Coral Reefs
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RESEARCH

Effects of light limitation on the photophysiology of the coral *Pachyseris speciosa* from Singapore's turbid reefs

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Abstract Light limitation caused by increased sedimentation and turbidity, mainly due to intense human activities, poses a particularly pronounced threat to coral reefs located near urban areas, such as those in Singapore. In this study, we investigated the photophysiological and bleaching responses of *Pachyseris speciosa*, a common reef building coral species found in Singapore's turbid reefs, under low-light conditions over a four-week period. The experimental treatments included intermittent light and complete darkness, simulating possible current and potential future light scenarios for Singapore's reefs under heightened turbidity due to coastal development and climate change. Our results showed that *P. speciosa* experienced declines in Symbiodiniaceae density, chlorophyll-a levels, and color scores under both treatment conditions, with severe bleaching occurring in complete darkness. However, corals exposed to intermittent light exhibited only tissue paling and significant photoacclimatory adjustments. Notably, these corals maintained the stability of the maximum quantum yield of photosystem II, increased their effective quantum yield, and decreased the saturating irradiance. This suggested a potential photoadaptation to intermittent light conditions and fluctuating light levels, allowing them to sustain elevated photosynthetic performance. Our findings highlighted and confirmed the resilience and ability of *P. speciosa* to tolerate various limited light conditions and enhanced our understanding of coral photoacclimation under extremely low-light scenarios.

Keywords Coastal development · Low-light stress · *Pachyseris speciosa* · Photophysiology · Singapore · Turbid reef

Introduction

Light is essential for maintaining of the mutualistic relationship between corals and their photosynthetic dinoflagellate Symbiodiniaceae, known as 'zooxanthellae,' and provides corals with a large proportion of their energy budget needed to grow and reproduce (Roth 2014; Stanley and van de Schootbrugge 2018). Therefore, the reduction in underwater light level can be stressful, lowering the energy production by algal endosymbionts that in turn can result in coral starvation, adversely affecting their growth, calcification, and other critical physiological processes (Anthony and Connolly 2004; Vogel et al. 2015; Iluz and Dubinsky 2015; Izumi et al. 2023). Moreover, low light can also lead to coral bleaching and related mortality (Titlyanov et al. 2001; DeSalvo et al. 2012; Bessell-Browne et al. 2017a, b; Strahl et al. 2019; Jones et al. 2020).

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Light availability for corals is significantly influenced by the turbidity of the water. High turbidity results in light attenuation and reduced photosynthetically active radiation (PAR) available for coral photosynthesis (Rogers 1990; Erftemeijer et al. 2012; Jones et al. 2015, 2016). An extreme example of low light availability can be found in the reef environment in Singapore, where decades of intense land reclamation, coastal development, dredging, and shipping activities have led to high levels of sedimentation and turbidity (Browne et al. 2014, 2015; Sin et al. 2016; Heery et al. 2018; Chow et al. 2019). Underwater visibility has decreased from an average of 10 m in the 1960s to 2 m or less in the last few years, in parallel to an increase in the sedimentation rate from 3 to 6 mg cm^{-2} day^{-1} in 1970s up to 10–30 mg cm^{-2} day^{-1} recently (Dikou and van Woesik 2006; Erftemeijer et al. 2012; Morgan et al. 2020). This situation, together with multiple bleaching events due to thermal stress (Guest et al. 2012; Chou et al. 2016; Ng et al. 2020), has caused a general decline in the cover and biodiversity of coral communities (Huang et al. 2009; Wong et al. 2018; Poquita-Du et al. 2019; Chan et al. 2024).

Despite the extremely turbid environment and limited light availability, some coral taxa have shown tolerance, growing and surviving under these conditions (Dikou and van Woesik 2006; Guest et al. 2016; Chow et al. 2019). For example, the laminar and depth-generalist coral *Pachyseris speciosa* (Agariciidae) is one of the most common species thriving on Singapore's turbid reefs (Ng and Chou 2014; Guest et al. 2016; Wong et al. 2018), where it is well acclimated to low-light condition (Chow et al. 2019; Morgan et al. 2020). In particular, *P. speciosa* is the most abundant species in terms of coral cover, accounting for > 20% of total coral cover across depths and being a close second in terms of number of colonies (Chow et al. 2019). Its tolerance to low light suggests that it possesses certain adaptations to be able to persist in low-light conditions and optimize photosynthesis under varying light intensities (i.e., photoacclimation). This was confirmed by previous studies investigating the effect of acute and short-term low-light condition on *P. speciosa* from turbid Singapore reefs (Browne et al. 2014, 2015), as well as from other locations (Piniak and Storlazzi 2008; DiPerna et al. 2018). In particular, Browne et al. (2014) showed that *P. speciosa* responded rapidly to decreased light availability by increasing the photosynthetic potential, or maximum quantum yield of photosystem II (PSII). Similarly, DiPerna et al. (2018) found that *P. speciosa* from the Great Barrier Reef displayed cycles of rapid declines in maximum quantum yield during high-light exposure, and subsequent recoveries during low-light, suggesting the species' preference for low-light environments and vulnerability to even short periods of high-light exposure. Although corals on turbid reefs have shown tolerance to low-light environments (Guest et al. 2016; Zweifler et al. 2021), their long-term survival will depend on their capacity to respond and adapt to persistent environmental changes (Law and Huang 2023), including further or prolonged reduction in light availability caused by natural turbid events or increasing sediment influx from anthropogenic activities that can subject corals to extreme low light levels or complete darkness up to several days in a row, as already observed in several reefs worldwide (Jones et al. 2015, 2016; Fisher et al. 2015; Bollati et al. 2022). Therefore, understanding the response of corals to long-term extreme low-light conditions and their adaptation limit is essential to predict the trajectory of coral cover and habitat change on turbid reefs.

In this study, we focused on the photophysiological and bleaching response of the coral *P. speciosa* to acute low-light stress regimes for four weeks. We examine two light scenarios that mimic possible current and potential future light conditions for corals on turbid reefs facing an acute low-light exposure. The first scenario simulates episodes of several days of complete darkness resulting from a transient increase in turbidity and sedimentation due to further coastal activities (e.g., dredging, land reclamation) or extreme coastal runoff events (e.g., after intense monsoon storms). The second scenario examines the response of *P. speciosa* to weeks of complete darkness, which represents an extreme future light scenario that could occur, especially in deeper reef areas, as a result of a combination of sustained, persistent and prolonged coastal development activities and climate anomalies leading to extreme sedimentation events (Morgan et al. 2020; Law and Huang 2023). Symbiodiniaceae density, chlorophyll *a* concentration, colony color changes, and various photochemical parameters were analyzed to assess the photosynthetic performance and efficiency of *P. speciosa* colonies under light stress. We hypothesized that *P. speciosa* could adapt to intermittent light conditions but would not survive four weeks of total darkness.

Our findings provided insights into the photoacclimatory response of corals thriving on turbid reefs exposed to a sustained decrease in light availability and the first observation of the photophysiological response of *P. speciosa* to a four-week period of complete darkness. However, it is important to emphasize that in our study, we experimentally modified only the light conditions to focus specifically on their impact, while in the real-world scenario, other factors, such as the high sedimentation contributing to turbidity, must also be considered.

