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Effects of Blue Light and Feeding on the Physiological Performance of Reef Corals, *Stylophora pistillata* and *Pocillopora damicornis*

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Previous studies have shown that culturing corals under controlled blue light can increase calcification rate and stimulate the production of pigments while reducing the photosynthetic capacity of the corals' symbiotic algae. Additionally, feeding coral can accelerate growth and enhance their resistance to environmental changes. However, most studies have left their combined effects on coral physiology largely unexplored. Here we investigate the effects of two blue light intensities and two feeding concentrations on coral growth rates and color expression during cultivation. We cultured *Stylophora pistillata* and *Pocillopora damicornis* under different blue light intensities and fed varying concentrations of enriched brine shrimp (*Artemia*) twice a week. Both species maintained high survival (100%) and photosynthetic efficiency (Fv/Fm > 0.6). *S. pistillata* exhibited the highest growth under high-light and high-feeding conditions, while *P. damicornis* showed no significant growth differences among treatments. However, both species displayed reduced color scores under high-light conditions, as indicated by elevated red-green-blue values. Together, these findings highlight coral species-specific responses to blue light intensity with feeding interactions and demonstrate that manipulating environmental regimes can optimize coral cultivation. This approach supports high-density ex-situ cultivation, advancing both reef restoration and production of corals for ornamental aquariums.

Keywords: Blue light intensity, Aquaculture, Coral growth, *Stylophora pistillata*, *Pocillopora damicornis*

BACKGROUND

Coral reefs are increasingly threatened by anthropogenic activities and climate change, driving the need for effective restoration and ex-situ cultivation strategies (Barton et al. 2017; Bellwood et al. 2004; Suggett et al. 2024). Reef-building corals rely on both photosynthetic input from their symbiotic dinoflagellates and the heterotrophic feeding by the host, which makes light conditions and food availability two of the most critical factors governing coral growth and survival (Fabina et al. 2012; Muscatine and Porter 1977).

Light is a critical factor influencing coral physiology, in which blue wavelengths are known to enhance calcification, growth, and bleaching resistance (Cohen et al. 2016; Goreau 1959; Roth 2014). However,

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the effects of blue light can vary across coral species and depths (Mass et al. 2010). For instance, a recent study on *Acropora* corals reported higher growth under spectra containing longer wavelengths (green/red), while reporting reduced growth under purely blue-dominant spectra (Izumi et al. 2023). These contrasting findings highlight the need for a more comprehensive assessment of the ecological role of blue light in shaping coral performance. In parallel, heterotrophic feeding is also essential, as it can increase coral growth, reproduction, and skeletal calcification (Ferrier-Pagès et al. 2003; Huang et al. 2020; Lam et al. 2023; Wall et al. 2020). Although the balance between autotrophy and heterotrophy is known to play a key role in the sustained growth of mixotrophic corals (Schubert and Wilke 2018; Sturaro et al. 2021), the interaction between blue light and feeding density in regulating coral growth remains unclear.

The reef-building corals, *Stylophora pistillata* and *Pocillopora damicornis* are widely distributed in Taiwan and around the globe and have been commonly used as experimental species in research. *Stylophora pistillata* has been used as a model coral for physiology studies since 1980, and over the past two decades has been used for stress response studies (Meziere et al. 2022). *Pocillopora damicornis* has been the focus of many foundational studies in coral physiology and ecology, which makes this well-understood organism an excellent model species for testing an ex-situ mesocosm system (Traylor-Knowles 2011).

Well-maintained ex-situ coral mesocosm systems present an opportunity to examine global-change simulations under controlled conditions, allowing for robust long-term experiments while avoiding the confounding effects of natural fluctuations commonly encountered in *in-situ* experiments (Schubert and Wilke 2018). For example, in ex-situ mesocosm systems, coral color scores provide a practical indicator of bleaching, while the maximum dark-adapted quantum yield (Fv/Fm) is widely used as a proxy for the photosynthetic efficiency of symbiotic algae and an serves as an overall indicator of coral health (Maxwell and Johnson 2000). Moreover, ex-situ coral mesocosm systems can easily manipulate light conditions to optimize species-specific cultivation and can readily incorporate customized feeding regimes. These features make ex-situ mesocosm systems particularly suitable for testing how key environmental drivers, such as light quality and feeding, interact to shape coral performance.

Therefore, in the present study, we exposed *S. pistillata* and *P. damicornis* nubbins to four culture treatments with factorial combinations of blue light intensities (high vs. low) and feeding densities (high vs. low) to understand the interactive effect of blue light intensities and feeding densities on coral growth. Coral performance under these treatment conditions was determined by assessing photosynthetic efficiency, buoyant weight, linear growth, and color scores. By clarifying how blue light intensity and feeding interact to influence coral performance, this study contributes to optimizing ex-situ cultivation strategies and informing coral reef restoration efforts under changing environmental conditions.

