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Optimization of Light Spectrum During Coral Grow-out

Daisy N. Ponce
Nova Southeastern University

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Daisy N. Ponce

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Approved:
Thesis Committee

Committee Chair: Joana Figueiredo, Ph.D.

Committee Member: Nicole D. Fogarty, Ph.D.

Committee Member: D. Abigail Renegar, Ph.D.

NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

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By

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Abstract

Direct and indirect anthropogenic stressors have led to a global decline of coral populations. Coral restoration aims to mitigate this loss and facilitate reef recovery. In particular, the sexual propagation of corals *ex situ* allows for the production and outplant of genetically diverse coral recruits on the reef. However, optimization at *ex situ* coral nurseries is required to scale-up production. This project aims to investigate and develop methods that reduce the duration of grow-out *ex situ* by determining the optimal light spectrum under which to rear for sexual recruits of the tropical scleractinian coral species *Pseudodiploria strigosa* and *P. clivosa*. Newly-settled corals of these species were reared under dim light (<50 μmol photons m^{-2} s^{-1}) and, after 4 weeks, shifted to one of three light spectra: blue-shifted spectrum produced by an LED light with a reef-depth light irradiance, reef depth spectrum produced by an LED light, or near surface depth light spectrum produced by natural sunlight with reef-depth irradiance levels achieved by using shade cloths. The three treatments were replicated in two tanks where survival and growth were quantified weekly from five to fourteen weeks post-settlement. *Pseudodiploria strigosa* demonstrated significantly higher survival and growth than *P. clivosa*, which may be due to their greater size at the time of settlement. Corals under LED lights exhibited faster growth rates than corals exposed to sunlight. The results suggest that light spectrum is an important factor in coral growth, and LED blue-shifted light spectrum may be a more suitable spectrum for coral grow-out 5 weeks after settlement. The manipulation of light spectrum during coral grow-out can reduce the time required at the *ex situ* nursery before outplanting and/or increase the size of the corals available for outplanting, thereby decreasing chances of mortality due to predation and overgrowth.

Keywords: aquaculture, irradiance, coral restoration, *Pseudodiploria*

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Introduction

Reef-building corals are integral architects of an intricate and diverse ecosystem, tropical coral reefs. Healthy coral reefs harbor a rich and abundant variety of fish and benthic invertebrate communities (Fisher et al., 2015; Plaisance et al., 2011). The structural complexity of coral reefs protects coastlines from erosion and damage caused by storms, by acting as a wave energy buffer (Hearn, 1999). Direct and indirect anthropogenic stressors pose challenges to corals by undermining their growth, survival, and population persistence (Côté et al., 2005; Bruno et al., 2007; Sebens et al., 1994; Thangaraj et al., 2019; Wilkinson et al., 1993). Since the 1950s, coral cover has been declining, and predictions indicate that 60% will be lost by the year 2030 (Bruno et al., 2019; Eddy et al., 2018; Hughes et al., 2017). The rapid decline of coral populations globally has led to a reduction of fish diversity and abundance along with a loss of structural complexity and integrity (Bruno et al., 2007; Côté et al., 2005). In regions where reef-building scleractinian corals are in peril, conservation strategies, such as habitat protection and active restoration, have been introduced to mitigate the loss of critical reef sites (Bruno et al., 2007). Restoration accelerates reef recovery and may, in the long term, contribute to increasing resilience to environmental change.

The use of asexual propagation of corals, such as fragmentation, can rapidly increase coral cover, however, it does not directly increase genetic diversity. This mode of propagation involves dividing an existing coral colony into smaller fragments and growing them either in land-based nurseries or ocean nurseries before outplanting them onto targeted reef sites. A single-parent colony can produce a high yield of coral biomass that can be outplanted, thereby aiding in the quick recovery of degraded reefs and promoting the local recruitment of coral species (Montoya-Maya et al., 2016). Despite the advantages of this methodology, the long-term effectiveness of this method may be somewhat limited. Asexual propagation produces genetic clones of the "parent" colony. Consequently, the resulting corals are susceptible to the same stressors that affect the "parent". The replication of genotypes that could lack resistance to stress or disease may result in mortality after outplanting. If these asexually propagated corals survive for at least a few years and demonstrate fecundity, strategically outplanting fragments of a diverse range of parental colonies in closed proximity on a designated "source reef" may

facilitate fertilization success and thus potential recruitment of genetically diverse corals to distant non-restored sites (King et al., 2023).

Sexual propagation of corals, on the other hand, facilitates reef recovery through the direct production of genetically diverse recruits to be outplanted on the reef. Genetic recombination creates variation within a population, potentially leading to the production of some individuals with greater resiliency, which may allow the populations to better adapt to a changing environment. Introducing unique individuals is the initial step toward the developing of a self-sustaining population. Newly outplanted corals are prone to predation from grazing fish; in some areas, nearly all are consumed within the first 30 days of outplanting (Kopecky et al., 2021). There is evidence that coral size significantly affects the likelihood of predation, with larger coral recruits being less predated upon (Christiansen et al., 2008; Kopecky et al., 2021; Koval et al., 2020; Raymundo et al., 2004). Maximizing the size of sexual recruits available for outplanting may increase their probability of surviving and contribute to the persistence of local populations. However, the process of rearing corals from larvae to a size suitable for outplanting is laborious, time-consuming, and costly. The production of larger corals for outplanting should not entail years in an *ex situ* nursery. The expedition of the grow-out stage would be possible through the enhancement of rearing conditions such as the establishment of algal symbionts, light regimes, favorable water quality parameters, and suitable diets. By enhancing these aquaculture methods, the sexual propagation of coral *ex situ* may prove to be a valuable approach to restoring coral populations and promoting genetic resilience and diversity in reef ecosystems.

Corals form a symbiotic relationship with phototrophic dinoflagellates known as zooxanthellae of the family Symbiodiniaceae. These endosymbionts exist as free-living forms within the water column and in sediments but can also form an association with other organisms (Cumbo et al. 2012; Mote et al., 2021). Depending on the species, the acquisition of algal symbionts by corals can occur either through vertical transmission or horizontal transmission (Yamashita et al., 2014; Yamashita et al., 2021), i.e., symbionts are acquired through maternal inheritance or the environment, respectively (Yamashita et al, 2014). The larvae of most scleractinian coral species lack zooxanthellae and uptake Symbiodiniaceae through horizontal transmission (Baird et al. 2009; Schwarz et al.,1999). Corals can establish a relationship with their symbionts through ingestion (Cumbo et al., 2012). The symbionts are phagocytosed into the

coral's cells which provide shelter and nutrients to the symbionts in exchange for energy from photosynthesis (Mote et al., 2021). Once the respiratory needs of the zooxanthellae are met, any surplus photosynthetic products are transported to the coral host to fuel its growth, other metabolic activities, or sexual development (Kuanui et al., 2014; Muscatine and Cernichiari, 1969).

Coral growth, their relationship to zooxanthellae, and the efficiency of photosynthesis, have been demonstrated to be influenced by the intensity of light or the density of photons (Kuanui et al., 2014; Main and Goodbody-Gringley, 2010; Rinkevich and Loya, 1984; Stambler and Dubinsky, 2005). The term light is typically used to describe the portion of the electromagnetic spectrum that is visible, also known as visible light (Osinga et al., 2008). However, the same portion of the spectrum is used by photosynthetic organisms for photosynthesis, which is called Photosynthetically Active Radiation (PAR). PAR and visible light are electromagnetic waves with wavelengths of 400 to 700 nm (Osinga et al., 2008). For corals, appropriate lighting conditions are essential for their physiology and ecology (Cheng et al., 2020). Suitable lighting plays a crucial role in the *ex situ* growth and maintenance of corals since it influences photosynthesis, which provides the energy needed for growth. While the importance of a stable symbiont community in adult scleractinian corals is well documented, the ideal light spectrum to rear newly settled corals remains an area of limited study.

Larvae and recently settled coral raised *ex situ* have been observed to exhibit a heightened sensitivity to high light irradiance (Fourney and Figueiredo, 2017). This may be related to the negative phototactic behavior displayed by larvae, which is then lost in the adult stage. The light irradiance experienced by adult corals varies with water depth and turbidity. For instance, reef-building corals found in very shallow waters are exposed to 2100 μmol photons m^{-2} s^{-1}, while corals at depths of 10m and 18m experience 400 and 25 μmol quanta m^{-2} s^{-1}, respectively (Lesser et al., 2000). While the acquisition of Symbiodiniaceae, occurs in early life stages (Schwarz & Weis, 1999; Weis et. al. 2001), the presence of pigmentation is contingent upon the establishment of an algal symbiont community (Dove et al., 2001; Kawaguti, 1944). Consequently, larvae preferentially settle in dim light areas, such as crevices of a substrate (Babcock and Mundy, 1996; Harrison and Wallace,1990), because they lack the pigmentation and proteins necessary to shield them from the damage caused by solar radiation. High irradiance can disrupt the larvae' ability to settle resulting in oxidative stress which can be detrimental to

their survival; similar responses are observed under high temperatures (Abrego et al., 2012; Putnam et al., 2008).