Materials and methods

Coral sampling and experimental setup

Fragments from four colonies of *Pachyseris speciosa* at least 0.5 m in diameter were collected by SCUBA at 5–7 m

depth (≥ 5 m apart) along the fringing reef around Kusu Island (1° 22′ 55″ N, 103° 85′ 85″ E, Fig. 1) in March 2023. Kusu Island reef is characterized by high levels of suspended sediments, which cause extreme light attenuation, limiting the reef slope to a maximum depth of about 8–10 m (Guest et al. 2012; Chow et al. 2019; Tanzil et al. 2019; Morgan et al. 2020). The in situ light and temperature level was measured through a HOBO Pendant MX Temperature/Light Data Logger (MX2202 Onset), in order to subsequently reproduce the same conditions in both the aquarium holding and experimental tanks, as described below.

The sampled colonies were first transported to the St John's Island National Marine Laboratory (SJINML), where they recovered after transportation and manipulation for two months in a common flow-through aquarium (holding tank; Alderdice et al. 2022), with water directly coming from the sea, under controlled conditions mimicking the in situ parameters of the Kusu Island reef. Each colony was then fragmented in nubbins of ~ 4 cm^2 using a Rotatory Tool Kit (Dremel 8200) equipped with a cut-off wheel to obtain a total of 68 fragments. Subsequently, they were fixed to Lego® cubes using Premium Aquatic Glue (Aquatic Exclusive).

Corals were then moved to an outdoor aquarium system (experimental tank) exposed to natural light and with the same physical and chemical conditions as the previous tank. To recover from the fragmentation process, nubbins were left in the same aquarium tank for ten additional days before the start of the experiment (= recovery period). During this recovery period, the chemical and physical parameters of the seawater were maintained at stable levels and consistently monitored. Additionally, coral fragments underwent regular visual inspections to detect any signs of bleaching, tissue degradation, mortality, or changes in gross morphology (Seveso et al. 2014, 2016; Montalbetti et al. 2021). Within days, tissue completely covered the cut regions, exhibiting normal pigmentation and a generally healthy appearance.

In both aquarium tanks (holding and experimental), the seawater temperature was set at ~ 30 °C as that of Kusu Island coral reef and kept constant using a water chiller HAILEA model HK-1000A. The photoperiod was set as the natural day-night cycle of 12 h:12 h (light/dark cycle). The mean light level was set to approximately 35 µmol m^{-2} s^{-1}

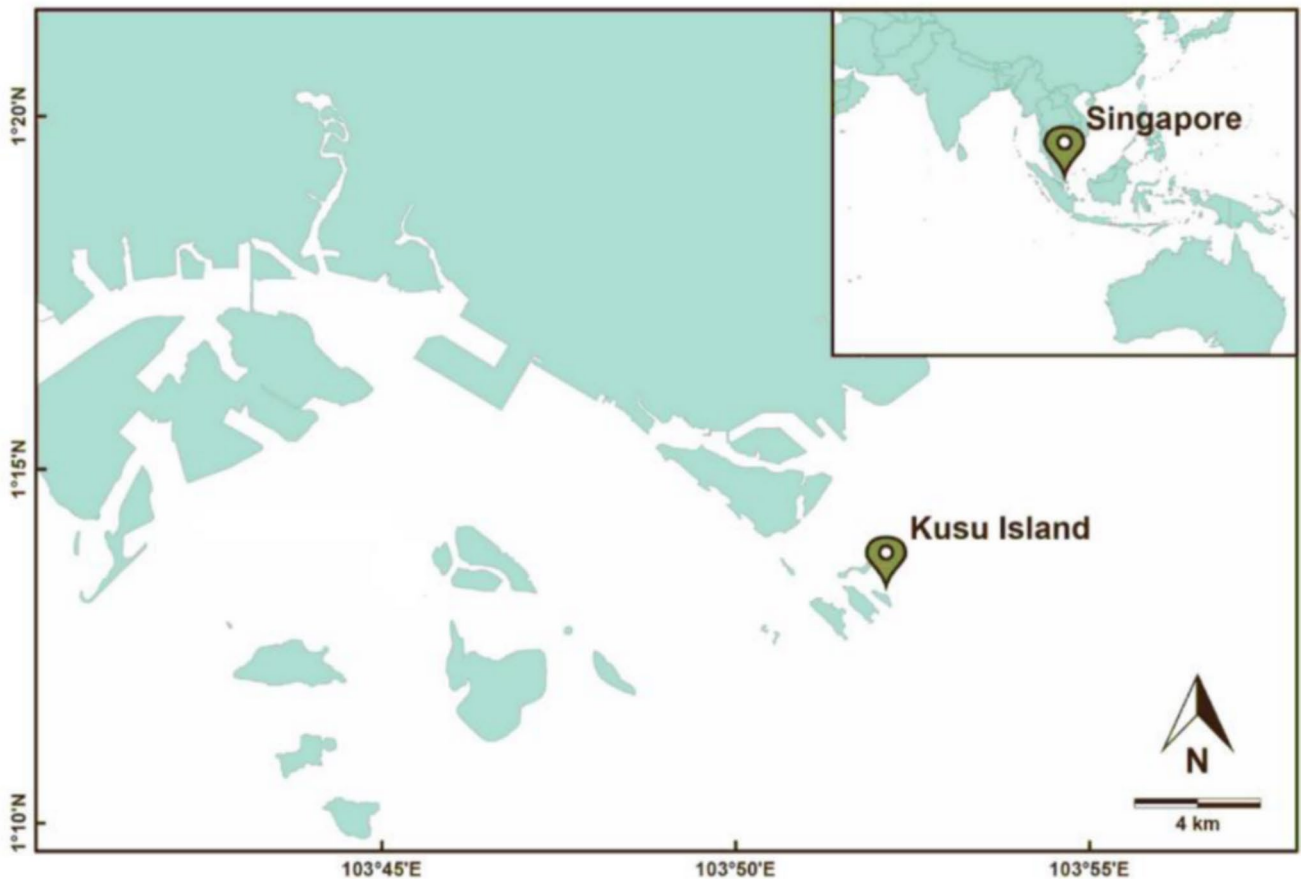

Fig. 1 Map of the study area showing the sampling site, Kusu Island, located 6.4 km south of Singapore's city center, from which colonies of *Pachyseris speciosa* were collected (modified from Maggioni et al. 2022)

between 7:00 AM and 7:00 PM (light period), simulating the normal in situ light level fluctuation recorded at a depth of 6–7 m at the sampling site (Chow et al. 2019; Morgan et al. 2020), (Supplementary Materials, Fig. S1A). In the holding tank, the light level was reproduced artificially, therefore keeping the average of 35 µmol m^{-2} s^{-1} constant during the light period. Instead, in the outdoor experimental tank, the simulation of the in situ light level was achieved by using two shading layers for natural light on top of the tank where the nubbins were located, and the daily light fluctuations more closely reflected the actual in situ scenario. The light level was measured and monitored using an quantum meter (Apogee Instruments, model MQ-510). To prevent additional light attenuation caused by sediment in the seawater, the incoming seawater at the aquarium facility was sand-filtered to approximately 200 µm to remove sediments from the often-turbid intake seawater. Corals were not additionally fed. Tanks were cleaned weekly to minimize algal growth.

Light treatments

After the recovery period, the 68 nubbins were randomly distributed among six PVC flow-through tanks (17 L) placed within the larger common flow-through experimental tank (Fig. S2A). Each tank contained 12 replicate nubbins, except for one tank, which had eight replicates. Four nubbins from this tank were in fact disregarded as they were not exhibiting optimum health prior to the start of the experiment. The tanks were arranged in a completely randomized order to avoid any bias (Fig. S2B). Three different light treatments were set up, each duplicated across two tanks, and the experiment was conducted for four weeks. In the Control treatment (C), nubbins were maintained under controlled conditions mimicking the in situ light level and fluctuation at the sampling site, as described previously.

