specific physiological controls over carbonate chemistry at the site of calcification strongly influence coral calcification rates (e.g. Comeau et al. 2018). Further research is required to identify the 'tipping point' where the benefits of mild warming and small changes in carbonate chemistry switch to become detrimental for coral growth and survival as further warming increases and lower aragonite saturation impedes coral growth.

If temperature and pCO₂ conditions continue to increase, the benefits observed under slightly elevated conditions can be reversed (Abrego et al. 2012), causing the well documented effect cascade of reduced Symbiodiniaceae cell division rates (Baghdasarian et al. 2017), followed by Symbiodiniaceae loss (bleaching) (Mason 2018, Suggett & Smith 2020) and consequent coral tissue mortality (Jones 2008, Lough & van Oppen 2018). Coral recruits grown in the high climate treatment of the present study had lower symbiont densities (early light attenuation treatment) and survival (Table S2) and were visibly pale compared to recruits grown in the other climate treatments (Fig. S4). Reduced F_v/F_m linked to thermal stress is exaggerated in low light adapted corals exposed to high irradiance (Jones & Hoegh-Guldberg 2001) and absence of effects of the high cli-

mate scenario on F_v/F_m may also indicate that photosystem II was not under high irradiance pressure during the experiment. Additionally, recruits in the high climate treatment were smaller and highly variable in size, which is consistent with numerous other studies showing that ocean acidification has detrimental effects on the calcification of juvenile and adult corals (Anthony et al. 2008, Albright & Langdon 2011), as well as on their skeleton structure and density (Cohen & Holcomb 2009, Foster et al. 2016, Mollica et al. 2018). The pressure imposed by ocean acidification can be even more severe when the photosynthesis is also hampered or inhibited due to shading or bleaching, with up to 164% lower calcification rates observed for adult corals due to additive effects of these stressors (Vogel et al. 2015, van der Zande et al. 2020).

Future climate conditions can also impair the photochemical efficiency (F_v/F_m) of corals, such as in *Seriatopora hystrix* (Noonan & Fabricius 2016, Davies et al. 2018). However, responses are species-specific (Noonan & Fabricius 2016, Noonan et al. 2022), and previous studies support that the F_v/F_m of adult *A. millepora* colonies only declines significantly in response to increases in temperature alone (by +3°C to 30.8°C) (Noonan & Fabricius 2016), but not when subjected to high pCO₂ alone (Vogel et al. 2015), or combined pCO₂ and temperature increases (Noonan & Fabricius 2016). This is in line with the present study, where no changes in the photochemical efficiency could be observed for *A. millepora* recruits across the climate treatments, when both the temperature and pCO₂ were manipulated together. The result also highlights that photosystem II of symbionts within *A. millepora* recruits was performing equally under all climate conditions tested in both the early and late light attenuation experiment.

4.2. Effects of light limitation on recruits

Light availability is critical to the success of coral-Symbiodiniaceae symbioses and, consequently, an extensive literature documents changes in coral performance in low light environments for juvenile and adult corals (e.g. Muscatine 1990, Hoogenboom et al. 2012, Bessell-Browne et al. 2017b, Jones et al. 2020b, 2021, Kuanui et al. 2020, Noonan et al. 2022), although clear thresholds have not been established. In the present study, the survival, size and Symbiodiniaceae quantities of 4 mo old recruits, which had experienced light attenuation between 2 and 3 mo of age, were all negatively affected by decreasing light

intensities, but there were no light attenuation effects on these metrics when the light was reduced earlier during recruit development (1–2 mo old). This occurred despite consistent increases in the photosynthetic efficiency of symbionts with decreasing light intensity in all climate treatments and within both age groups. The low F_v/F_m values observed at the baseline light intensity (4 mol photons $m^{-2} d^{-1}$) is typical for cultured *Cladocopium goreaui*, with values between 0.3 and 0.5 observed for this genotype in culture and *in hospite* (Chakravarti & van Oppen 2018, C. Alvarez Roa pers. comm.); however, the influence of this low yield on the contribution of *C. goreaui* to the symbiotic partnership is not known.