MATERIALS AND METHODS

Coral sampling

Total seven partial colonies (~15–20 cm in diameter) of *S. pistillata* and *P. damicornis* (*S. pistillata* = 3; *P. damicornis* = 4) (Fig. 1) were randomly collected, using a hammer and a chisel, from a depth of 3-5m from Waimushan Seaside in northern Taiwan (25°16385'N, 121°72715'E). All colonies were sourced from the same environmental conditions. However, this study did not specifically account for potential genetic variability among individual colonies, which may influence the results and should be considered a limitation. The corals were placed in a 120-L rearing tank in an aquaculture room at the Institute of Fisheries Science for four weeks for recovery and acclimation. The recirculating tank was kept under full spectrum light (140–280 μmol quanta $m^{-2}s^{-1}$), and seawater temperature was maintained at 25 ± 1°C by an air conditioner. After acclimation, a total of 144 3–5 cm nubbins (72 nubbins per species, with *S. pistillata* yielding 24 ± 4.55 nubbins per colony and *P. damicornis* yielding 18 ± 8.57 nubbins per colony) were prepared by cutting the branches off of the colonies and gluing them to ceramic bases (Oceanexus, Taiwan). All nubbins were evenly distributed amongthree separate circulating water systems with wide spectrum of blue light (150 μmol quanta $m^{-2}s^{-1}$) for two additional weeks for acclimation.

Culture system

Four independent culture tanks (120 × 60 × 60 cm; length×width×height) were used in this experiment; each tank was connected to a life support tank situated below the culture tank to form a recirculating aquaculture system (RAS). Three culture tanks were used as experimental tanks and received the assigned treatments, while one tank served exclusively as a feeding tank to culture and supply feed to the experimental tanks (no corals were maintained in feeding tank). Each RAS contained a total of 25 kilograms of live rocks and 15 kilograms of

live sand. Water movement in each culture tank was facilitated by circulation pumps (Sun Sun, JDP10000, China) providing a water flow rate of ~3000 L H^{-1} and a wave maker (Maxspect, F350, China) with a wave strength fluctuating every 6 hours from weak current (4 ± 1 cm s^{-1}) to strong current (8 ± 1 cm s^{-1}). Each life support system contained cotton for physical filtration, a protein skimmer (Bubble Magus, A9, China), a primary pump (Sun Sun, JDP10000, China), a chiller (Resun, CL650, China) and a heater (Ista, I-H880, Taiwan) to maintain temperature, and a titration system (Simalai, D4, China) to stabilize both the alkalinity, and concentration of the ion Ca^{2+} and Mg^{2+}. The salinity was maintained by periodically adding fresh reverse osmosis water at 35 ppt using a marine salinity tester (Hanna, HI98319, Italy). The basic maintenance of the aquarium included replacing 30% of the seawater and testing water quality parameters using aquarium test kits (Salifert, Netherlands) every month, and using temperature loggers (HOBO, MX2201, USA) and an aquarium pH test pen (Sun Sun, APH-300, China) to ensure the temperature and pH values were stable. Throughout the experiment, water quality parameters remained within ranges suitable for coral culture—temperature, salinity, pH, alkalinity, Ca^{2+}, Mg^{2+}, and dissolved inorganic nitrogen and phosphorus were monitored regularly; summary statistics and full time series are provided in table S1.

Light and feeding treatments

Nubbins were equally placed into three 432-L tanks with a circulating water system (24 nubbins $species^{-1}$ $tank^{-1}$). To exclude ambient light, the experimental area was fully enclosed with opaque black blackout curtains, and room lights remained off; thus, the tanks were in complete darkness except for the controlled blue-LED illumination (Next Generation Aquarium Control and Lighting System). Illumination followed a 12 h light:12 h dark photoperiod (L:D 12:12), controlled by programmable timers. The tanks were then divided into four treatment groups. The duration of the treatment was 75 days (Fig. 2). Nylon ropes were used to suspend the nubbins in the tank and according to the method of previous study (Huang et al. 2020) for dividing two blue light intensity: high light (HL, 420 ± 3.5 µmol photons m^{-2} s^{-1}) and low light (LL, 280 ± 5.1 µmol photons m^{-2} s^{-1}) (Hammer system, Taiwan). During the experiment, a full-spectrum underwater quantum meter (Apogee, MQ-510, USA) was used to monitored the light intensity. The nylon thread also separated the feeding group while feeding, so two nubbins on the same nylon thread share the same feeding group.

In the experiment, enriched 2-day-old *Artemia salina* were used as feed. Different weights of dried *A. salina* eggs —5 g (low-feed; LF) and 10 g (high-feed; HF) (Huang et al. 2020)—were added to a two-liter hatching bucket, and the eggs were incubated for 48 hours at 25 degrees in seawater with a salinity of 35 psu. At 36 and 42 hours (Tagliafico et al. 2017), a nutrient solution (Omega, PACK BOOST enrichment diet, Chuan Kuan Enterprise, Taiwan) was added to the hatching bucket to enrich the nauplii; the