For sexual recruits raised *ex situ*, light is provided through either artificial light sources or exposure to sunlight in outdoor systems. A variety of artificial light sources are used to imitate natural sunlight to provide the PAR required by zooxanthellae corals in captive settings (Osinga et al., 2008). These artificial light types have been designed to recreate the different wavelengths and intensities of light found in natural marine environments. They are also commonly used by hobbyists to highlight fluorescent pigments. Metal halide lamps and fluorescent lighting have been commonly favored choices, though recent advancements in technology have prompted a swift transition towards LED lighting among hobbyists and researchers alike (Osinga et al., 2008). Each type of artificial light source presents a unique set of advantages and disadvantages that are crucial to consider. Metal halide lamps are singular light sources that offer a scattering effect reminiscent of natural sunlight. Fluorescent lighting creates a diffuse and even light pattern (Osinga et al., 2008). In comparison, LED lighting offers uniform illumination and an extensive range of customization. The manipulation of light spectra can be achieved easily using computer and mobile applications that allow manual adjustment or by changing the Kelvin settings. Kelvin is a unit used to measure the color temperature of light, with lower values indicating warmer light with longer wavelengths, such as red, and higher values indicating cooler, blue light. The use of LED lighting for coral grow-out offers several advantages over other lighting forms, including energy efficiency, customizability, uniformity of illumination, and the ability to adjust light spectra to cater to specific needs. This flexibility is particularly useful for adjusting to the needs of corals at different stages of development.

Juvenile corals initially exhibit greater survival rates under low light levels, such as those not exceeding 20 μmol photons m^{-2} s^{-1} (Abrego et al.,2012; Fourney and Figueiredo, 2017). As corals mature, their light irradiance requirements increase, aligning with the establishment of an algal symbiont community (Krebs et al., 2019; McMahon et al., 2018). This increase in irradiance is closer to the conditions found at reef depth (5-10 m), typically 150-200 μmol photons $m^{-2}s^{-1}$ (Lesser et al., 2000; Sinniger et al., 2019). The optimal light spectrum to rear coral recruits has not yet been investigated. Coral recruits in *ex situ* nurseries have been reared indoors under artificial lights that mimic light irradiance and spectrum typical on the reef (often using the light manufacturer's setting for a specific region) and outdoors under natural light (using shade

cloths to reduce light irradiance). However, rearing corals outdoors exposes corals to an atypical light spectrum. Since the outdoor tanks commonly used in nurseries are relatively shallow, they allow for the presence of light waves that would otherwise be absorbed with greater depth, such as those within the red and orange portions of the light spectrum, while corals in natural ocean settings are exposed to a broad blue spectrum. As zooxanthellae have evolved in tandem with the spectral characteristics of their environments, the growth and health of cultured corals may be negatively impacted by exposure to an "unnatural" light spectrum. Concomitantly, aquarium hobbyists claim that a light spectrum richer in blue (more than what is measured on the reefs) promotes faster growth of corals. The chlorophyll, the primary pigment used in photosynthesis, in Symbiodiniaceae can readily absorb wavelengths of 440nm to 675nm. The wavelength of blue light is between 450 nm to 495nm hence why photosynthesis may be more successful under blue light. Conversely, red lighting appears to yield less favorable results, with corals exposed to blue light displaying higher survival rates and greater Symbiodiniaceae density than those exposed to red light (Kinzie et al., 1984; Wijgerde et al., 2014). Therefore, it is possible that certain lighting regimes promote the highest efficiency for photosynthesis and, in turn, enhance coral growth and health. Nonetheless, the application of blue-shifted light during early grow-out, i.e. the first 12-16 weeks after settlement, is yet to be quantitatively assessed.

This study was designed to evaluate the effects of different light spectra on coral recruits, aiming to assess their impact on both survival and growth during early grow-out. Ultimately, the objective is to scale-up coral production by optimizing the grow-out period of corals, allowing for the cultivation of corals within a reduced timeframe thereby, enhancing the efficacy of coral restoration efforts. Specifically, this research seeks to identify the optimal light spectrum to increase the number and reduce the time required to raise sexually-produced corals in land-based nurseries or increase the size of genetically diverse corals to outplant. By testing different light spectra, this research has the potential to contribute to the success of conservation strategies aimed at preserving invaluable coral reef ecosystems.

Methods

Spawning, larval rearing and settlement

Pseudodiploria strigosa and *P. clivosa* are two abundant species of hermaphroditic broadcast-spawning scleractinian coral found in the Caribbean. These species are anticipated to spawn a week after the full moon in August (Acosta et al., 1997). On August 8, 2022, *P. strigosa* spawned at the Florida Aquarium (FLAQ)'s Center for Conservation in Apollo Beach, Florida, and *P. clivosa* spawned at the University of North Carolina Wilmington (UNCW) on August 17, 2022 (Table S1). After fertilization, larvae were reared until they started rotating (2 days) and were then transported to Nova Southeastern University's Oceanographic Campus in Dania, Florida, in a 0.96 L wide mouth leak-proof plastic bottles. To ensure that no larvae were lost upon lid removal, the bottle was gently agitated to encourage the buoyant larvae at the top to sink before opening the bottle. Next, the larvae were washed using 6 L of filtered artificial seawater to remove any unwanted debris and to change the water they were transported in, thus reducing the chances of bio contamination. After rinsing, the competency of coral larvae were inspected by observing their ability to swim.

Swimming larvae were counted and subsequently placed into rectangular settlement tray and maintained at 28°C using a water bath (Figure 1). Each container's bottom surface was entirely covered with Ocean Wonders Ceramic Coral Frag Tiles (31.75mm × 31.75mm × 7.9mm) which provided a hard substrate for the larvae to settle upon. These tiles were conditioned for six weeks prior to the spawning period by immersing them in tanks that housed adult corals, thereby fostering the growth of a biofilm that induces settlement of larvae. As planulae display a preference for settling in substrate crevices (Harrison and Wallace, 1990; Peterson et al., 2005), the textured side of the tiles was positioned facing upwards within the settlement trays. Furthermore, crustose coralline algae (CCA), a secondary settlement cue, was gathered from tanks containing adult colonies, crushed into a fine dust with a mortar and pestle, and then dispersed onto the textured tiles using a 3 mL pipette. To assess the occurrence of settlement and metamorphosis, tiles from each settlement tray were observed once every 24 hours under an Olympic SZ51 stereoscope.

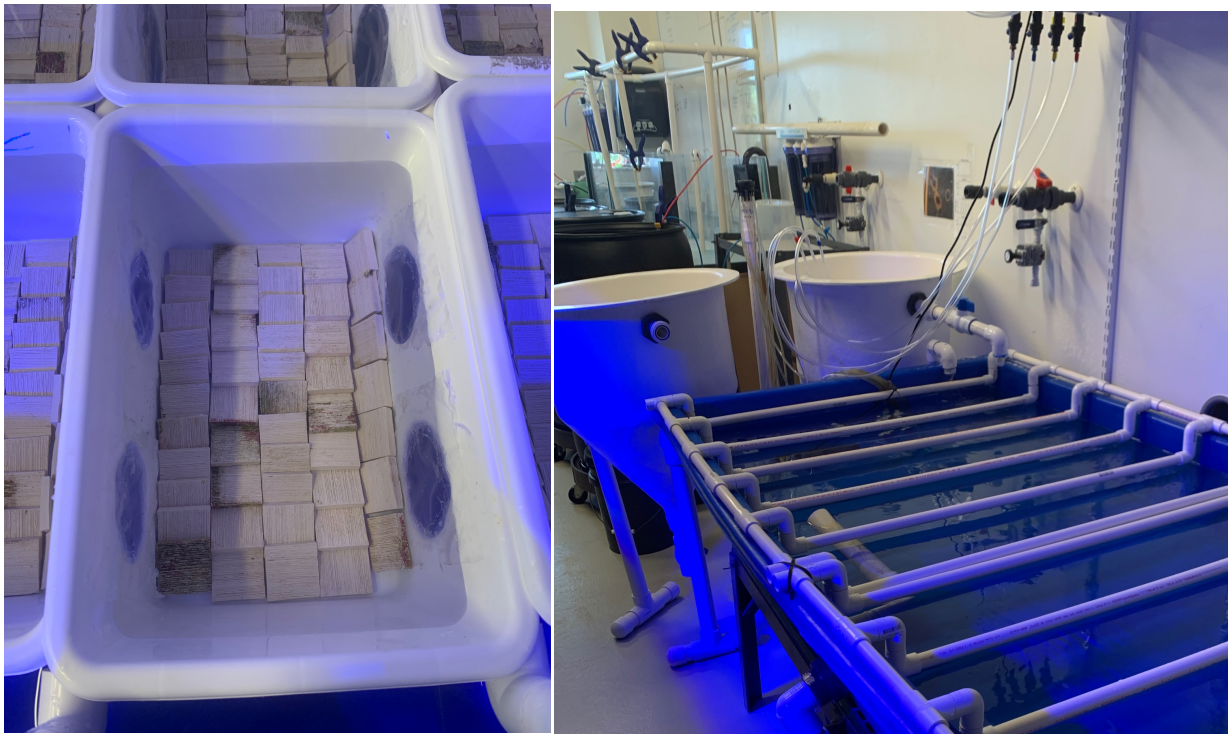

Figure 1. Settlement tray (left) and larval settlement system (right).
The settlement trays used were rectangular plastic bins with circular 10 cm holes cut out along each long side, covered by 105 µm mesh to permit water exchange and prevent larvae loss. Larval settlement system was equipped with PVC racks used to hold the trays in place.

Recruit rearing

After larvae settled and metamorphosed, the tiles were randomly assigned to one of three adult coral colony tanks for a four-week period, allowing for the acquisition of zooxanthellae shed by the adults. Each tank was equipped with a four Radion XR30 G5 PRO LED light fixtures and black polystyrene curtains, which separated the young recruits from the adult counterparts and prevented the excess light from fixtures above the adults, which would be too intense for the recruits. To prevent damage to the young recruits, the irradiance was regulated using the Ecotech Mobius app since they are particularly sensitive to irradiance at this stage. A week after settlement, the LED lights were adjusted to 20 µmol photons m^{-2} s^{-1}, and each week, the PAR was increased to 10 µmol photons m^{-2} s^{-1} until moved to experimental tanks at the start of week 5 (Table 1). PAR was measured using a LI-COR LI-250A Light Meter, positioned at the

same depth as the corals. Each conditioned tile, containing 3-8 recruits, was trimmed to remove any vacant surrounding space using tile nippers. Then, it was adhered to an unconditioned tile marked with a unique identification label that randomly assigned it to a light treatment (Figure 2). One week prior to the placing of the tiles in the outdoor tanks, the recruits on the selected tiles were photographed and mapped (Figure 2).