Light attenuation only negatively affected symbiont densities of recruits exposed to light attenuation later (2–3 mo old), suggesting that the need for light intensities required to support symbiont cell division and proliferation with coral tissues increases between 2 and 3 mo post settlement, consistent with the concept that there is an increased demand for a functioning coral–Symbiodiniaceae symbiosis in older recruits (Babcock & Mundy 1996). In turbid environments, coral recruits benefit in their early development from settling on downward-facing surfaces for protection from sediment smothering (Maida et al. 1994, Babcock & Mundy 1996, Ricardo et al. 2017). However, with a greater demand for uninterrupted light availability to support autotrophic feeding processes, recruits that were at least 2–5 mo (Hancock et al. 2021) or 5–9 mo (Babcock & Mundy 1996) old significantly profited in their growth and survival from greater light levels. This pattern is consistent with responses between the tested age groups of this study, which indicates that coral recruits begin to require higher light quantities for successful growth and survival as early as 2 mo old. Increased recruit survival, but not growth, with higher light levels has also been reported for recruits of *A. tenuis* and *A. hyacinthus* exposed to 2 climate scenarios and 9 wk long light attenuations at approximately the same recruit ages as used in the present study (Noonan et al. 2022). However, in that study, the overall recruit survivorship and growth trends were inconsistent, and reduced survival was more strongly associated with red algae (*Peyssonnelia* spp.) which became more dominant on surfaces in their low light treatments.

Where light intensities are chronically reduced, corals may suffer from nutritional undersupply (Falkowski et al. 1990, Warner et al. 1999) indicated by reduced lipid (Jones et al. 2020b, 2021, Luter et al. 2021) and protein content (Noonan et al. 2022), which may be coupled with decreasing respiration (Vogel et al. 2015) and calcification rates (Franzisket

1970, Rogers 1979, Humanes et al. 2017a, Noonan et al. 2022), ultimately leading to bleaching, reduced growth and mortality if the light limitation persists (Rogers 1979, Bessell-Browne et al. 2017a,b, Jones et al. 2020b, 2021, Luter et al. 2021, Noonan et al. 2022). For example, light attenuation experiments with different coral morphologies, involving *A. millepora* (corymbose), *Porites* spp. (massive) and *Montipora capricornis* (foliaceous) fragments, showed that after 28 d of light limitation (~ 1.1 mol photons $m^{-2} d^{-1}$), discolouration and partial mortality were observable (Bessell-Browne et al. 2017a). Furthermore, exposure to almost complete darkness (< 0.2 mol photons $m^{-2} d^{-1}$) resulted in a 50% decline of coral health along with severe bleaching (Bessell-Browne et al. 2017a,b). Despite the detrimental effects extreme low light quantities or qualities may pose, adult corals may effectively adapt by shifting to a heterotrophic diet (Anthony & Fabricius 2000, Houlbrèque & Ferrier-Pagès 2009, Bessell-Browne et al. 2014). These studies reporting shifts from autotrophy to heterotrophy generally focus on large adult coral colonies. In the present study on coral recruits, shifts of feeding mechanisms were not quantified (e.g. integration of marked carbon acquired through heterotrophic feeding), and therefore possible changes cannot be fully explained. However, the observation that older recruits suffered significantly more from light limitation than recruits shaded at a younger age could be explained by reports that corals commence heterotrophic feeding about 2 d following settlement (Toh et al. 2013), whereas photosynthetic processes often fully commence weeks to months later (Tomaschik & Sander 1987, Babcock & Mundy 1996).

4.3. Ecological implications and application

Suspended sediments released by dredging may cause periods of complete darkness (i.e. up to 20 d yr^{-1}) (Fisher et al. 2015) or prolonged twilight periods (i.e. over 340 d yr^{-1}) (Fisher et al. 2015, Jones et al. 2015a, 2016). Natural resuspension events (Anthony et al. 2004, Cooper et al. 2008, Luter et al. 2021) and river runoff (Cooper et al. 2008) on nearshore reefs can also attenuate light dramatically, but generally for shorter periods, and the degree of attenuation depends on the particle size, colour and amount of sediment in the water (Storlazzi et al. 2015). Coral reefs affected by such chronic light limitation may consequently suffer from declining reef functions and a narrowing habitat availability due to decreasing zones of optimal light conditions, as observed