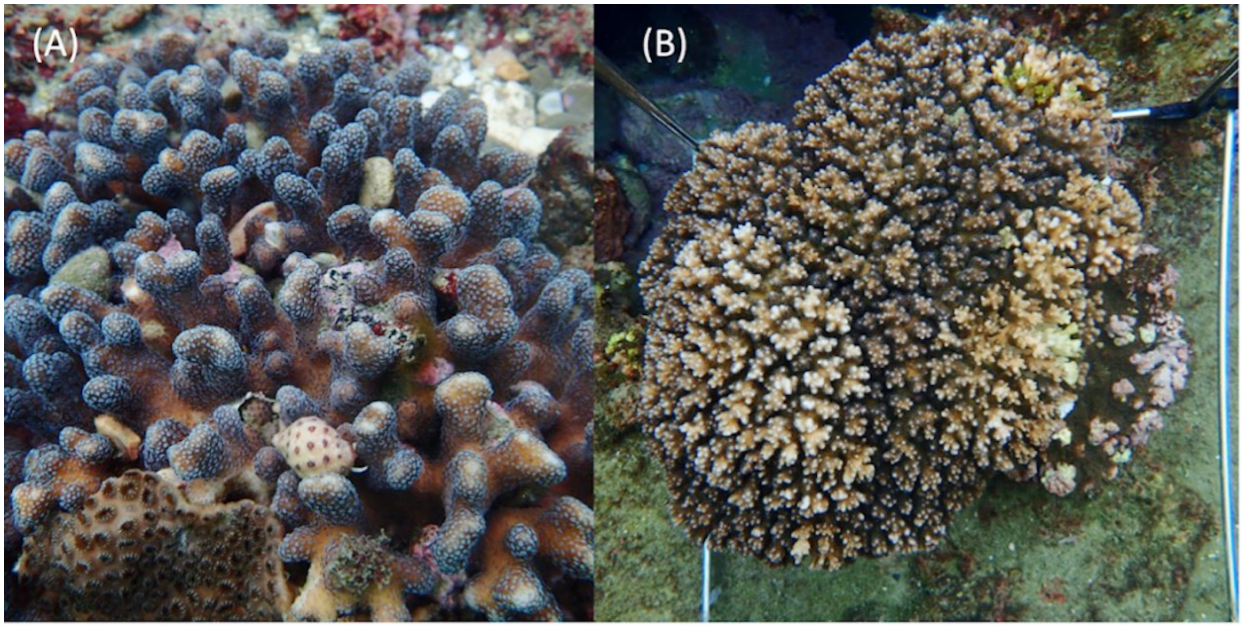

Fig. 1. The colonies of *S. pistillata* (A) and *P. damicornis* (B).

nutritional composition of this commercial enrichment is summarized in table S2. At 48 hours, the 2-day-old *Artemia nauplii* were collected using a 200 μm filter at the bottom of the bucket, rinsed with clean seawater to remove the nutrient solution and added to another independent system according to different feed concentrations: high feed (HF: 50 ± 2.6 ind ml^{-1}) and low feed (LF: 28 ± 1.2 ind ml^{-1}). This feeding tank system otherwise has the same equipment that was used for the experimental; however, a macro algae reactor (Tunze, 3182, Germany) and media reactor (Bubble Magus, MF60, China) were added to reduce nitrate levels. Two polycarbonate cage nets (150-mesh; 30 × 17 × 17 in) were placed in feeding tank to prevent artemia went in to the feeding system. During feeding, two cage nets will be put in the feeding tank, one is for high feed group and the other is for low feed group, the nubbin would be put in the cage net in feeding tank for acclimation and dark adaptation about thirty minutes. Then pouring two different densities of artemia in two cage nets with bubble stones placed at the corners of the tank to allow for even water mixing and to increase the dissolved oxygen. Ten minutes later, 10 ml of water in three different depth (2, 8 and 14 inches) was taking out for artemia density checking. After 4 h, all coral nubbins were rinsed with seawater to remove the residual nauplii