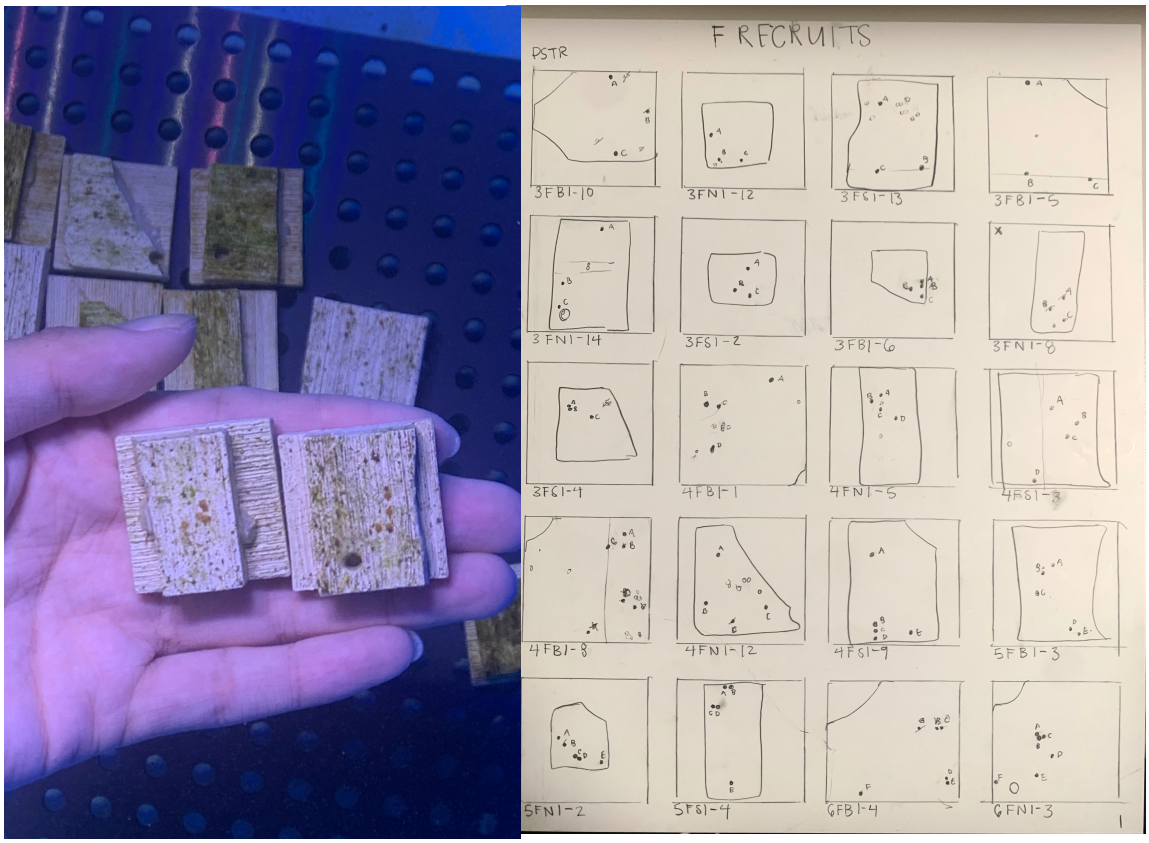

Figure 2. Tile maps
Conditioned tile with recruits were glued on top of an unconditioned tile labeled with an identification label (left). Map drawings of tiles (right) with tile identification, coral position and number of each recruit per tile.

Experimental set up

The investigation spanned a period of nine weeks and was carried out in two distinct, but equally equipped, outdoor water systems (Tanks E and F). Each system comprised a large, recirculating fiberglass tank measuring 3.05 m × 1.07 m × 0.61 m and a sump. The tank raceway, which incorporated a chiller and two titanium heaters, held 911 L of UV sterilized artificial seawater maintained at a temperature of 28°C. Additionally, water flow was evenly distributed throughout the tank using three small submersible water pumps situated at the front, middle, and end of the tank. Water in the sump underwent biological, mechanical and chemical filtration using two bags of bioballs, a protein skimmer (Red Sea RSK 900 Reefer Internal Protein Skimmer), and a carbon filter (PhosBan Reactor 150). Phosphate and alkalinity levels were maintained with the help of a phosphate reactor (PhosBan Reactor 550) and a calcium reactor (AquaMaxx cTech T-2 Calcium Reactor), supplemented by manual adjustments of alkalinity, calcium and magnesium as necessary to maintain healthy level for corals. Water recirculation between the sump and the raceway was achieved using a circulation pump (MRC LP4200 HydroTek). Overhead shade structures provided coverage for the outdoor raceways, which allowed for the draping of blackout curtains and shade cloths.

The coral juveniles were randomly assigned to a treatment group and subjected to a specific light spectrum: natural sunlight with near-surface (tank depth) spectrum (treatment S), LED light mimicking a spectrum at reef depth (approximately 3m) (treatment R), and LED with blue-shifted light spectrum (treatment B). Each tank was divided into three equal sections, with two-thirds of each tank covered by a blackout tarp, necessitating the use of overhead light fixtures (Radion XR30 G5 PRO LED), except for the section allocated to treatment S, which was illuminated naturally but covered with a shade cloth (Figure 3 & 4). The cloth reduced the irradiance but did not alter the light spectrum, which remained consistent with the spectrum present at the tank's depth.

The LED light fixtures hung 53.34 centimeters from the bottom of the tank, providing specifically regimented light sources for treatments B and S. Black shower curtains were installed to partition each section within the tank and prevent bleed-over from neighboring light treatments (Figure S3). LED treatments followed a programmed schedule with the same sun rise/set and moon intensities based on time, date, and location to ensure all treatments followed the same day night schedule. The photosynthetically active radiation (PAR) was increased

incrementally by 10 µmol photons m^{-2} s^{-1} weekly using Ecotech's Mobius app (Table 1). In treatment B, the point intensity slider was raised to achieve increased PAR, while in treatment R, irradiance was increased using a combination of point intensity and Kelvin (Table S3, Figure S2 and S3). However, by ten weeks post- settlement, the maximum threshold for treatment R was reached, preventing the increase in PAR without increasing Kelvin too high (Table S3, Figure S3). Consequently, the PAR had to remain at 110 PAR between weeks ten to fourteen for LED treatments. The irradiance in treatment S was controlled by utilizing shade cloths of varying reduction levels. A shade cloth that reduced irradiance by 75% covered the tanks between weeks five and seven, which was then replaced by a 50% reduction cloth starting from week eight until the end of the experiment. The entire light spectra experiment comprised 480 juvenile coral individuals, with each outdoor tank containing 86 *P. strigosa* and 74 *P. clivosa* juveniles per treatment group. All corals were target-fed a slurry four times a week, consisting of 1.1 grams of Polyp Lab's Reef Roids, 1.1 grams of Aquatic Food's Golden Pearls (5-50µm), 1 mL American Marine Selcon, 9 mL Brightwells Aquatics CoralAminos, and rotifers enriched with RotiGrowTM Plus (~1 hr prior to feeding) diluted in 0.5 L of seawater. The food was prepared in a plastic 3L pitcher and distributed using a 3 mL pipette for targeted feeding for the duration of the study.

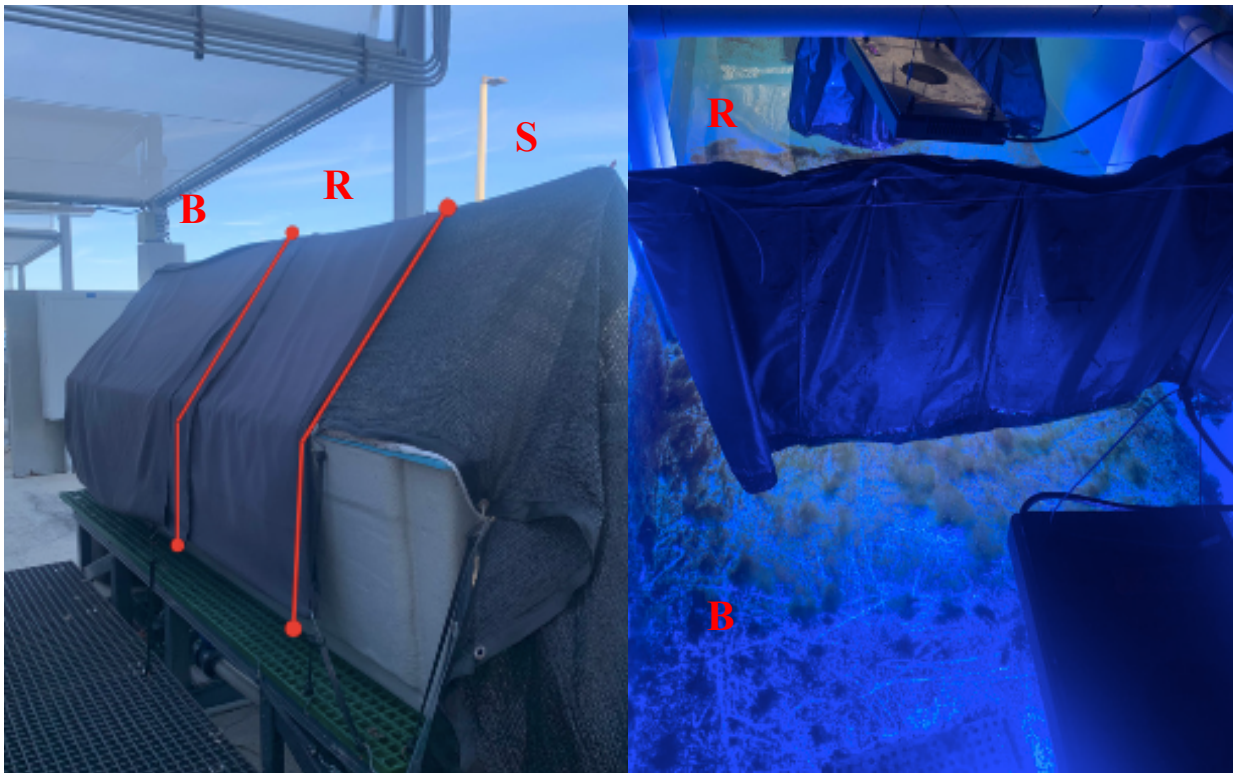

Figure 3. Experimental set up.
One of two outdoor tanks (Tank E, on the left) with a black out tarp covering the LED lights for the Blue-shifted spectrum (B) and Reef-depth spectrum (R), and a shade cloth covering the Sunlight (S) treatment. The set up on the right illustrates the treatment arrangement within each tank, with black shower curtains separating each light treatment to prevent bleed-over. Both tanks follow the same light treatment sequence: Blue-shifted on the inflow side, Reef-depth in the middle, and Sunlight on the outflow side of the tank.