In the Intermittent Light treatment (IL) nubbins were exposed to complete darkness (~ 0 µmol m^{-2} s^{-1}) for five non-consecutive days a week, while in the remaining two days tanks were uncovered and exposed to control light conditions. This treatment mimicked an environmentally realistic scenario, that can occur in Singapore especially during the northeast monsoon that bring heavy storms characterized by high rainfall and significant cloud cover. During this period, monsoon surges can persist for up to five days, often occurring multiple times. As a result, total irradiance is reduced due to the cloud cover, and seawater turbidity increases because of elevated runoff as well as coastal development activities. In particular, at depths of around 6–7 m, the photosynthetically active radiation levels can drop to zero for several consecutive days, though they can increase again once the storms subside. The effects of these activities can persist for several days (Dikou and van Woesik 2006; Tanzil et al. 2019; Morgan et al. 2020).

Lastly, a Dark treatment (D) was set up where nubbins were completely shaded and maintained in complete darkness (~ 0 µmol m^{-2} s^{-1}) for the entire four-week period. This scenario, while not currently real, could mimic a potential extreme outcome resulting from a combination of increased coastal development activities and severe climatic events that lead to significant sedimentation, as previously suggested (Morgan et al. 2020; Law and Huang 2023).

Complete darkness was achieved by placing a dark chamber around the intermittent light and dark treatment tanks. The chamber was made from black plastic corrugated boards of 3 mm thick (Fig. S3). In each tank, the seawater quality parameters and temperature were monitored daily and maintained constant throughout the experiment. This ensured that stable conditions were maintained in all the tanks, except for light. A HOBO Pendant MX Temperature/Light Data Logger (MX2202 Onset) was put in each tank to measure PAR (µmol m^{-2} s^{-1}) and temperature (°C) every 10 min for the entire length of the experiment. All the loggers were calibrated against a LI-1500 Light Sensor (LI-COR, USA). Seawater temperature over the four weeks of the experiment was similar between the three different light treatments (KW $\chi 2(2) = 521.735$, $p \geq 0.05$; Fig. S1B). In particular, the mean value recorded in control treatment tanks was 30.90 ± 0.31 °C, for IL treatment tanks was 30.89 ± 0.29 °C, and for D treatment tanks was 30.98 ± 0.20 °C. The mean value of light intensity recorded between the 12 h of daylight (7:00 AM to 7:00 PM) during the four weeks of the experiment was 32.5 ± 1.2 µmol m^{-2} s^{-1} for C treatment, 7.1 ± 0.6 µmol m^{-2} s^{-1} for IL treatment, and 1.7 ± 0.3 µmol m^{-2} s^{-1} for D treatment. Light intensity was significantly different between all the three treatments (Kruskal–Wallis $\chi 2(2) = 123.283$, $p < 0.01$; Fig. S1C).

Chlorophyll fluorescence measurements

Chlorophyll fluorescence associated with Photosystem II (PSII) of all nubbins was measured with a DIVING-PAM Underwater Fluorometer (Heinz Walz GmbH, Germany) at the beginning (T0) and at the end (T4) of the experiment. At T0, PAM measurements were taken during the light phase on the final day of the recovery period, just before the start of the four-week experimental stress phase. At T4, measurements were again taken during a light phase, immediately after the experiment stress period was concluded, as shown in Fig. S4, in order to make results comparable. The Diving-PAM was connected to a 6 mm diameter fiber-optic probe and a Miniature Spectrometer MINI-SPEC (Heinz Walz GmbH, Germany) used to record separately the spectra of PAR in the visible and far-red range. Diving-PAM settings for T0 were as follows: distance between clip and notch = 5.5 cm, light intensity = 1, light frequency = 1, gain = 1, damping = 1, and ETR-Factor = 0.84. Rapid Light

Curves (RLCs): width = 10, intensity = 1, and length = 12 (from 1 to 13). Diving-PAM settings for T4 were modified for optimum fluorescence signal measurements, as follows: distance between clip and notch = 5.5 cm, light intensity = 5, light frequency = 1, gain = 3, damping = 1, ETR-Factor = 0.84 and for RLCs: width = 10, intensity = 1, length = 12 (from 1 to 13). Five different sets of photophysiological parameters were recorded in coral nubbins: Maximum Quantum Yield (MQY, Fv/Fm), Effective Quantum Yield (EQY, ΔF/Fm'), Maximum Electron Transport Rate (ETR_{max}), and photoacclimation parameters such as Minimum Saturating Irradiance (Ek) and Photochemical Efficiency at Low Light Intensity (Alpha, α).

The photophysiological parameters of both D and IL treatment groups were measured concurrently during the light phase. This ensured that all photophysiological parameters were measured under the same light conditions, making them directly comparable across the two time points (T0 and T4). For both T0 and T4, MQY was measured before sunrise at 4:30 AM following approximately seven hours of overnight dark adaptation, and at 1:00 PM EQY was measured under natural outdoor ambient light. RLCs were subsequently performed (after approximately 1 h from EQY) on the light-adapted nubbins. Given the extended duration of the measurement process, coral nubbins were temporarily transferred for the RLC analysis to an indoor aquarium tank, filled with water from the same source tank and kept under identical chemical-physical and light parameters. Light intensity was measured before the start of the RLCs acquisition and the value was maintained in the indoor tank (approximately between 60 and 100 µmol m^{-2} s^{-1}). This ensured consistent light irradiation throughout the RLC measurements, avoiding errors from varying outdoor irradiance. RLCs were measured by illuminating the corals at increasing irradiance levels from 0 to 1500 µmol photons m^{-2} s^{-1} (PAR) with a 10 s incubation at each irradiance step (Ralph and Gademann 2005). From the fitted RLCs, ETR_{max}, Ek, and Alpha (α) were calculated by plotting ETR versus PAR and fitting the data of the RLCs using the exponential-saturation model by Platt et al. (1980).

Coral bleaching assessment

Sample preparation

Fragments for coral bleaching assessment were sampled at both the beginning (T0) and the end of the experiment (T4). A 1 cm^2 fragment was cut from each *P. speciosa* nubbin and immediately frozen at − 80 °C (Guest et al. 2016). Coral tissue was removed from the fragments using a WP-660 Water Flosser (Waterpik, UK) with Milli-Q water (Fitt et al. 2000; Louis et al. 2016). The suspension was decanted in a glass beaker and homogenized for ~ 20 s using a QIAGEN TissueRuptor. The total volume of the suspension was measured, and 10 ml used for Symbiodiniaceae count. The remaining suspension was centrifuged at 4,500 rpm for 15 min at 4 °C to obtain a pellet for chlorophyll *a* quantification.

Symbiodiniaceae density The 10 ml suspension was homogenized, and 10 µl was used to count Symbiodiniaceae cells from five independent counts using a hemacytometer (Improved Newbauer) under a light microscope (Olympus, Japan). The cell density was calculated for 1 ml of suspension (Ladrière et al. 2014).

Due to the flat morphology of the small nubbins used and the total absence of coral tissue in the underside part of each nubbin epoxied on the support, the planar surface area of fragments was estimated, as also performed in previous studies (Kikuzawa et al. 2018; McLachlan and Grottoli 2021; Sam et al. 2021). In detail, fragments were placed next to a calibrated quadrat and pictures using an Olympus TG6 under stable and optimal light conditions and at constant distance from the fragment were taken. Afterward, images were processed using ImageJ (version 1.54 g, National Institutes of Health, USA) and the planar surface area calculated. The Symbiodiniaceae cell counts for each replicate were normalized to the total coral planar surface area and therefore the Symbiodiniaceae density was obtained by dividing the cell number by the respective estimated surface area (Isa et al. 2024).