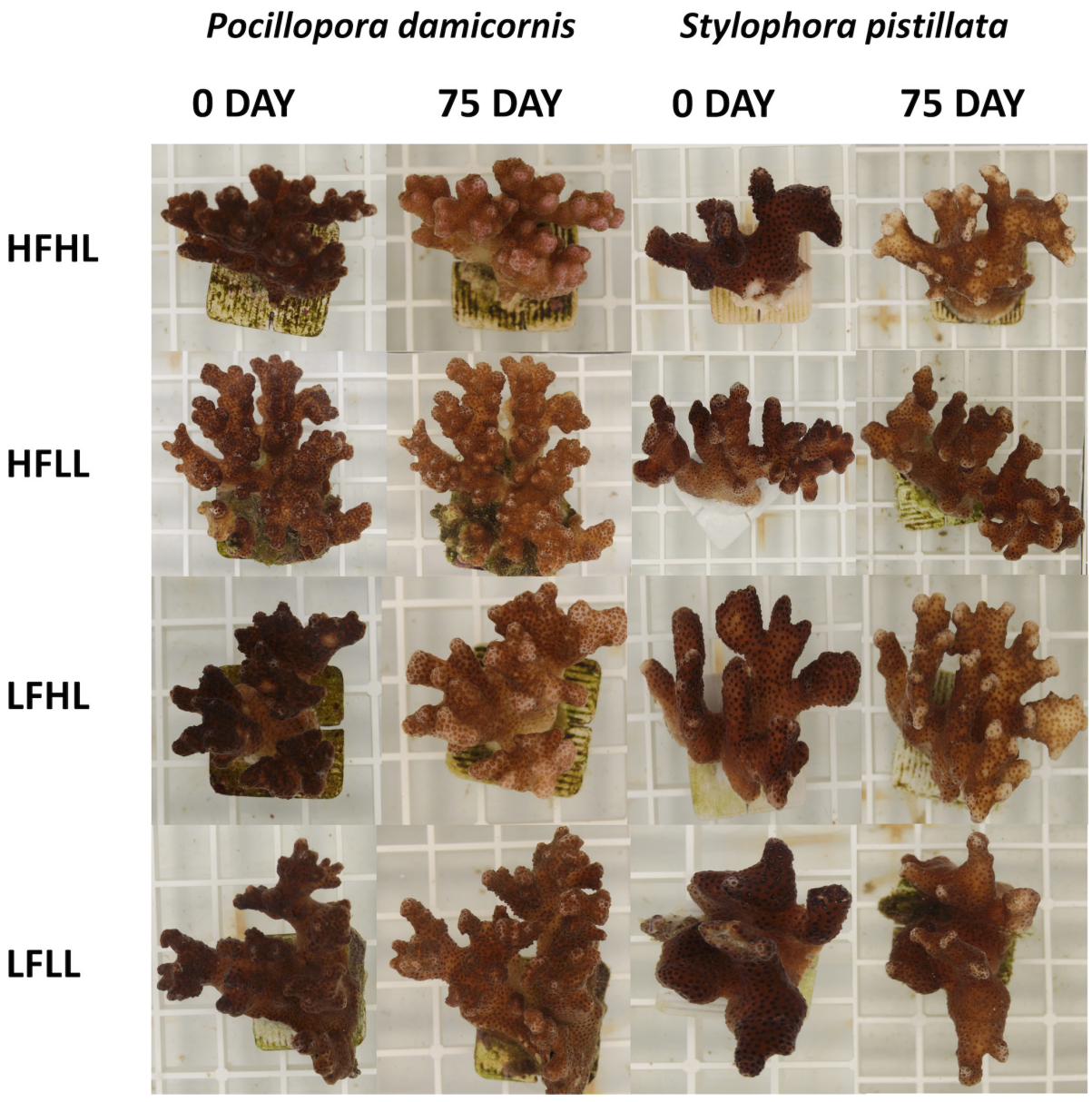

Fig. 2. Photos of *S. pistillata* and *P. damicornis* branches under the different treatments at 0 days and 75 days. HFHL, high feeding regimes with high light; HFLL, high feeding regimes with low light; LFHL, low feeding regimes with high light; LFLL, low feeding regimes with low light.

and returned to their respective suspended positions in the experiment tanks.

Each tank also configured 57 nubbins of *Acropora hemprichii*, 30 nubbins of *P. damicornis*, 10 nubbins of *S. pistillata* at the bottom as a biotope aquarium in each tank, and one *Tripneustes gratilla*, one *Ctenochaetus tominiensis*, one *Holothuria atra*, two *Conomurex luhuanus* as functional organisms to control algae in the tank.

Pulse-Amplitude-Modulation (PAM) Fluorometry

Coral nubbins were dark-adapted for at least 30 min before measurement. The fiber optic cable was placed 2 mm on the vertical stem/stalk of nubbins and recorded the value of Diving-PAM (Germany) for measurement.

Buoyant weight of coral

Short-term coral growth was hard to determine until the development of the buoyant weighing technique by Davies (Spencer Davies 1989). This method does not remove corals from the seawater, and thus prevents the organisms from experiencing measurement-induced stress. The method involves measuring the weight of coral using a barb under a scale which is placed in the seawater.

Buoyant weight was measured before the experiment and every two weeks during the experiment using a scale (Shimadzu, AUX220, Japan) with a jacketed beaker below. Temperature of the seawater in the beaker was stable according to a thermostat (Firstek, B401, Taiwan). The salinity and temperature were converted to density of seawater. Then the scale measurement was converted into the weight of the coral using Eq. (1) below. The specific growth rate (SGR, % day^{-1}) was calculated following Huang et al. (2020) as: $SGR = (\ln(W_f) - \ln(W_i)) / \Delta t \times 100$, where W_i and W_f are the coral fragments' buoyant weights (g) at the beginning and end of the measurement interval, and Δt is the number of days.

Weight of object in air = Weight of object in seawater / $[1- (D_{seawater}-D_{object})]$ (1)

Linear growth of coral

The maximum length, width and height of branches were measured with vernier calipers before the treatment and every four weeks during the treatment. The data were converted into total linear growth using a formula published by Huang (Huang et al. 2020) as total linear growth (mm yr^{-1}) = $(L_f - L_i) \times 365 / \Delta t$, where L is the total linear extension of each nubbin (sum of the maximum branch length + width + height, in mm); L_i and L_f are the initial and final values, and Δt is the number of days between measurements.

Color measurement of coral

Before measuring buoyant weight, the nubbins' base label, branch sides and branch facades were placed in the photo studio (40 × 40 × 40 cm) under consistent light intensity to photograph with a camera (Canon, EOS-650d, Japan). All parameters of the camera were the same for all nubbins and the white balance was also done using a color card (Kodak, Q-13, USA) before photographing.

The photos were analyzed by the dripper tool of Adobe Photoshop CS6 to calculate the red (R), green (G), and blue (B) channel intensities of the RGB color model. The RGB system is like the human visual system which uses three kinds of 8-bit integers (0–255), from full black (0) to full color (255) to represent color intensity.

For RGB analysis we randomly selected 9 nubbins per species per treatment at the last timepoint (total $n = 9$ per group) and analyzed corals' growing point and coenosarc by taking the average of each of three points from the lighter sight of growing point and the brown coenosarc tissue between every polyp.

Color score of coral

Nubbins were placed in a storage box (25 × 16 × 8 cm) with Coral Health Monitoring Chart (Siebeck et al. 2006). There are four color shades on the chart, and each side is divided into a numeric scale of 1 (light) to 6 (dark) points. The change of scale reflects a change in symbiotic algae in corals and also represent the bleaching state of the corals.

Statistical analysis

All analyses were performed within each coral species (no between-species comparisons). For variables measured repeatedly on the same fragments (*e.g.*, linear growth, buoyant weight), we used linear mixed-effects models (LMMs) with fixed effects of light intensity (High/Low), feeding concentration (High/Low), time, and their interactions, and fragment identity as a random effect. For single-value, per-fragment outcomes (*e.g.*, specific growth rate/annual linear growth when summarized to one value per fragment), we used two-way ANOVA with light and feeding as factors. Estimated marginal means and Tukey-adjusted pairwise contrasts were obtained using the *emmeans* package. Significance was set at $\alpha = 0.05$. Analyses were

conducted in R (version 4.3.2) using *lme4*, *lmerTest*, *car*, and *emmeans*.