Table 1. LED Photosynthetically active radiation (PAR) regime for weeks 1-14 post- settlement. Corals were exposed to different light treatments between the ages of 5-14 weeks post-settlement.

Week	1	2	3	4	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
PAR (µmol photons m^{-2} s^{-1})	20	30	40	50	60	70	80	90	100	110	110	110	110	110

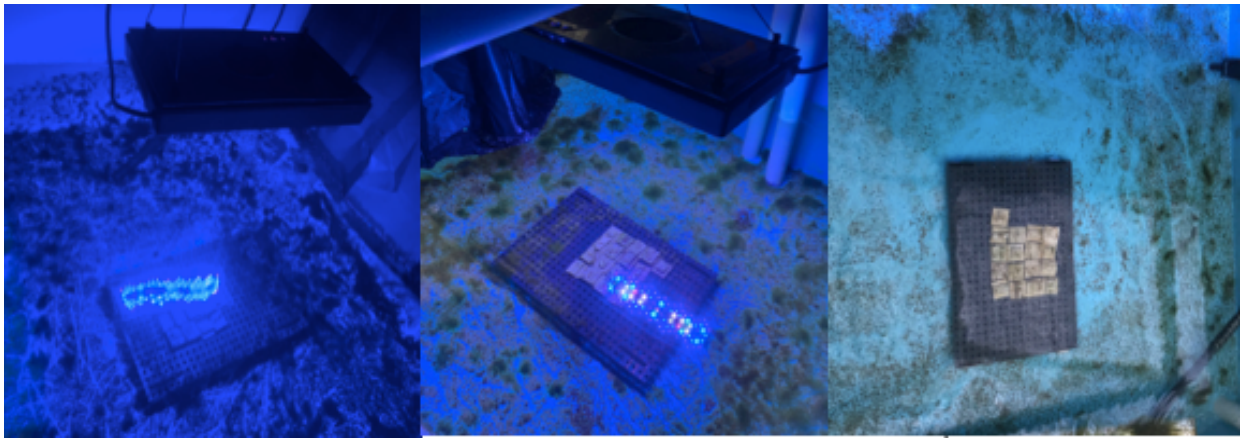

Figure 4. Coral juveniles under to LED blue-shifted (left), LED reef-depth (middle), and sunlight near-surface (right) spectra.
Each rack each held 17 tiles, eight of which contained *P. clivosa* (37 corals total) and nine contained *P. strigosa* corals (43 corals total) per treatment. Images taken at 14-weeks post-settlement on Tank E.

Routine care

To maintain a healthy environment for the corals, temperature and salinity were monitored and recorded daily. To prevent excess algae growth, a cleaning routine was implemented for both the tiles and tanks. The tiles were cleaned once a week between 1-4 weeks post-settlement, and twice a week once placed in outdoor systems. The tiles were transferred into a 12.7 cm x 10.16 cm x 15.24 cm rectangular container placed under an Olympic SZ51 stereoscope, minimizing the risk of puncturing the coral tissue during cleaning. The algae on tiles was removed using an angled eyeliner brush and a needle attached to a syringe. The walls and floor of the outdoor tanks were scraped off using a razor with a plastic blade weekly. In addition to algal removal, a portion of the water in the tank was siphoned out and replaced with new seawater to maintain water quality. The water quality in the tanks, i.e. the levels of calcium, alkalinity, phosphate, ammonium, nitrates, and nitrites, was monitored once a week.

Survivorship and growth measurements

Throughout the 9-week duration of the study, meticulous data on the survival and growth of coral juveniles were recorded weekly. To enable effective observation, tiles were purged of excess algae one day prior to data collection. These tiles were placed in a 12.7 cm x 10.16 cm x 15.24 cm rectangular container containing a 600mL of seawater with the addition of 2 mL of Coral Aminos to promote the expansion and opening of coral juveniles for measurement (Figure 5). Surface area measurements were taken at each time point using the advanced CellSens image analysis program, which allowed for the measurement of each juvenile's surface area, while excluding tentacles (Figure 6). In addition to these measurements, tile maps were employed to systematically monitor and track the fate of individual juveniles, thus enabling insights into the mortality of each species under different treatment conditions.

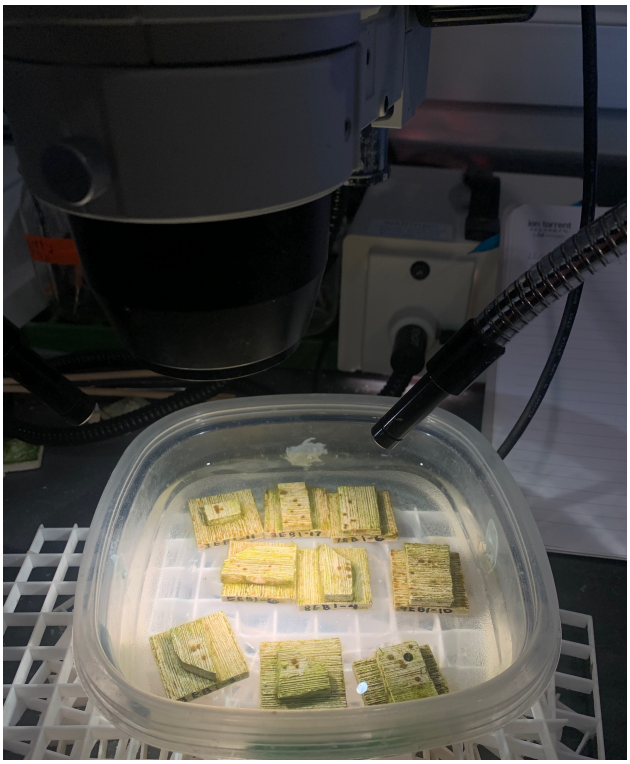

Figure 5. Weekly growth measurement and survivorship assessments.
A plastic container was used to hold tiles under a stereoscope for weekly growth measurements and survival assessments using CellSens software.

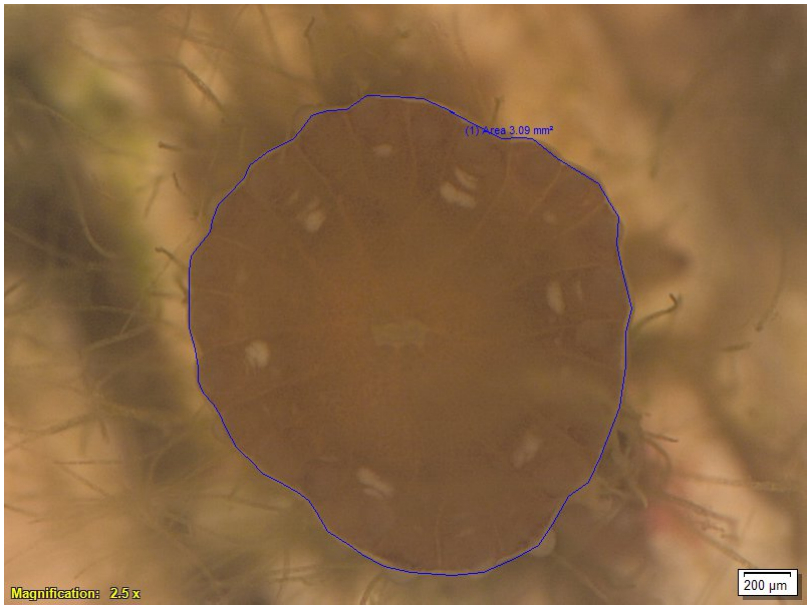

Figure 6. CellSens software
Corals were photographed and traced carefully using measurement tool. Image shows *P. clivosa* at 10 weeks post-settlement. Measurements did not include tentacles.

Data analysis

To investigate the effect of light spectra and species (fixed factors) on survival over time, a survival analysis, specifically a Cox proportional hazard model, was used. The Kaplan-Meier estimator was utilized to generate survival curves and visualize mortality among treatment groups.

A generalized linear mixed effect model (GLMM) with a Gamma distribution and a log link function was used to compare the growth of juvenile corals (surface area over nine weeks) among different light spectra treatments. A GLMM was chosen to account for the effects of random factors, including the random intercept and slope of tile and individual coral, which may cause variation over time. The most complex model was built, including all fixed predictors (light spectrum, species, and time) and their interactions. A backward stepwise method was used to remove non-significant and multicollinear variables and interactions from the model.

All statistical analyses were conducted using R version 3.5.1 (RPubs with code for all analysis in Supplementary Material).