Chlorophyll a quantification The pellet was resuspended in 8 ml (or multiples) of 99% ethanol (Ritchie 2006, 2008) and homogenized for approximately 20 s using a QIAGEN TissueRuptor. The solution was then incubated for 24 h at 4 °C. Following incubation, the extract was centrifuged at 4,500 rpm for 15 min at 4 °C before proceeding with the spectrophotometric analysis. Absorbance was measured at 632 nm, 649 nm, 665 nm, and 696 nm. These values were applied to dinoflagellate-specific equations to determine the chlorophyll concentration (Jeffrey and Humphrey 1975; Contardi et al. 2023). Chlorophyll *a* concentrations were normalized to the coral planar surface area of the respective fragments (cm^2), indicated as [Chl *a*]/ cm^2, and to the Symbiodiniaceae density (cell), indicated as [Chl *a*]/cell.

Color chart

Coral bleaching was visually assessed using a coral color chart (=Color Reference Card) as described by Siebeck et al. (2006). The color reference card was placed next to the coral nubbin, and the color brightness was recorded on a scale from 1 to 6, to the nearest 0.5 units (Montano et al. 2010; Seveso et al. 2020). The color reference card uses a 6-point scale for brightness/saturation across four color hues to document changes in bleaching status. Shifts of two units or more indicate variations in symbiont density and chlorophyll *a* content,

corresponding to changes in coral bleaching status (Siebeck et al. 2006).

Statistical analysis

Each replicate's RLC was fitted using the R package "phytotools" and the model by Platt et al. (1980). The Shapiro–Wilk test was used to assess the normality distribution of all data. For both coral bleaching parameters (Symbiodiniaceae density, [Chl *a*]/cm^2, [Chl *a*]/cell and color score) and photochemical parameters (MQY, EQY, ETR_{max}, Ek, α), one-way ANOVA tests followed by Tukey's HSD post hoc tests for multiple pairwise comparisons of means were performed to assess significant differences between the different light treatments and, within each treatment, between the different exposure times (T0 and T4) tested. If either the assumption of homogeneity of variances or data normality was not met, Kruskal–Wallis (KW) nonparametric tests followed by pairwise comparisons were performed. Significant differences between the light treatments in temperature and light values recorded throughout the experiment were assessed using KW nonparametric tests followed by pairwise comparisons. Pearson's correlation coefficient was used to test the correlation between the bleaching parameters. All the data were analyzed using IBM SPSS Statistics software, version 29.0.1.0. A multivariate analysis was performed using the statistical package PRIMER-E v.7 (Clarke and Gorley 2015) with the permutational multivariate analysis of variance (PERMANOVA) + add on (Anderson et al. 2008), to investigate together the change of the parameters investigated, both the photosynthetic ones and some of those related to bleaching (Symbiodiniaceae density, [Chl *a*]/cm^2 and color score) in response to light treatments and the exposure time. Data related to the levels of all the parameters were standardized to calculate a matrix based on the Euclidean distance. To test for differences in parameter levels among light treatments and time and the combination of both, a nonparametric PERMANOVA was performed using 999 permutations with partial sum of squares and unrestricted permutation of raw data. Treatments and time were selected as fixed factors. Pairwise PERMANOVA tests were conducted to assess differences between treatments at T0 and T4 and between times within each light treatment. To visualize effects of light treatments and exposure times, non-metric multidimensional scaling (nMDS) was performed based on Euclidean distance.

Results

Coral bleaching assessment

At the end of the four-weeks treatment period, bleaching was observed for the D treatment, while corals subjected to IL showed paling (Fig. S5) and no partial or total mortality was observed for any of the coral nubbins in any treatments. Symbiodiniaceae density, [Chl *a*]/cm^2, and coral color score showed similar trends during the experiment (Fig. 2). Additionally, considering together all samples, a positive and significant correlation was observed between these three bleaching parameters ($p < 0.01$), with a significant positive correlation between Symbiodiniaceae density and [Chl *a*]/cm^2 ($r^2 = 0.417$), Symbiodiniaceae density and color score ($r^2 = 0.733$), and [Chl *a*]/cm^2 and color score ($r^2 = 0.474$) (Fig. S6). Overall, statistically significant differences were detected between the different treatments and times analyzed for Symbiodiniaceae density (ANOVA, $F(5, 129) = 30.115$, $p < 0.01$), for [Chl *a*]/cm^2 (KW, $\chi^2(5) = 56.840$, $p < 0.01$) and for color score (KW, $\chi^2(5) = 80.072$, $p < 0.01$), while no statistically significant differences for these parameters were observed at T0 between treatments ($p \geq 0.05$).

Specifically, nubbins subjected to C treatment did not show any significant change in Symbiodiniaceae density, [Chl *a*]/cm^2 and color score between T0 and T4 (Fig. 2A–C). The largest decrease in coral bleaching parameters was observed in colonies subjected to the D treatment. In particular, a statistically significant decrease in Symbiodiniaceae density of 32% ($p < 0.01$) was observed for the IL treatment between T0 and T4. In comparison, a greater reduction of approximately 70% ($p < 0.01$) was recorded in corals subjected to the D treatment (Fig. 2A). Similarly, a significant decrease in [Chl *a*]/cm^2 of approximately 47% ($p < 0.01$) and 75% ($p < 0.01$) was observed in the IL and D treatments, respectively, between T0 and T4 (Fig. 2B). Additionally, a slight but significant paling of the corals was noted at the end of the IL treatment, with an average loss of one color score (from about 5 to approximately 4), which, however did not indicate significative bleaching as previously reported (see paragraph 2.4.2 and Siebeck et al. 2006). In contrast, more evident bleaching was recorded in the corals subjected to the D treatment, which lost approximately three color scores (from about 5 to about 2) ($p < 0.01$) over the four weeks of treatment (Fig. 2C, Fig. S5).

Finally, no statistically significant differences were detected between the different treatments and times analyzed for [Chl *a*]/cell (KW, $\chi^2(5) = 72.335$, $p \geq 0.05$), (Fig. 2D).

Photosynthetic parameters

All five photochemical parameters analyzed in *P. speciosa* nubbins displayed significant variations between the different treatments and time points (KW, χ^2 (5) = 12.265, $p < 0.05$ for MQY; KW, χ^2 (5) = 25.339, $p < 0.01$ for EQY; ANOVA, $F(5, 127) = 26.841$, $p < 0.01$ for ETR_{max}; KW, χ^2 (5) = 53.988, $p < 0.01$ for Ek and KW, χ^2 (5) = 77.739, $p < 0.01$ for alpha), (Fig. 3). At the start of the experiment (T0), no significant differences were observed in all the five parameters between the different light treatments ($p \geq 0.05$)