RESULTS

Pulse-Amplitude-Modulation (PAM) Fluorometry

At the beginning of the experiment, the pulse-amplitude-modulation fluorometry values for the four treatment groups of *S. pistillata* were between 0.75 to 0.8, while the values decreased to 0.71 to 0.73 at 28 days, then increased slowly after 28 days of the experiment. At the end of the experiment, all groups' PAM fluorometry values of each group were higher than 0.6, indicating that the corals were healthy (Fig. 3A). Meanwhile, the values of *P. damicornis* dropped to 0.68 from 0.72 after 56 days of the experiment, but the values of all groups were higher than the health standard of 0.6 (Fig. 3B).

Buoyant weight and linear growth of corals

Across treatments, *S. pistillata* showed numerically higher specific growth rate and annual linear growth rate than *P. damicornis*. Buoyant weight increased across the experimental period in all four treatment groups for both species (Fig. 4). When analyzed as repeated measures, linear mixed-effects models with fragment ID as a random effect detected no main effects of light intensity or feeding concentration and no light with feeding interaction on either buoyant weight or linear extension in either species (all $p > 0.05$). For both species, specific growth rate also did not differ significantly among the four treatment groups (two-way ANOVA; all $p > 0.05$; Fig. 4A–B). When per-fragment linear extension was summarized to total annual linear growth, *S. pistillata* showed significant light with feeding interaction (two-way ANOVA, $p < 0.05$): post-hoc Tukey tests showed the HFHL group had higher total annual linear growth than each of the other three groups (all $p < 0.05$; Fig. 4C). For *P. damicornis*, no main effects or interaction

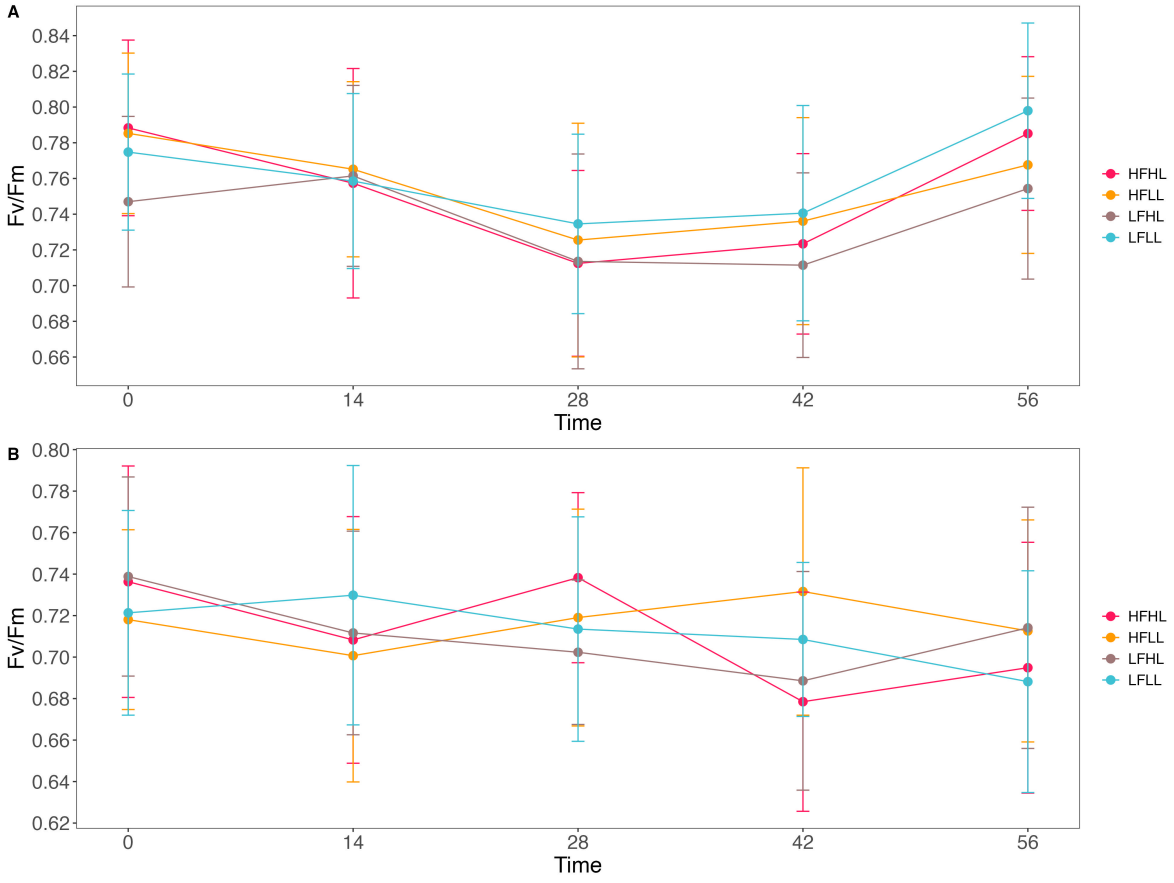

Fig. 3. Time course of maximum quantum yield (Fv/Fm) during the experiment. *S. pistillata* ($n = 72$) (A) and *P. damicornis* ($n = 72$) (B) assigned to four treatments: HFHL (high feeding, high light), HFLL (high feeding, low light), LFHL (low feeding, high light), and LFLL (low feeding, low light). Fv/Fm was measured every 14 days (days 0, 14, 28, 42, 56) after 30-min dark acclimation using a Diving-PAM fluorometer. Points show mean ± SE ($n = 18$ fragments per group); lines connect time points for clarity.

were detected for total annual linear growth and no pairwise differences among groups were found (two-way ANOVA, all $p > 0.05$; Fig. 4D).