Spectral analysis

Spectral measurements were performed using the Ocean Insight Flame Spectrometer and analyzed with OceanView software. These measurements were conducted in another tank with an identical experimental setup, replicating the exact conditions of each light treatment at 5 and 14 weeks post-settlement. This involved matching the light fixture height and water depth. The Mobius application was utilized to replicate the settings for the LED treatments (Figure S2 & S3), ensuring they aligned with the target PAR levels (Table 1). PAR was measured using a LI-COR LI-250A Light Meter, positioned at the same depth as the spectrometer. To minimize potential interference of sunlight during LED treatment spectral measurements, tests were conducted at night. Sunlight measurements were taken within the same tank, at noon. Shade cloths were strategically employed to adjust sunlight PAR until the sensor's depth reached the target readings. Spectral measurements for each light treatment at 60 PAR and 110 PAR were visualized using R version 3.5.1.

Results

Survival

Survival differed significantly between species (p-value = 6×10^{-3}**)**. *Pseudodiploria strigosa* had higher survival rates compared to *Pseudodiploria clivosa.* Additionally, *P. clivosa* consistently exhibited smaller sizes and higher mortality rates across treatments, in contrast to *P. strigosa*. At 95% confidence level, survival among light spectra treatments could not be considered statistically significant, but since the same exact ranking of light spectra was observed in both species and the p-value for this test (p-value = 0.086) was very close to rejection threshold (0.05) and would be considered significant if a 90% confidence level had been applied. Therefore, we will report the results as at least indicative of a likely trend that requires further investigation. Both species exhibited the highest survival rates when exposed to sunlight at surface depth, with *P. strigosa* displaying 97.7% survival and *P. clivosa* exhibiting 83.8% survival. Following this, the blue-shifted spectrum showed the next highest survival rates, with 84.9% for *P. strigosa* and 83.8% for *P. clivosa*. The reef-depth spectrum exhibited the lowest but still notable survival rates, with *P. strigosa* at 84.9% and *P. clivosa* at 71.6% (Figure 7 and 8).

Table 2. Cox proportional hazards model investigating the effect of light spectrum and species on the survival of individuals over time. The total sample size (n) was 480 with 73 events (deaths) observed. The results show that species had a significant different survival ($p = 6\times10^{-3}$), but light spectrum did not have significantly affected it (p = 0.086).

	coef	exp(coef)	se(coef)	z	Pr(>|z|)
Light spectrum	-0.2463	0.7817	0.1433	-1.719	0.086
Species	-0.6622	0.5157	0.2407	-2.751	**6×10^{-3}**

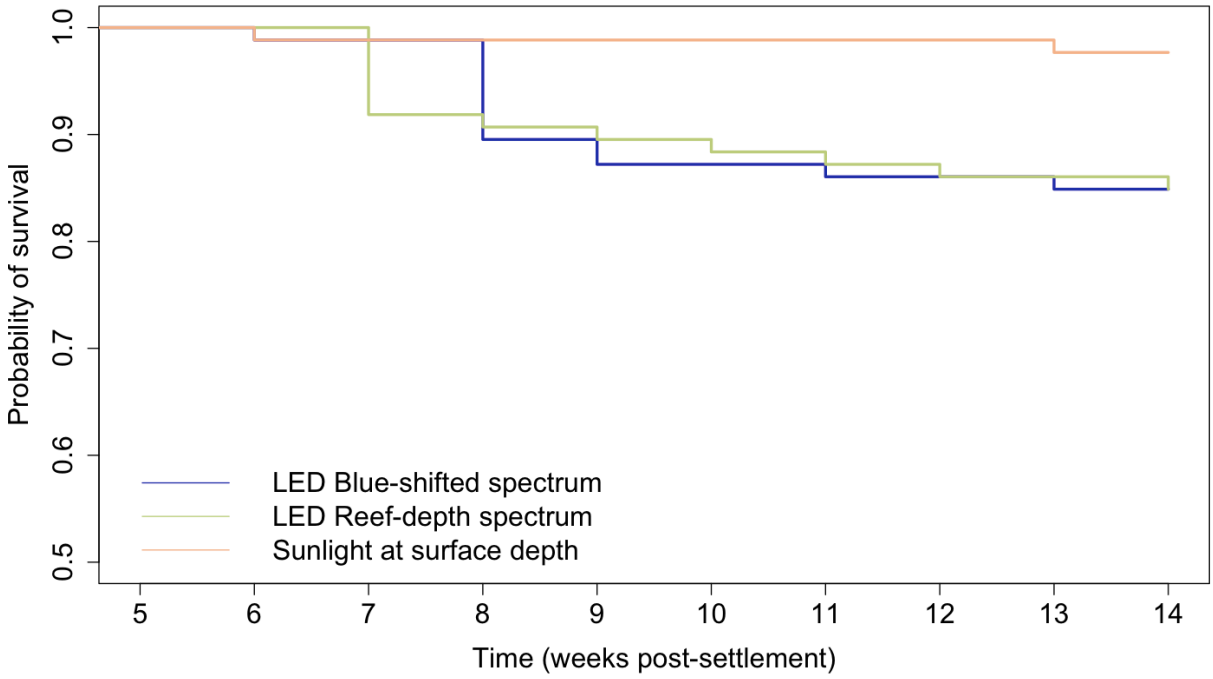

Figure 7. Probability of survival of Pseudodiploria strigosa juveniles over time. Survival curves generated using Kaplan-Meier estimator. Among treatments, thirteen mortalities were observed under Blue-shifted and Reef-depth spectrum, while only two occurred under the Sunlight spectrum at surface depth (n=258).

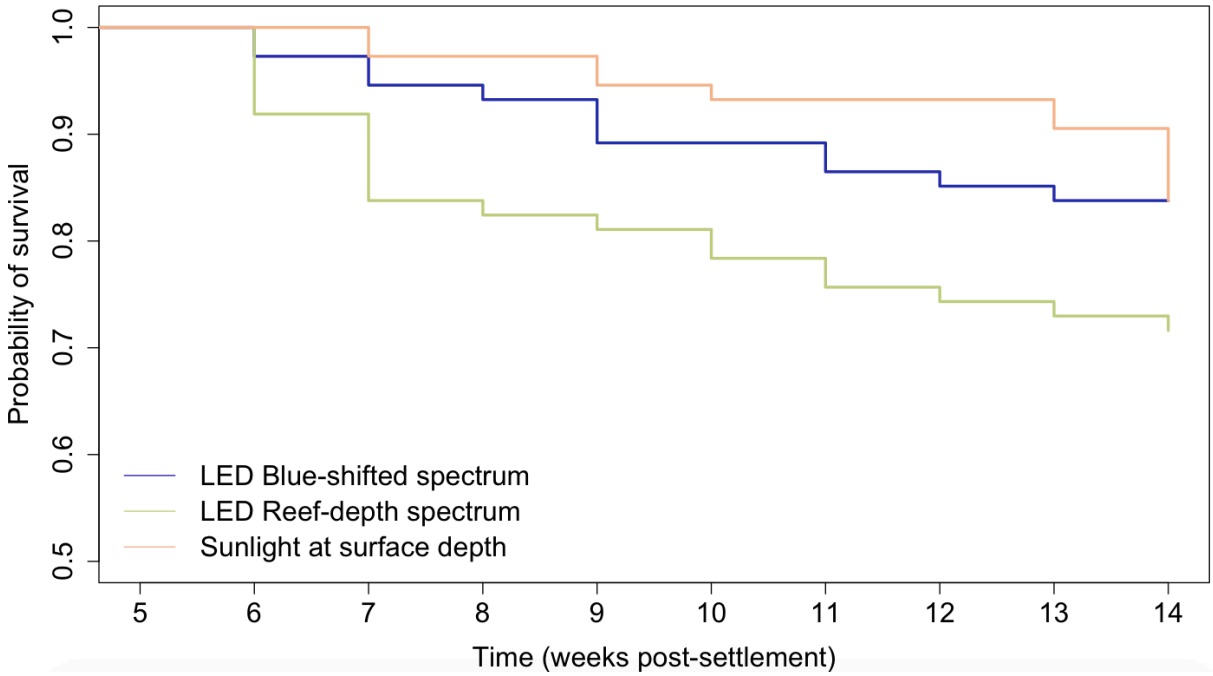

Figure 8. Probability of survival Pseudodiploria clivosa recruits over time.
Survival curves generated using Kaplan-Meier estimator. Among treatments, the Reef-depth spectrum resulted in highest mortality, with twenty-one mortalities. While, twelve mortalities were observed under the Blue-shifted and Sunlight spectrum at surface depth (n=222).

Growth

Coral size varied significantly over time between light spectrum, species, and their interactions. Specifically, the effect of light spectrum treatment on coral surface area is significant (df= 2, p-value: 8.166×10^{-4}), as is the effect of species (df= 1, p-value= 7.116×10^{-8}) and age (df=1, p-value= 3.823×10^{-14}). Furthermore, the interactions between treatment and age (df:2, p-value=2.949×10^{-4}) and species and age (df=1, p-value= 2.769×10^{-5}) were significant (Table 3).