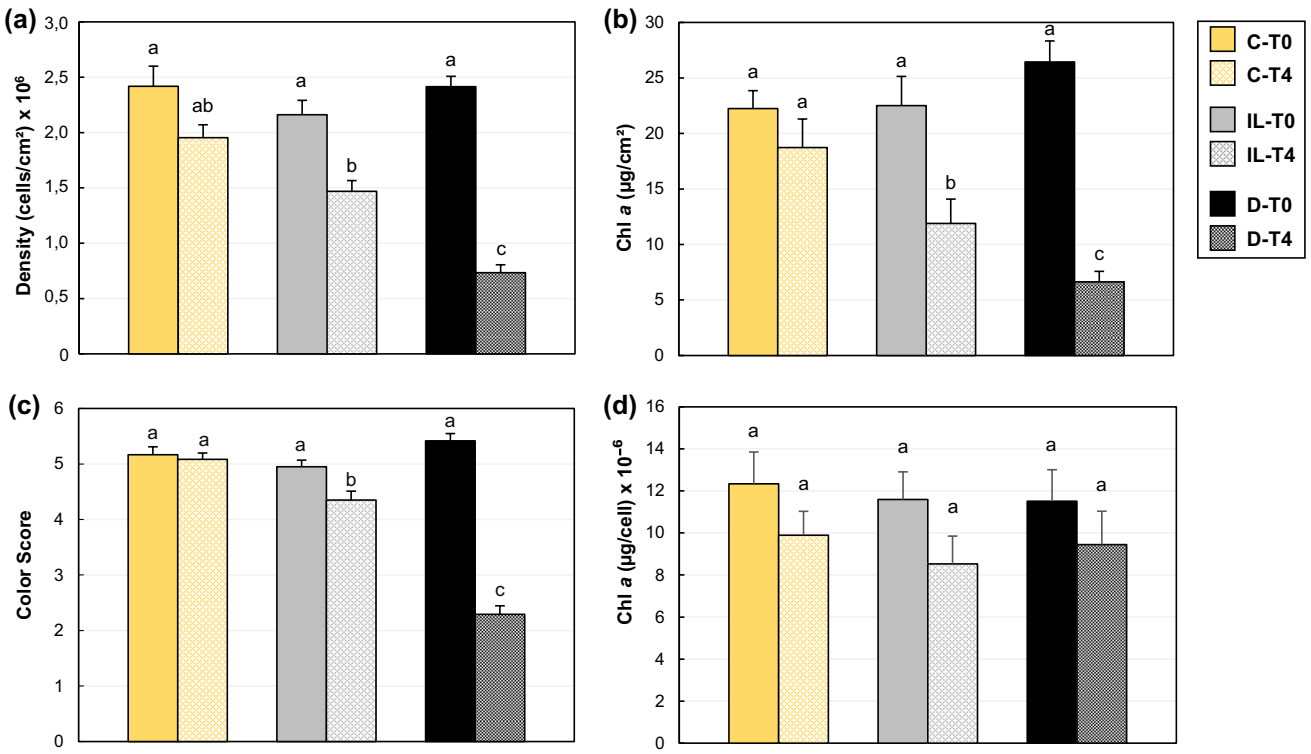

Fig. 2 Symbiodiniaceae density (**A**), concentration of chlorophyll *a* per planar surface area ([Chl *a*]/cm^2; **B**), color score of the Color Reference Card (**C**), concentration of chlorophyll *a* per Symbiodiniaceae cell ([Chl *a*]/cell; **D**) in *P. speciosa* nubbins at the beginning (T0) and after four weeks of exposure (T4) at the different light treatments (C: Control; IL: Intermittent Light; D: Dark). Data are expressed as mean ± SEM (n = 24 for treatments C and D; n = 20 for treatment IL). Significant differences between treatments were evaluated through one-way analysis of variance (ANOVA) or Kruskal–Wallis (KW) test followed by Tukey's pairwise tests. Letters denote statistically significant differences between the different treatments ($p < 0.05$). The same letter indicates no significant difference ($p \geq 0.05$)

(Fig. 3). No common trend was observed at the end of the experiment, as each photosynthetic parameter responded differently to the various treatments.

Specifically, the Maximum Quantum Yield (MQY) of *P. speciosa* nubbins did not change significantly in both the C and IL treatments from the beginning to the end of the experiment. However, a significant decrease of approximately 17% was measured in the D treatment ($p < 0.01$) (Fig. 3A).

The Effective Quantum Yield (EQY) of *P. speciosa* nubbins remained constant in the C treatment throughout the experiment. However, nubbins exposed to IL treatment exhibited a considerable increase in approximately 86% ($p < 0.01$) by the end of the treatment period, representing the highest EQY value recorded in the experiment (Fig. 3B). Conversely, there were no significant changes in EQY observed for samples subjected to the D treatment (Fig. 3B).

For the Maximum Electron Transport Rate (ETR_{max}), no significant change was observed in the C treatment (Fig. 3C). However, a significant decrease was observed at the end of both IL and D treatments. ETR_{max} value was halved between the start and end of both treatments (-50% $p < 0.01$, and -43% $p < 0.01$, respectively), (Fig. 3C).

The minimum saturating irradiance (Ek) significantly decreased in nubbins subjected to C and IL treatments after four weeks of the experiment, with a decrease of 20% ($p < 0.01$) and 41% ($p < 0.01$), respectively. The lowest Ek value was recorded in nubbins subjected to the IL treatment (Fig. 3D). Conversely, no significant change in the minimum saturating irradiance was observed in nubbins subjected to the D treatment (Fig. 3D).

Finally, the photochemical efficiency of photosynthesis (alpha, α) changed significantly in all treatments by the end of the experiment (Fig. 3E). In the C treatment, α increased by approximately 15% ($p < 0.01$). In contrast, α decreased in nubbins subjected to IL and D treatments over the four-week period. The greatest decrease in α was observed in nubbins exposed to complete darkness for four weeks, with a reduction of 53% ($p < 0.01$) (Fig. 3E).