Color measurement and color score

In *P. damicornis* at the final time point, the RGB values of the high-light group (HFHL, LFHL) significantly exceeded those of the low-light group (HFLL, LFLL) for both the growing point and coenosarc (two-way ANOVA with Tukey-adjusted pairwise comparisons, $p < 0.05$; Fig. S1). In the case of the *S. pistillata* at the final time point, both feeding concentration and light intensity affected the RGB values, and the RGB values of the growth points in two coral species were higher than those of the coenosarc. In terms of color scores, two coral species remained within the healthy range after each experimental treatment. However, a decreasing trend in color scores was observed as the experiment progressed (Fig. 5A, 5B). At the final time point (Fig. 5C, 5D), color score differed by light: both high-light groups (HFHL, LFHL) were lower than the low-light groups (HFLL, LFLL) (two-way ANOVA with Tukey-adjusted pairwise comparisons, $p < 0.05$) in both species while feeding had no effect within a light level (two-way ANOVA with Tukey-adjusted pairwise comparisons, $p > 0.05$). These results of color score correspond to the results of color measurement, while higher values of RGB mean that coral's color becomes lighter under higher-light treatment.

DISCUSSION

Our study demonstrates that the combined effects of feeding and light intensity influenced coral growth and coloration in species-specific ways. *S. pistillata* exhibited the strongest synergistic response, with the highest specific and linear growth observed in the high-feeding, high-light (HFHL) treatment, whereas *P. damicornis* showed more modest improvements primarily linked to feeding. Despite these growth differences, both species maintained photosynthetic efficiency (Fv/Fm > 0.6) throughout the experiment, indicating that they remained physiologically healthy. Moreover, higher light levels led to lighter tissue coloration in both species, reflecting shifts in symbiont density or pigment concentration.

These findings are broadly consistent with previous studies on the combined roles of feeding and light in coral physiology. Previous study reported that heterotrophic feeding strongly enhanced buoyant weight, specific growth rate, and pigmentation of *P.*

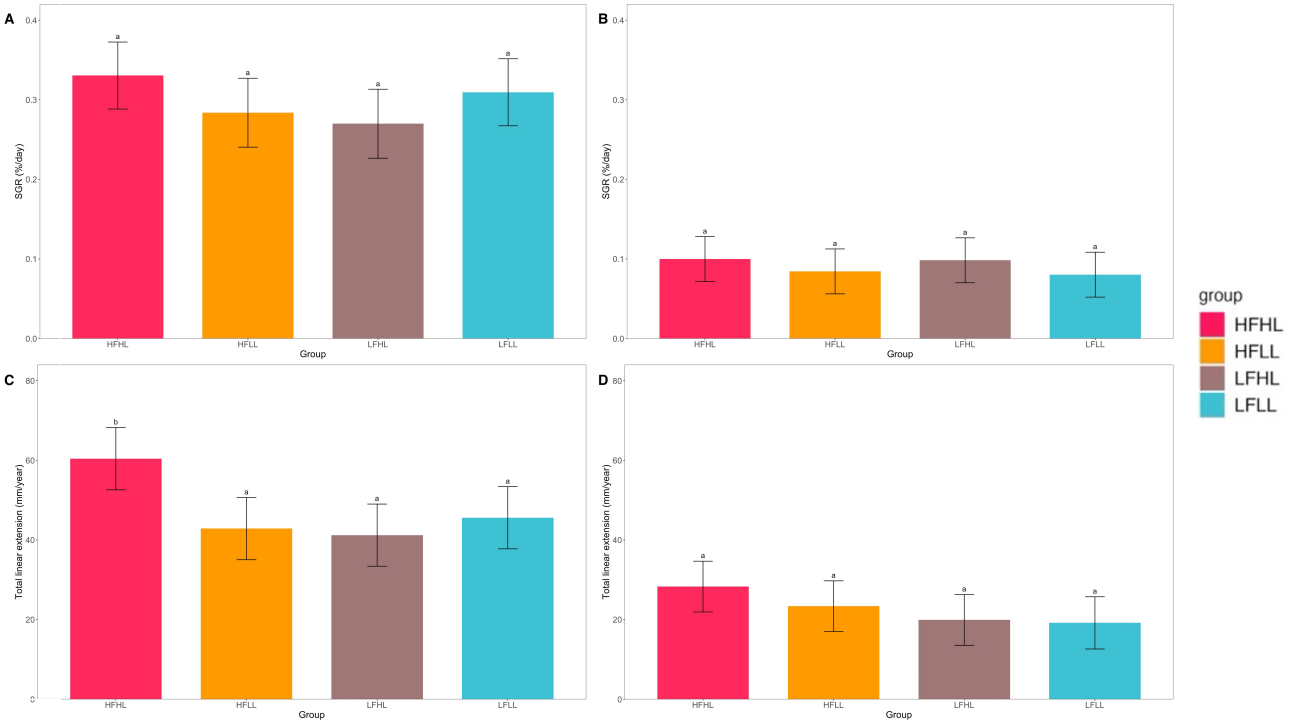

Fig. 4. Specific growth rate and total annual linear growth across treatments. Specific growth rate (% day^{-1}; A–B) and total annual linear growth rate (mm yr^{-1}; C–D) for *S. pistillata* (A, C; $n = 72$) and *P. damicornis* (B, D; $n = 72$) under HFHL, HFLL, LFHL, and LFLL. Bars show mean ± SE ($n = 18$ fragments per group). Different letters indicate significant pairwise differences at $p < 0.05$.