By the end of the experiment (fourteen weeks post-settlement), *P. strigosa* and *P. clivosa* individuals under LED reef-depth light spectrum were the largest (1.22 ±0.80 mm^2 and 1.06 ±0.83 mm^2, respectively) (Figure 9). Those under LED blue-shifted light spectrum were very closely sized (1.33 ±0.84 mm^2 and 0.90 ±0.69 mm^2, respectively), while the smallest were those receiving sunlight near-surface spectrum (0.91 ±0.53 mm^2 and 0.56 ±0.39 mm^2, respectively). However, *P. strigosa* displayed a higher average surface area (0.57± 0.014 mm^2), since the beginning of the experiment, five-weeks post-settlement. While *P. clivosa* tended to be below average (0.48 ±0.018 mm^2) (Figure 9) and, for each species, the average size among treatments also differed. The differences in coral size at the end of the experiment (14 weeks post-settlement) is not indicative of the effect of the light spectrum on growth. Instead, a more accurate indication of their effect can be observed by comparing growth rates, which involved calculating the change in surface area (mm^2) over time (week), represented by the slope of the models. Blue-shifted light spectrum treatment led to significantly faster growth on both species (*P. strigosa:* 4.86×10^{-2} mm^2 $week^{-1}$; *P. clivosa:* 1.47×10^{-2} mm^2 $week^{-1}$) compared to the sunlight at surface depth light spectrum treatment (*P. strigosa:* 2.16×10^{-2} mm^2 $week^{-1}$, *P. clivosa*: -4.08×10^{-3} mm^2 $week^{-1}$, $p = 4.0\times10^{-4}$; $p = 8.0\times10^{-4}$, respectively; Table 4) but were not significantly different from the growth under the reef-depth light spectrum (*P. strigosa:* 4.04×10^{-2} mm^2 $week^{-1}$; *P. clivosa:* 7.43×10^{-3} $mm^2 week^{-1}$, p=0.4880 and p=0.4880 respectively)(Figure 10).

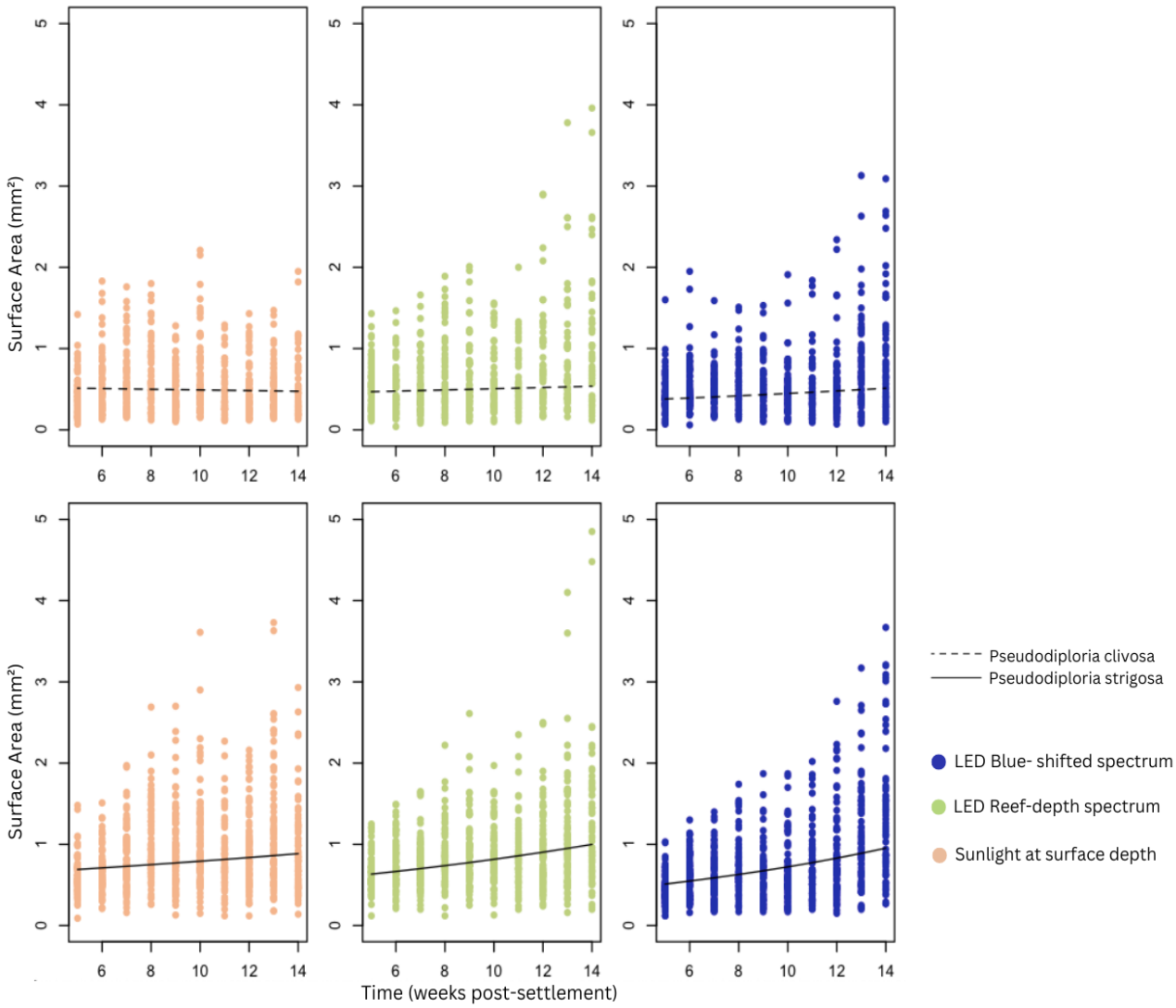

Figure 9. Surface area (mm^2) of corals over time for Pseudodiploria clivosa (top row) and Pseudodiploria strigosa (bottom row) under different light spectrum treatments.
Dots represent the observations and the line represents the best fit model.

Table 3. Analysis of Deviance Table (Type II Wald chi-square tests) of the simplified model. An ANOVA was performed on the Generalized Linear Mixed Model used to analyze growth of corals over time. All predictors had a significant effect on growth.

	Chisq	**Df**	**Pr(>Chisq)**
Treatment	14.221	2	8.166×10^{-4}
Species	29.033	1	7.116×10^{-8}
Time	57.258	1	3.823×10^{-14}
Treatment: Time	16.258	2	2.949×10^{-4}
Species: Time	17.570	1	2.769×10^{-5}

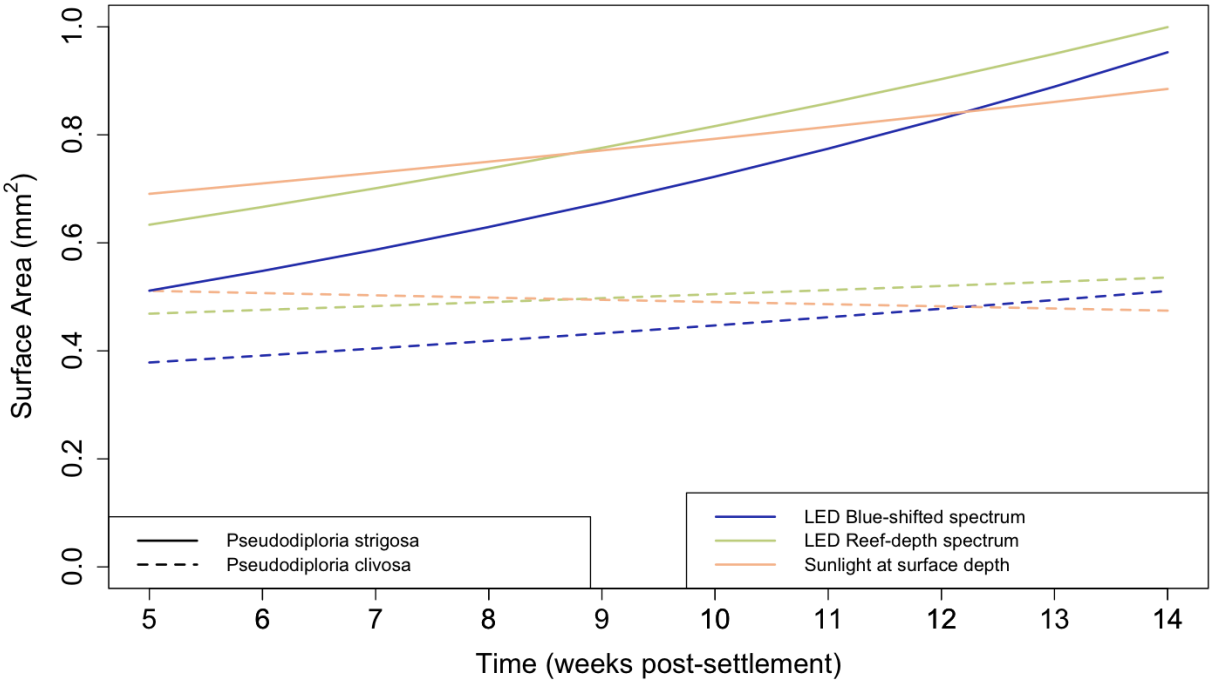

Figure 10. Predictive Size model.
Generalized linear mixed effects model used to predict the surface area of *P. strigosa* and *P. clivosa* from ages 5- 14 weeks post-settlement under various light spectra.

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Table 4. Pairwise comparison of the effects of light spectrum on the growth of P. clivosa and P. strigosa.