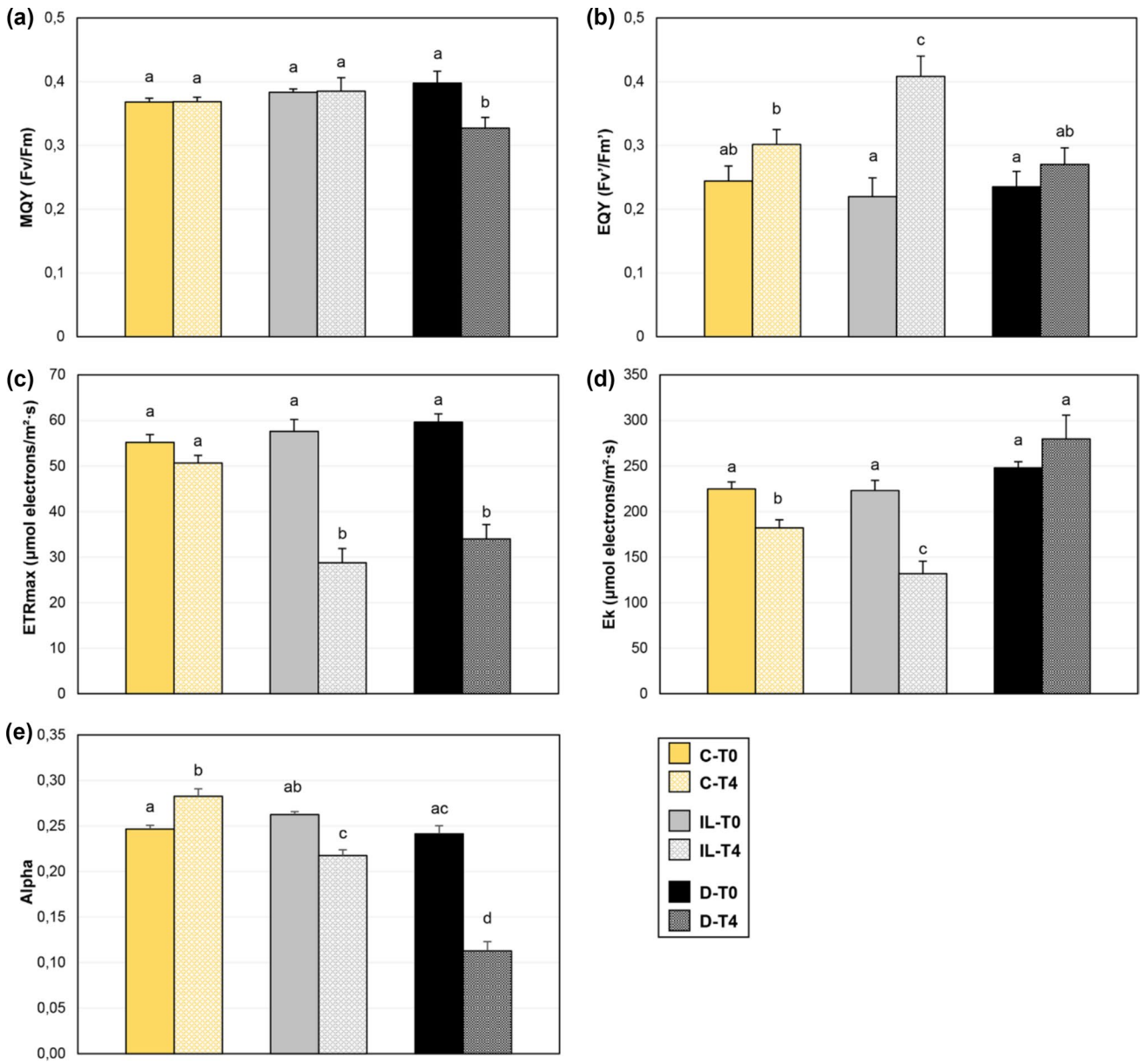

Fig. 3 Maximum Quantum Yield (MQY; **A**), Effective Quantum Yield (EQY; **B**), Maximum Electron Transport Rate (ETR_{max}; **C**), Minimum saturating irradiance (Ek; **D**) and Photochemical Efficiency at low light intensity (Alpha; **E**), in *P. speciosa* nubbins at the beginning (T0) and after four weeks of exposure (T4). Data are expressed as mean ± SEM (n = 24 for treatments C and D; n = 20 for treatment IL). Significant differences between treatments were evaluated through one-way analysis of variance (ANOVA) or Kruskal–Wallis (KW) test followed by Tukey's pairwise tests. Letters denote statistically significant differences between the different treatments ($p < 0.05$). The same letter indicates no significant difference ($p \geq 0.05$)

Multivariate analysis

PERMANOVA revealed significant differences in parameter levels among treatments, exposure times, and a combination of both (Table 1). Specifically, all treatments exhibited similar parameter levels at the start of exposure (T0) (Table 2A). In contrast, by the end of the experiment (T4), the levels of the analyzed parameters differed significantly between treatments (Table 2A). Additionally, there was a significant change in most parameters throughout the experiment, except for controls.

The nMDS analysis indicated that all T0 samples were most similar, regardless of the light treatment, demonstrating similar levels of the analyzed parameters at T0 (Fig. 4). By the end of the experiment (T4), C treatment samples remained grouped with T0 samples, while samples exposed to IL treatment showed a slight distinction, primarily driven by an increase in EQY and a decrease in Ek. In contrast,

Table 1 Results of the PERMANOVA testing the effects of the light treatments (C, IL and D) and exposure times (T0 and T4) on the coral bleaching parameters (Symbiodiniaceae density, [Chl *a*]/cm^2, color score) and photochemical parameters (MQY, EQY, ETR_{max}, Ek, α) of *P. speciosa* obtained by permutations (perm) for each group

Source of variation	df	SS	MS	F	*p*	Perms
Treatment	2	9.8333	4.9167	10.738	**0.001**	999
Time	1	22.241	22.241	48.572	**0.001**	998
Treatment x Time	2	11.208	5.6042	12.239	**0.001**	999
Error	130	59.526	0.4578			
Total	135	102.91				

Significant p values ($p < 0.05$) are in bold

Table 2 Results of the PERMANOVA pairwise comparisons between light treatments at T0 and T4 (**A**), and between exposure times within each light treatment (**B**) obtained by permutations (perm) for each group

	Groups	t	P (perm)	Perms
A				
Time T0	C vs. IL	0.75411	0.689	998
	IL vs. D	1.1237	0.266	999
	C vs. D	0.9934	0.374	998
Time T4	C vs. IL	3.274	**0.001**	998
	IL vs. D	5.7286	**0.001**	999
	C vs. D	4.8506	**0.001**	998
B				
Treatment C	T0 vs. T4	1.7659	0.071	999
Treatment IL	T0 vs. T4	4.8462	**0.001**	999
Treatment D	T0 vs. T4	6.6922	**0.001**	998

Significant p values ($p < 0.05$) are in bold

dark-treated samples (D) displayed a clear distancing due to a significant decrease in bleaching parameters (Symbiodiniaceae density, [Chl *a*]/cm^2, color score) as well as in ETR_{max} and α (Fig. 4).

Discussion

In this study, we subjected the widespread coral species in Singapore turbid reefs *Pachyseris speciosa* to intermittent light and complete darkness conditions for four weeks to test its photopysiological response and its potential for photoacclimatization under possible light limitation scenarios. After four weeks of both treatments, *P. speciosa* nubbins showed a reduction in zooxanthellae density, chlorophyll *a* concentration per planar surface area, and color score, while this was not recorded in coral maintained in control light condition. However, a higher decrease in these parameters, and therefore a significant and strong bleaching, was observed in colonies subjected to dark treatment, i.e., exposed to 1.7 ± 0.3 µmol m^{-2} s^{-1} mean daylight intensity during the four-weeks experiment. This was expected, as it has long been known that corals and others cnidarians can lose their algae symbionts during prolonged (several days) incubation in constant darkness or very low light (Yonge and Nicholls 1931; Franzisket 1970; Kevin and Hudson 1979; Hoegh-Guldberg and Smith 1989; Titlyanov et al. 2001; DeSalvo et al. 2012; Tolleter et al. 2013; Bessell-Browne et al. 2017a,b). Previous studies indicated that corals exposed to complete darkness could quickly shift into a hypoxic state, followed by a nearly anaerobic condition, due to high metabolic activity of the zooxanthellae and polyp tissue (Kühl et al. 1995; Gardella and Edmunds 1999; Jones and Hoegh-Guldberg 2001). If the hypoxia in coral tissues under extremely low light is linked to the metabolic activity of the symbiotic algae, then removing them from the polyps (generating bleaching), appears to be the only survival strategy (Bessell-Browne et al. 2017a). Alternatively, bleaching could be also due to unstacking and structural changes of the thylakoid membrane, leading to reduced electron transport and photosynthate translocation from the algal symbionts to the host and this inefficiency can prompt polyps to expel the algae to reduce the energy burden (Masuda et al. 1993; DeSalvo et al. 2012).