acuta, with the fastest growth occurring under high-light with feeding treatments (Huang et al. 2020). Similarly, a study of *Acropora* spp. demonstrated that light intensity, photoperiod, and spectral composition jointly regulate calcification and photo acclimation (Izumi et al. 2023), highlighting the importance of light as a dominant driver of growth with species-specific responses. In line with these studies, our results underline that feeding universally supports growth, while light primarily governs photo acclimation, with the two factors interacting differently across coral species. Importantly, by comparing two coral species, our study extends these findings by demonstrating that the magnitude of light with feeding interactions is itself species-specific, with *S. pistillata* showing strong synergistic responses while *P. damicornis* adopted a more conservative growth strategy.

We found that the coral color scores of two coral species were lower under high light conditions than under low light conditions. The coral health chart has been used as a coral health indicator based on the color of corals, which represents the abundance of symbiotic algae in the coral (Siebeck et al. 2006). Under high light conditions in natural environments, the colors of stony corals are usually lighter because their symbiotic algae densities are lower (Dubinsky et al. 1984; Falkowski and Dubinsky 1981; Mass et al. 2010). Meanwhile, the concentration of symbiotic algae in *P. damicronis* decreases as light intensity increases (Dobson et al. 2021). Under higher light conditions, symbiotic algae are easily damaged by light, causing them to divide more quickly and resulting in smaller or younger symbiotic algae populations (Dustan 1982; Titlyanov et al. 2001). At the same time, higher values of RGB, indicating lighter colors of coral, were also present in our results. However, coral coloration is not determined solely by symbiont density but also influenced by host- and symbiont-derived pigments (*e.g.*, GFP-like proteins, chromoproteins, chlorophylls) (Mass et al. 2007; Salih et al. 2000) and skeletal light scattering (Smith et al. 2017).

The regulation of growth in corals by autotrophic and heterotrophic feeding is highly complex and species-specific (Osinga et al. 2011). It is widely believed that heterotrophic feeding can provide essential organic compounds that corals cannot obtain from autotrophic feeding, and that can improve autotrophic efficiency (Davies 1991; Ferrier 1991; Muscatine and Porter 1977). For example, supplementation with enriched *A. salina* nauplii has been shown to promote