This output is the result of running a pairwise comparison *using `emmeans` R package* of the effects of three different treatments (LED blue-shifted spectrum, LED reef-depth spectrum, and sunlight at surface spectrum) on two different species (*P. clivosa* and *P. strigosa*). Contrast that shows significant differences between the treatment and species pairing are emphasized with bolded *p*-values. Positive estimate values signify that the first paring exhibits a larger size relative to the second pairing, whereas negative values indicate that the second factor surpasses the first pairing in size.

contrast	estimate	SE	df	t.ratio	p-value
Blue-shifted *P. clivosa* – Reef-depth *P. clivosa*	0.01857	0.01052	4345	1.766	0.4880
Blue- shifted *P. clivosa* - Sunlight *P. clivosa*	0.04159	0.01035	4345	4.018	**0.0008**
Reef-depth *P. clivosa* – Sunlight *P. clivosa*	0.02302	0.01047	4345	2.199	0.2383
Blue-shifted *P. strigosa* - Sunlight *P. strigosa*	0.04159	0.01035	4345	4.018	**0.0008**
Blue-shifted *P. strigosa* - Reef-depth *P. strigosa*	0.01857	0.01052	4345	1.766	0.4880
Reef-depth *P. strigosa* - Sunlight *P. strigosa*	0.02302	0.01047	4345	2.199	0.2383
Blue-shifted *P. clivosa* – Blue-shifted *P. strigosa*	-0.03584	0.00855	4345	-4.190	**0.0004**
Reef-depth *P. clivosa* – Reef-depth *P. strigosa*	-0.03584	0.00855	4345	-4.190	**0.0004**
Sunlight *P. clivosa* - Sunlight *P. strigosa*	-0.03584	0.00855	4345	-4.190	**0.0004**

Discussion

Manipulating light spectrum allows optimization of the grow-out of juvenile corals. Corals under sunlight at surface depth exhibited higher survival but grew slower indicating a potential trade-off between survival and growth under a light environment in which photosynthetically active radiation (PAR) naturally fluctuates. Corals exposed to LED blue-shifted light spectrum and LED reef-depth spectrum exhibited faster growth during grow-out. Recruits of the species *P. clivosa* had a smaller initial size and experienced significantly higher mortality rates during grow-out compared to *P. strigosa*, suggesting a potential size advantage for survival between species.

Corals grown under LED lights had, on average, faster growth rates than corals grown under sunlight. Both reef-depth light spectrum and blue-shifted light spectrum demonstrated comparable effects on coral growth throughout the study. The LED lights were programmed to replicate certain environmental light parameters that the corals under sunlight experienced specifically, the same photoperiod. This replication included a gradual ramping up of light intensity from morning to peak sun and corresponding decrease from afternoon to sunset. The lighting schedule also considered moonlight, adjusting its intensity per the current phase of the moon. However, the uninterrupted and constant irradiance provided by the LED lights during the daytime offers them greater stability and an advantage over corals exposed to sunlight. The LED lights closely adhered to the intended target irradiance levels for each subsequent week (Table 1), a consistency that shade cloths could not achieve (Table S2). Weekly PAR readings (Table S2) revealed that corals exposed to natural sunlight experienced greater changes in irradiance. These fluctuations can be attributed to various influencing factors such as cloud cover, shading from the nearby building, or even the tank walls at specific times of the day. Such variations in light availability impact the energy supply accessible to corals and can potentially induce stress. In contrast, an environment with consistent irradiance enables corals to optimize their energy acquisition and allocation strategies, maintain their symbiotic relationships, and reduce stress, thereby facilitating growth and calcification over time. Consequently, the stability provided by LED lights, characterized by precise and consistent irradiance in the daytime, created a more favorable condition for growth and support for metabolic activities, in contrast to the fluctuating light conditions experienced by corals under sunlight.

The LED blue-shifted spectrum promoted a significantly higher growth rate in corals compared to those exposed to sunlight. Corals are adapted to utilize the available light in their environment, particularly blue light, which can penetrate deeper into the water column compared to other visible colors (Mass et al., 2010). Chlorophyll a, the primary photosynthetic pigment of the coral symbiont, zooxanthellae, exhibits its highest absorption peak within a large part of the blue region of the light spectrum (Szabó et al., 2014), highlighting its critical role in driving biochemical reactions (Cheng et al., 2020; Ralph et al., 2004; Szabó et al., 2014; Wangpraseurt et al., 2019;). Blue light has also been demonstrated to increase zooxanthellae density, chlorophyll a content, photosynthesis, and calcification rates, which all contribute to coral growth (Cohen et al., 2015; D'Angelo et al., 2008; Kinzie et al. 1984; Wijgerde et al., 2014;). The influence of blue light has been shown to be particularly important for zooxanthellae, specifically by influencing photosynthesis (Cohen et al., 2015; D'Angelo et al., 2008; Kinzie et al. 1984; Kinzie et al. 1987; Izumi et al., 2023; Wijgerde et al.,2014). This intricate relationship between coral host and their photosynthetic symbionts is a crucial determinant of coral growth and likely underlies the observed growth-promoting effects of the blue-shifted light spectrum (Cohen et al., 2015; D'Angelo et al., 2008; Kinzie et al. 1984; Izumi et al., 2023; Wijgerde et al.,2014). In comparison, the sunlight spectrum at tank depth exposes corals with higher intensity red wavelengths (Figure S5 and Figure S6), which are not commonly experienced at reef-depth (5-10 m). The rapid attenuation of red light within the water column occurs at an approximate depth range of 1-5 m (Osinga et al., 2004). Chlorophyll a can absorb red light and utilize it for photosynthesis (Wijgerde et al., 2014), potentially contributing to the promotion of coral health and growth by facilitating the production of certain pigments and protective compounds. However, excessive quantities of red light can yield adverse effects such as decreased rates of zooxanthellae reproduction, repression of chlorophyll a synthesis, and instances of bleaching and necrosis (Cheng et al., 2020; Kinzie et al. 1984; Kinzie et al. 1987; Wang et al., 2008; Wijgerde et al., 2014). The differential growth observed between corals exposed to sunlight and those under LED treatments may be attributed to the higher abundance of red, orange, and green wavelengths which may repress survival and growth (Kinzie et al. 1984; Wang et al., 2008; Wijgerde et al., 2014). Conversely, corals exposed to a light spectrum with a higher proportion of shorter wavelengths, such as the blue-shifted spectrum, exhibited faster growth over the span of nine weeks. Growth rate, as measured by the slope of surface area over time, is a key indicator

of coral growth, with a steeper slope indicating faster growth. Furthermore, the reef-depth light spectrum treatment may be a viable alternative to near surface sunlight for growth as it includes more blue wavelengths and fewer red and green. The potential trade-off between energy allocation towards growth and survival should be considered as well. For instance, a coral must balance the energetic demands of building their skeletons and tissue, which promote growth, with the need to maintain basic physiological functions, defense, or adaptation, which are crucial to survival. In this context, the type of light environment that corals are exposed to can have an impact on their energy allocation patterns.

Corals under sunlight at surface depth were observed to be darker and smaller than those exposed to the LED blue-shifted spectrum (Figure S1). The adaptive response of corals to their environment involves the regulation of zooxanthellae types and quantities they harbor (Falkowski et al., 1984; Hoogenboom et al., 2012; Levy et al., 2003; Tagliafico et al., 2022). In habitats characterized by reduced light, such as shaded or mesophotic environments, corals tend to have higher zooxanthellae densities compared to those in well-lit areas to enhance light absorption (Titlyanov, 1991). However, self-shading also serves as a response to high light levels and offers UV protection (Roth et al., 1988). The observed changes in pigmentation may potentially be attributed to stress induced by low or high UV radiation, or fluctuation between the two. Furthermore, the heightened intensities of red light within the sunlight spectrum may have imposed additional stress. The compounds produced by corals, apart from primary metabolites which are involved in essential processes such as photosynthesis, respiration, and nutrient uptake (Ferrier-Pages et al., 2010; Suggett et al., 2017; Wangpraseurt et al., 2019), play additional roles that offer benefits the organism. These benefits include defense against predators, competition for resources, or adaptation to environmental stressors (Bayer et al., 2012). These compounds, referred to as secondary metabolites, serves functions that are not directly involved in the primary metabolic process. Therefore, it is plausible that the corals under sunlight may have been allocating their energy resources toward the maintenance of their symbionts as an adaptation to their light environment, as a survival strategy rather than allocating energy towards growth. This energy allocation pattern may explain the observed lower growth rates in the sunlight treatment but higher survival rates compared to the other LED treatments, albeit not significant. To enhance the comprehensiveness of this study, evaluating coral pigmentation, quantification of Zooxanthellae per coral cell, and conducting more frequent PAR

measurements (specifically in the sunlight at surface depth treatment) would have provided valuable in evaluating health, identifying stress thereby facilitating a deeper exploration of the trade-offs between survival and growth dynamics.

Interspecific differences in survival and growth of coral recruits were observed, with *P. strigosa* exhibiting a larger size average at settlement, potentially providing them an advantage (Ligson et. al., 2022). While *P. strigosa* survived more than *P. clivosa* it was uncertain whether this was due to genetic advantages, size advantage, or other factors. A genetic advantage would suggest that *P. strigosa* recruits are better adapted to the aquarium environment and may possess genetic traits that are specific to the species or genotype of the *P. strigosa* larvae in this study. These traits could allow them to cope better with stress than *P. clivosa*. A size advantage would indicate the relationship between size, energy content, and food capture could have provided large recruits a competitive advantage over smaller ones. Similar to larvae, larger coral recruits typically possess higher lipid energy reserves, allowing them to better withstand and cope with challenges from environmental stressors (Richmond & Hunter, 1990; Wiesner & Lasker, 2017). Although larger corals may possess more energy, they also come with potential physiological costs. For example, larger corals may have increased respiratory and energy demands for tissue regeneration and calcification (Keister, 2023) but this could be compensated by better feeding ability. In addition, the origin of the larvae used may have influenced their health and development, as the health of the newly settled coral is closely tied to the conditions experienced as larvae and the health of the parental colonies (Hartmann et al., 2017; Richmond et al., 2018). Diet plays a role in this relationship, as corals accumulate energy reserves through photosynthesis and nutrient uptake prior to spawning. Providing a diet that supports the production of viable gametes containing ample lipid reserves is vital for the early development of larvae. The transportation of larvae from the Florida Aquarium (FLAQ) to the Oceanographic Campus (NSU), with a travel time of 4 hours, and from the University of North Carolina (UNCW) via priority one-day shipping may have introduced varying stress levels to the larvae. *P. clivosa* larvae from UNCW, experiencing a prolonged travel time, might have incurred higher energy expenditure during the larval stage in comparison to *P. strigosa* larvae from FLAQ. Stressed larvae generally exhibit reduced survival rates compared to unstressed individuals, and increased vulnerability during this phase can lead to higher mortality rates (Hughes et al., 2019; Ross et al., 2013). Additionally, the *P. clivosa* larvae were four days older than *P.* strigosa (Table

S1) and the transportation-induced delay in settlement prolonged the period of stress during which their energy reserves are depleting (Graham et al., 2013). These stressors can have latent repercussions, such as growth impairment, persisting throughout the life of the corals by depleting energy reserves and resulting in reduced growth rates. Growth impairments can impact the corals' ability to effectively compete for resources (Ritson-Williams et al., 2016; Ross et. al., 2013). In summary, the observed differences in survival and growth between coral species can be influenced by a combination of genetic factors, size advantages, energy reserves, larval health, and stress. These factors collectively shape the trajectories of coral recruits and have implication for their long-term survival and resilience in dynamic ecosystems.