In contrast, an intermittent light scenario, represented by an alternation of complete darkness and in situ light condition (mean daylight intensity of 7.1 ± 0.6 µmol m^{-2} s^{-1} considering the four-weeks treatment), produced a slight bleaching or paling. In a recent study, three different coral species *Turbinaria mesenterina*, *Porites lutea*, and *Goniopora cellulosa* showed significant reduction in Symbiodiniaceae and chlorophyll (and also mortality for *G. cellulosa*) after seven-days exposure to 9 to 10 µmol m^{-2} s^{-1} (Juhi et al. 2021). In another study, *P. speciosa* subjected to low-light and variable light treatments alternating between high and low conditions every five days, displayed an increase in chlorophyll level under low light and no significant changes under variable light after 20 days (DiPerna et al. 2018). These evidences highlight as the coral bleaching response to low light or intermittent light conditions is highly variable among species, and it also appears to be strongly affected

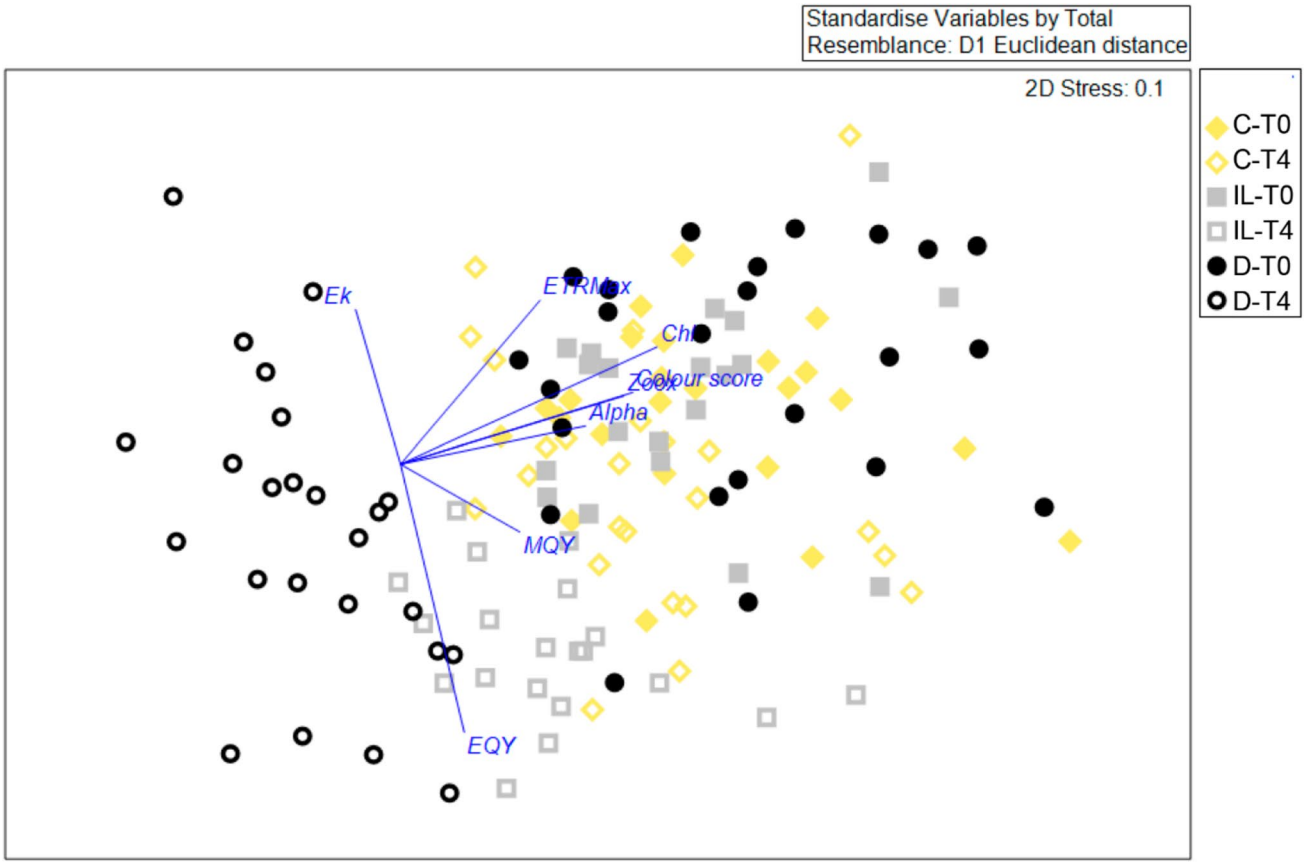

Fig. 4 Non-metric multidimensional scaling plot (nMDS) showing the response pattern of all the *P. speciosa* parameters analyzed by the different light treatments and exposure times, with vectors (Pearson's correlations ≥ 0.7) representing the variables that drive significant resemblances among experimental conditions. In the figure, the vector named "Zoox" refers to the Symbiodiniaceae density parameter and Chl*a* to [Chl *a*]/cm^2

by several factors, such as the experimental light intensity, the exposure time and the basal light level in the coral natural environment, making it difficult to make a reliable comparison between the various studies. In addition, other coral intrinsic factors as the growth forms, the photoacclimatization capabilities and strategies and the heterotrophic plasticity may influence the different response of coral species (Anthony and Fabricius 2000; Hennige et al. 2008; Treignier et al. 2008; Hoogenboom et al. 2009; DiPerna et al. 2018; López-Londoño et al. 2024; Luo et al. 2024). Finally, it is also important to considered that our corals subjected to IL treatment, during the light days were not exposed to a constant light irradiation, but to fluctuating light intensity, which could change suddenly and rapidly, ranging from a few µmol m^{-2} s^{-1} to peaks of about 100 µmol m^{-2} s^{-1} (with an average of ~ 32 µmol m^{-2} s^{-1}, Fig. S1). This aspect should be taken in account when analyzing the bleaching and the photophysiological response of IL corals.

Surprisingly, our results also showed that, while the chlorophyll concentration significantly decreased per planar surface area, it did not significantly change per Symbiodiniaceae cell after four-weeks of both light treatments. The stability of the chlorophyll concentration per cell ratio over the time and between treatments could suggest that *P. speciosa* may not concentrate chlorophyll within the remaining zooxanthellae as a photoacclimation response to intermittent light and darkness, contrary to what is widely known and reported in the literature for corals subjected to reduced light availability (Titlyanov et al. 2001; Rodolfo-Metalpa et al. 2008; Lesser et al. 2010; Mass et al. 2010). Instead, it could photoacclimatize by enhancing the photosynthetic efficiency of the remaining zooxanthellae cells. On the other hand, previous studies showed that pigment content per cell was relatively constant in *Leptoseris fragilis* colonies located at different mesophotic depths, and therefore subjected to different light regimes (Fricke et al. 1987), and that [chl *a*] per zooxanthellae cell in *Stylophora pistillata* colonies reciprocally transplanted at different depths remained equal to those recorded in the original depths (Cohen and Dubinsky 2015).

MQY (Fv/Fm), the maximum quantum efficiency of PSII, is the most commonly used indicator for determining the algae zooxanthellae's physiological state, and it serves as a