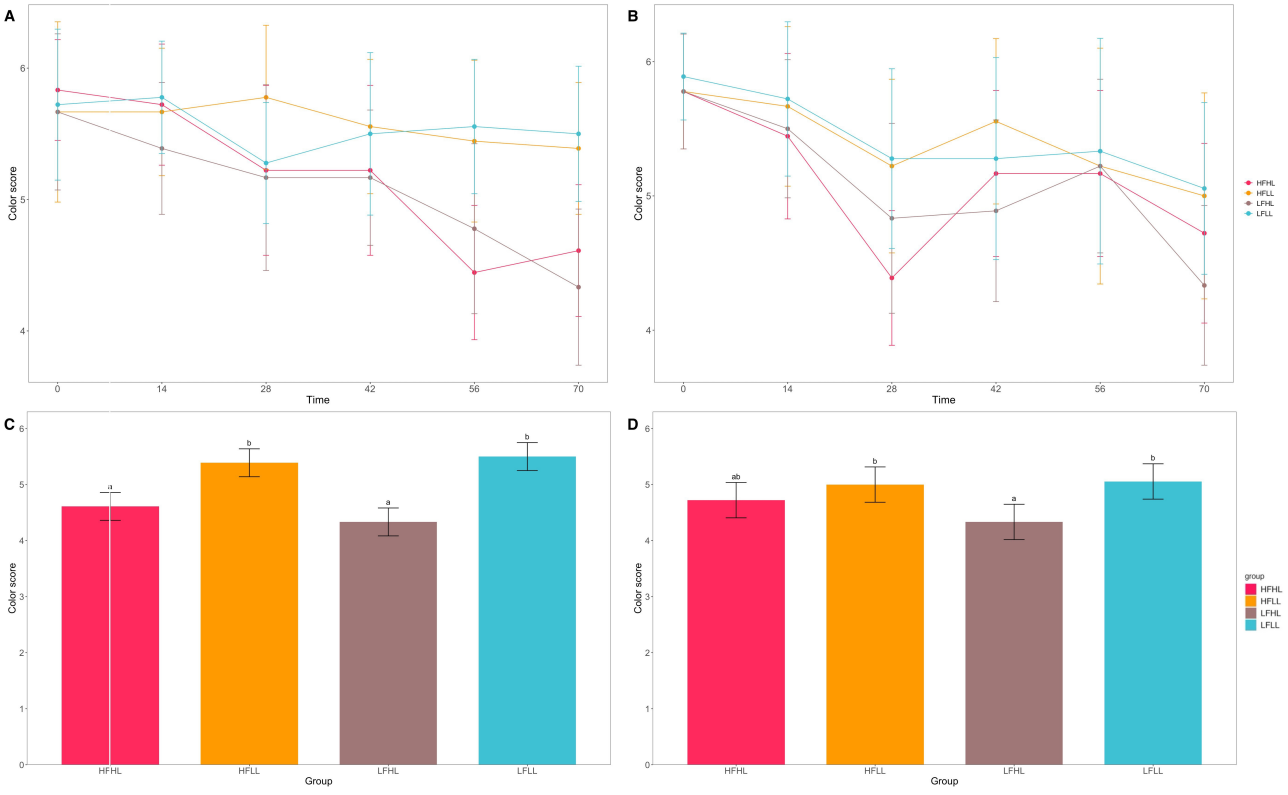

Fig. 5. Time course and endpoint of color score across treatments. The variety of color scores of *S. pistillata* ($n = 72$) and *P. damicornis* ($n = 72$). The variety of color scores in 70 days of *S. pistillata* (A) and *P. damicornis*, (B) measured every 14 days. Last measurement of color score of *S. pistillata* (C) and *P. damicornis* (D). Points/bars show mean ± SE ($n = 18$ fragments per group). Different letters indicate significant pairwise differences at $p < 0.05$.

the growth of *S. pistillata* (Houlbrèque et al. 2003), a pattern also evident in our experiment where feeding treatments increased growth. In contrast, in Dobson's study in 2021, it was found that *P. damicornis* exhibits poor utilization of enriched *A. salina* due to its preference for smaller planktonic prey (300–400 μm). In this study, the *A. salina* offered were approximately 1000 μm in size, which likely limited their nutritional benefit for *P. damicornis*. Moreover, *P. damicornis* is known to rely more heavily on autotrophy, with heterotrophy mainly supporting host maintenance rather than driving rapid growth (Al-Sofyani and Floos 2013; Cunning et al. 2015; Lizcano-Sandoval et al. 2018). Nevertheless, in our experiment, the growth rates in *P. damicornis* under feeding treatments exceeded those reported for wild conspecifics, suggesting that while enriched *A. salina* may not represent the optimal food source, it can still enhance growth relative to natural conditions.

Beyond feeding, light wavelengths and intensity are also crucial factors influencing coral physiology. For instance, blue light can stimulate photosynthesis in corals, promoting coral growth and health as well as adaptive capacity (Wijgerde et al. 2014). Under the blue light, the contraction of coral polyps is most effective (Levy et al. 2016), so in this study, we suggested that feeding under blue light conditions can promote the heterotrophy of corals. Besides, light intensity can cause stress to corals, and the degree of stress varies depending on the coral species. Previous studies have indicated that the lower portion of *S. pistillata* has a higher maximum photosynthetic yield in areas that are not fully illuminated by light, while the upper portion that receives full light exposure has a lower yield (Shick et al. 2011). In this study, under the blue light condition, it was found that the maximum photosynthetic yield of corals subjected to low light with low feeding was higher than that of corals subjected to high light with low feeding, indicating that high light intensity is a form of stress for *S. pistillata*. Other studies have shown that *S. pistillata* subjected to heterotrophic treatment under thermal stress has a higher maximum photosynthetic yield compared to those without feeding (Ferrier-Pagès et al. 2010). Similarly, in our study, although the stressor was high light intensity rather than temperature, we also observed that higher feeding concentrations led to higher maximum photosynthetic yields. This indicates that feeding can help corals mitigate stress and sustain photosynthetic performance under adverse environmental conditions. About *P. damicornis*, this species is known to rely more heavily on autotrophy (Al-Sofyani and Floos 2013; Cunning et al. 2015; Lizcano-Sandoval et al. 2018), which may explain its greater tolerance to high light. Consistent with this, our results showed that feeding did not affect its maximum photosynthetic yield of *P. damicornis* under high-light conditions. However, under low-light conditions, *P. damicornis* relied on heterotrophy to maintain photosynthetic yield, suggesting that the benefit of feeding is more pronounced when light availability is limited. Taken together, our findings suggest that the extent to which feeding supports corals under light stress depends strongly on the coral species identity.

CONCLUSIONS

In this investigation, two common reef-building corals in Taiwan were successfully cultured under different intensities of blue light and feeding concentrations. For *S. pistillata*, a higher growth rate was observed, and it was found that light intensity and feeding amount both influenced the corals' color performance. For *P. damicornis*, there was no significant difference in growth among the different treatment groups, but the light intensity was found to significantly affect the corals' color performance. Therefore, we suggest that adjusting blue light and feeding influences the color of corals and improves their growth and health during the process of coral cultivation. As high-density culture methods can meet the demand for large quantities of corals in the market and reduce the damage caused by wild collection, we believe that our study can contribute to both the artificial cultivation of corals and to coral research and reef restoration efforts.

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and weight measurements. SHY and TYF conceived and designed the experiments, and participated in manuscript writing and interpretation of the results.

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Supplementary materials

Fig. S1. RGB values by species, tissue region, and treatment. Bar plots show mean ± SE of Total (R+G+B), Red (R), Green (G), and Blue (B) values for *P. damicornis* (PD) and *S. pistillata* (SP), separated by tissue region (coenosarc vs. growing point) and treatment group (HFHL, HFLL, LFHL, LFLL). Different letters denote Tukey-adjusted pairwise differences among the four groups within each panel (one-way ANOVA on group; $\alpha = 0.05$). Sample sizes were $n = 9$ fragments per group. (download)

Table S1. Comparison of seawater parameters across tanks. (download)

Table S2. Nutritional composition of the enrichment emulsion (Omega, PACK BOOST Enrichment Diet; Chuan Kuan Enterprise, Taiwan) used to fortify *Artemia nauplii*. (download)