with an over 60% inshore reef degradation around Singapore (Zweifler et al. 2021). However, turbid environments have been frequently suggested as refuges for corals against (temporarily) rising temperatures (Anthony et al. 2007, Morgan et al. 2017, Sully & van Woesik 2020, Zweifler et al. 2021). For example, during the mass coral bleaching event in the GBR in 2016, inshore reefs were less affected than offshore reefs, as their location potentially promoted survival through shading (i.e. turbidity), greater food availability (i.e. heterotrophy) and local thermal acclimation (i.e. symbiosis with more heat-tolerant Symbiodiniaceae strains) (Morgan et al. 2017). Accordingly, about 12% of the world's reefs are presumed to act as potential temperature refuge (Anthony et al. 2007, Sully & van Woesik 2020). However, these benefits might only be true for adult coral colonies, since in turbid waters coral larvae generally tend to settle on vertical walls or underneath overhangs to escape direct sediment stress during and after attachment to the reef (Rogers 1990, Babcock & Davies 1991, Maida et al. 1994, Ricardo et al. 2017). The protective effect of partially shaded areas may become detrimental as recruits grow larger and require higher light availability to support a functioning coral–Symbiodiniaceae symbiosis, which cannot be satisfied in shaded areas unless these corals are able to grow out of the shade (Babcock & Mundy 1996, Ricardo et al. 2017). In addition, depositing sediments are even more detrimental to the survival of coral recruits (Jones et al. 2015b). This is particularly the case where future climate scenarios (similar to those applied in the present study) impose further pressure, causing coral recruits to be more sensitive to sedimentation than in current climate scenarios (Brunner et al. 2021).

In the present study, the most severe effects on coral recruits were under combined climate and light limitation conditions, with the lack of significant statistical interactions between the effects of light limitation and climate indicating additive, rather than synergistic outcomes. For older coral recruits in this study, the effects of light limitation (commonly associated with suspended sediments) were found to be more detrimental than the effects of climate pressures. However, the applied climate treatments were modest in comparison to many other studies that apply climate conditions (Ban et al. 2014, Uthicke et al. 2016). Future work assessing a broader range of scenarios is needed to identify whether synergistic effects with light limitation occur beyond a more severe future climate threshold. Conversely, the strong effects of light attenuation may be less

severe if the energy needs of the recruit can be met by greater heterotrophy (Anthony & Fabricius 2000). Future studies should also include suspended sediments in their multifactorial experiments, as the direct effect of sediment particles (not apparent under current climate conditions) (Bessell-Browne et al. 2017a) may be more serious under future climate scenarios. Sediment-associated nutrients and contaminants may also pose additional hazards (Humanes et al. 2017a,b) not addressed in this study. Additionally, in the present study, only 1 coral species was investigated. Although *A. millepora* is a common model organism as it is highly abundant and an important ecosystem engineer (Babcock et al. 1986, Veron 2000), light quality and quantity preferences (regardless of the mechanism) are likely to be species-specific (Mundy & Babcock 1998, Vogel et al. 2015, Ricardo et al. 2021, Noonan et al. 2022), and some coral species might be more adapted than others due to factors including greater lipid stores (Anthony et al. 2007). Similarly, the use of corals inoculated with various Symbiodiniaceae species that are more heat-tolerant may affect the reliance on carbon acquisition (Cantin et al. 2009, Scheufen et al. 2017) and should therefore be tested in conjunction with predicted climate scenarios.

5. CONCLUSIONS

Combined effects of ocean warming or acidification and light limitation have been commonly reported for adult corals; however, only few studies exist on juvenile corals (e.g. Abrego et al. 2012, Humanes et al. 2017b, Noonan et al. 2022). The present study is the first to examine the independent and combined impacts of light limitation and simultaneous ocean warming and acidification pressure on the survival and performance of coral recruits, and no interactions could be identified. In comparison to recruits grown under current climate conditions, survival, size and symbiont densities increased in the medium future climate conditions and decreased in the high future climate conditions. The negative impacts of light attenuation only for older recruits highlights their increasing vulnerability to light attenuation in the months after settlement. Therefore, water quality management actions should consider the timing of activities that attenuate light to support the replenishment of reefs into the future.

Data availability. The data reported in this study are available at <https://doi.org/10.26274/FRPN-TA60>.

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