useful proxy for assessing photodamage and possible photoacclimation, as it is directly correlated to the photosynthetic performance of the coral (Maxwell and Johnson 2000; Levy et al. 2016; Bhagooli et al. 2021). In general, a reduction in MQY could indicate a decrease in algal productivity that could lead to a drop in the nutrition, growth, reproduction and calcification rate of the organism and finally bleaching and mortality, as observed in previous studies (Anthony and Hoegh-Guldberg 2003; Bhagooli and Hidaka 2004; Mass et al. 2007; Erftemeijer et al. 2012; Jones et al. 2020). Our findings showed as *P. speciosa* nubbins subjected to the complete dark treatment displayed a decrease in MQY, as previously observed for *Euphyllia paradivisa* (Eyal et al. 2015), *T. mesenterina*, *P. lutea*, and *G. cellulosa* (Juhi et al. 2021), and this reduction occurred alongside coral bleaching, while it remains unclear if other physiological parameters were also affected. In contrast, a previous study on *P. speciosa* reported an increase in the Fv/Fm with rising turbidity, which corresponds to decreased light intensity, with the maximum quantum yield observed at 72% light attenuation (Browne et al. 2014). However, in that study, the colonies were exposed to low light for a significantly shorter duration and experienced a higher level of sedimentation, condition that were not replicated in the current experiment, making comparisons challenging. Not surprisingly, *P. speciosa* corals that were subjected to continuous and prolonged sedimentation instead exhibited a significant and persistent decline in Fv/Fm (Browne et al. 2015). On the other hand, the stability of MQY in *P. speciosa* nubbins exposed to the intermittent light treatment, despite five days of full darkness, could suggest the ability of the species to tolerate fluctuating light conditions while maintaining the integrity and functionality of the coral photosynthetic apparatus. In a previous study, under variable light conditions, *P. speciosa* proved to be resilient to short periods of high light intensity regulating MQY and recovering rapidly thanks to up-regulation of the xanthophyll pigment cycle used to dissipate excess light energy (DiPerna et al. 2018). This resilience highlights the species' capacity for photoacclimation, ensuring sustained photosynthetic efficiency under varying light conditions. In addition, the observation that in our experiment EQY reached MQY levels under four-weeks of intermittent light treatment further indicated that *P. speciosa* was able to reach its maximum photosynthetic rate despite the adverse light environment, even when its photosystems were not dark-acclimated.

Pachyseris speciosa colonies exposed to the intermittent light treatment also showed a significant increase in EQY, accompanied by a significant decrease in ETR_{max}, Ek, and α. The increase in EQY implies a better photosynthetic efficiency, as also seen in other coral species such as *E. paradivisa* (Ben-Zvi et al. 2020), *Montastraea cavernosa* and *Porites astreoides* (Carpenter et al. 2022), suggesting that *P. speciosa* was able to adapt to the new adverse conditions by maximizing the use of the limited light available. Such modification could have occurred by regulating the number of available reaction centers associated with PSII (Gorbunov et al. 2001; Lesser and Gorbunov 2001) and/or by changing effective antenna size—antenna pigments per photosynthetic unit (Falkowski and Dubinsky 1981; Franklin et al. 1996; Dubinsky and Stambler 2009; Einbinder et al. 2016). In general, the photoacclimation to decreasing light conditions is also characterized by a decrease in Ek (Hennige et al. 2008; Frade et al. 2008; Lesser et al. 2010; Langlois and Hoogenboom 2014). In our study, this parameter showed the greatest decrease after four-weeks of intermittent light treatment, indicating that *P. speciosa* required less light to saturate its photosystems, thereby enhancing its photosynthetic efficiency. In addition, a decrease in ETR_{max} suggested that corals exhibit a capacity for acclimation to low-light environments by lowering its electron transport rate. A similar behavior was recorded for corals subjected to 80–90% photosynthetic active radiations reduction for seven days (Yongzhi et al. 2024) and for the sponge *Lamellodysidea herbacea* transplanted to a 97% shaded environment for five days (Biggerstaff et al. 2015). Overall, although all these adjustments indicated a reduced photosynthetic capacity under intermittent light condition, they may reflect an adaptive response whereby the coral could optimize its photochemical apparatus to handle sporadic light availability, by using the mechanisms previously reported. On the other hand, corals subjected to the complete dark treatment, despite showing a decrease in ETR_{max}, were not able to parallelly decrease also their Ek values, as for corals under intermittent light, indicating that the light required to saturate the photosystems did not decrease, reflecting the corals' inability to acclimate to the dark condition.

Finally, the parameter Alpha (α) represents the photosynthetic efficiency at low light levels and is a measure of how effectively the coral can convert light into chemical energy under sub-saturating light conditions (Falkowski and Raven 2013). An increase in α under low-light conditions is typically attributed to enhanced light harvesting efficiency, possible due to an increase in antenna size, and to shade adapted corals (Björkman 1966; Perkins et al. 2006; Dubinsky and Stambler 2009; Rocha et al. 2013; Laverick et al. 2019). However, in this study, a decrease in α was observed at the end of both intermittent light and dark treatments, with a significantly greater reduction in the dark-treated samples. Other previous studies have also shown a decline in coral α under decreased light or shading conditions (Juhi et al. 2021; Tunala et al. 2019; Tamir et al. 2020; Ellis et al. 2025), while to the best of our knowledge, to date no studies analyzed the change in α under intermittent or variable light scenarios. The strong reduction in α in coral subjected to dark treatment could be explained with a partially inactivated

photosynthetic apparatus, reflecting the inability of the coral to photo acclimate. On the other hand, for corals subjected to intermittent light we hypothesized that they might not able to adapt their antenna size due to the fact the corals during the light days were not exposed to constant low light irradiation, but to fluctuating light intensity that also reached higher peaks compared to the average. In this context, the slighter reduction of α in IL samples could be linked to a possible photoprotection mechanism during the shift from complete darkness to light by inactivating some photosynthetic active centers. In this regard, while photoprotection analysis was not within the scope of this research, it could be interesting to also investigate a parameter like non-photochemical quenching (NPQ) in future studies on intermittent or variable light conditions.

Overall, our results indicated that, although both intermittent light and dark treatments caused a decrease in coral coloration and symbiosis integrity over four weeks, colonies exposed to intermittent light treatment showed (1) milder change in bleaching parameters and (2) possible photoacclimation to the new light condition by increasing EQY, decreasing ETR_{max} and Ek, and maintaining MQY. Interestingly, no coral mortality was observed at the end of the experiments, indicating that *P. speciosa* can survive up to four weeks in complete darkness, contrary to what we initially hypothesized. However, due to the evident bleaching and the lack of photoacclimatization to dark treatment, it can be hypothesized that prolonged exposure to complete darkness may probably lead to mortality, although it cannot be excluded that a return to better environmental/light conditions may also lead to coral recovery. Additionally, it is important to note that our study focused solely on light as the changing variable, keeping constant all the other environmental factors. However, in its natural environment, a coral exposed to high turbidity levels that result in complete darkness or intermittent light for long periods, would likely perish due to smothering, abrasion, diseases and other physical damages associated with excessive sedimentation (Tuttle and Donahue 2022), rather than solely from low light. Therefore, the response of *P. speciosa* to sedimentation and smothering could probably be very different from the observed response to intermittent low light or darkness only (Browne et al. 2014, 2015).

Nonetheless, our results suggested that *P. speciosa* from Singapore's turbid reefs can adapt to a light level that simulates, for four weeks, episodes of complete darkness alternating with days of normal ambient light as we initially hypothesized, showing some potential to tolerate slight further light reduction and confirming its overall remarkable tolerance for low-light conditions. Therefore, although other turbidity-related variables and stressors besides low light need to be taken into account, *P. speciosa* deserves special attention and should be considered for transplantation in extremely low-light conditions (as also documented by Afiq-Rosli et al. 2017) to aid the conservation of Singapore's reef ecosystems in the face of rapid urbanization and climate change.

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Author contributions LMT: Writing—original draft; Project administration; Conceptualization; Formal analysis;. Data curationMethodology; Software; Validation YDL: Investigation; Supervision; Writing—review and editing;. Data curation DS: Investigation; Supervision; Writing—review and editing; Validation; Visualization;. Data curation EM: Supervision; Visualization; Writing—review and editing JKCH: Conceptualization, Investigation, Methodology WLOY: Conceptualization, Investigation, Methodology DH: Funding acquisition; Conceptualization; Project administration; Supervision; Writing—review and editing JT: Funding acquisition; Conceptualization; Project administration; Supervision; Writing—review and editing; Data curation.

Data availability Data will be made available on request.

Declarations

Competing Interests The authors declare no competing interests.

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