Differential algal growth between treatments was expected to impact coral survival and growth as the rapid accumulation of algae was observed on tiles, racks, and tank walls, specifically under the LED reef-depth light spectrum (Figure S4) and blue-shifted spectrum, especially the latter. While blue-shifted spectra are produced faster coral growth, algae also exhibited accelerated growth rates. This could be attributed to the consistent PAR levels maintained under LED treatments, which inadvertently promoted algal growth. To mitigate the effects of algal overgrowth, biweekly tile cleaning, and weekly tank maintenance were deemed necessary to prevent algal smothering, which can impede coral survivorship. It is worth considering that accumulated algae on tiles beneath the LED lights may result extended cleaning time, potentially leading to more frequent occurrences of acute shock over time when transferring corals out of their holding aquarium or during the process of algal removal. However, the exact effects of such conditions are poorly explored. Acknowledging the impact of environmental conditions on coral recruits' physiology and immune system, including the presence of algae, is essential. These conditions could potentially alter growth rates and reduced survivorship (Thompson et al., 2014). Algal overgrowth poses a dual threat to corals, as it competes for space and nutrients, while also contributing to degraded water quality (Bellwood et al., 2004; Brown et al., 2018). The application of LED lights to accelerate coral grow-out must, therefore, be accompanied by a methodical cleaning regimen to avoid algal overgrowth-induced mortality and competition. These findings also highlight the trade-off between fast coral growth and maintenance requirements and raise important questions about the feasibility and efficiency of optimizing grow-out for reproduction. In this study, no herbivores such as snails and urchins

were introduced to assist with algae control. Future research should explore strategies, such as the introduction of herbivores, to mitigate the labor costs associated with faster growth.

This study represents a novel contribution to the field of coral research, as it is the first to investigate the impact of light spectrum on the survival and growth of juvenile coral whereas, previous studies focused on the effect of irradiance and spectra on adult coral (Abrego et al., 2012; Cheng et al., 2020; Cohen et al., 2015; D'Angelo et al., 2008; Dove et al., 2001; Izumi et al., 2023; Kinzie et al., 1984; Krebs et al., 2019; Osinga et al., 2008; Wijgerde et al., 2014). The outcomes of this study can be utilized to promote the survival and growth of corals during grow-out and possess important implications for the conservation and restoration of coral reefs. While blue light was found to be the most effective in promoting growth, it is critical to consider other factors, such as survivorship, when designing coral culture systems or restoring coral reefs. In other words, prioritizing growth rate alone may not always result in the most successful or sustainable outcomes, if other factors, such as algal overgrowth, are neglected. Further research is also needed to fully comprehend the underlying mechanisms behind these results, such as the interaction between symbiont densities and light treatment. Thus, all factors that can affect coral health and survival must be considered when making such decisions. By identifying the most effective light treatment for promoting coral growth and survival, this research offers valuable insights that can be used to guide the design of coral culture systems and coral reef restoration efforts.

Supplementary Material

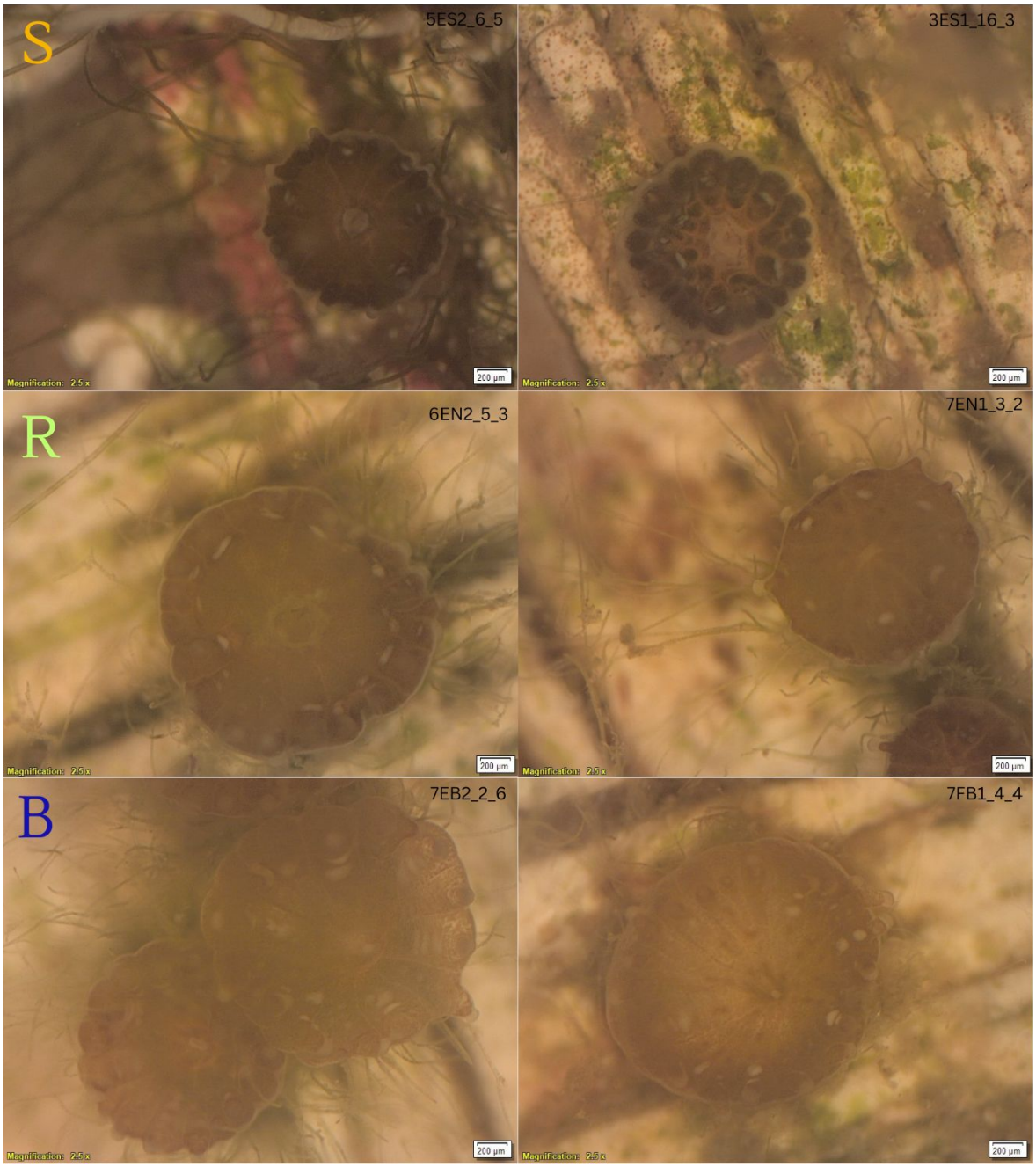

Figure S1. Microscopic images of corals under different lights treatments at fourteen weeks post-settlement.
The top row (S) show corals exposed to sunlight at surface-depth, the middle row (R) shows corals exposed to LED reef-depth light spectrum treatment (11,100 Kelvin), and the bottom row shows corals in the LED blue- shifted light spectrum treatment (20,000 Kelvin). All images are shown at the same scale (200 um) and includes three individuals of each coral species, *P. strigosa* (right column) and *P. clivosa* (left column).

Table S1. Spawning and settlement details.
P. strigosa settled 40 hours after spawning and *P. clivosa* recruits settled 87 hours after spawning.

	LOCATION	**SPAWNING DATE**	**SETTLEMENT DATE**
P. STRIGOSA	Florida Aquarium's Center for Conservation (Apollo Beach, Florida)	6:45PM on 8/20/2022	8/22/2022
P. CLIVOSA	University of North Carolina Wilmington	12:00AM on 8/17/2022	8/20/2022

Table S2. Irradiance recordings during experimental weeks (5-14).

Age of coral (weeks post-settlement)	**TANK**	**PAR/treatment**		
		Blue-shifted	**Reef-depth**	**Sunlight**
5	E	61	61	50
	F	62	61	75
6	E	73	73	65
	F	71	73	80
7	E	80	79	99
	F	79	79	105
8	E	90	90	40
	F	90	90	59
9	E	103	99	98
	F	105	100	101
10	E	110	108	78
	F	109	112	93
11	E	110	108	115
	F	109	112	107
12	E	110	108	101
	F	109	112	115
13	E	110	108	95
	F	109	112	120
14	E	110	108	80
	F	109	112	93

Table S3. Kelvin recordings during experimental weeks (5-14) for LED light treatments.

Age (weeks post-settlement)	**LED Spectrum Settings (Kelvin)**	
	Reef-depth	Blue-shifted
5	7,000K	20,000K
6	8,000K	20,000K
7	8,300K	20,000K
8	9,500K	20,000K
9	11,000K	20,000K
10	11,100K	20,000K
11	11,100K	20,000K
12	11,100K	20,000K
13	11,100K	20,000K
14	11,100K	20,000K

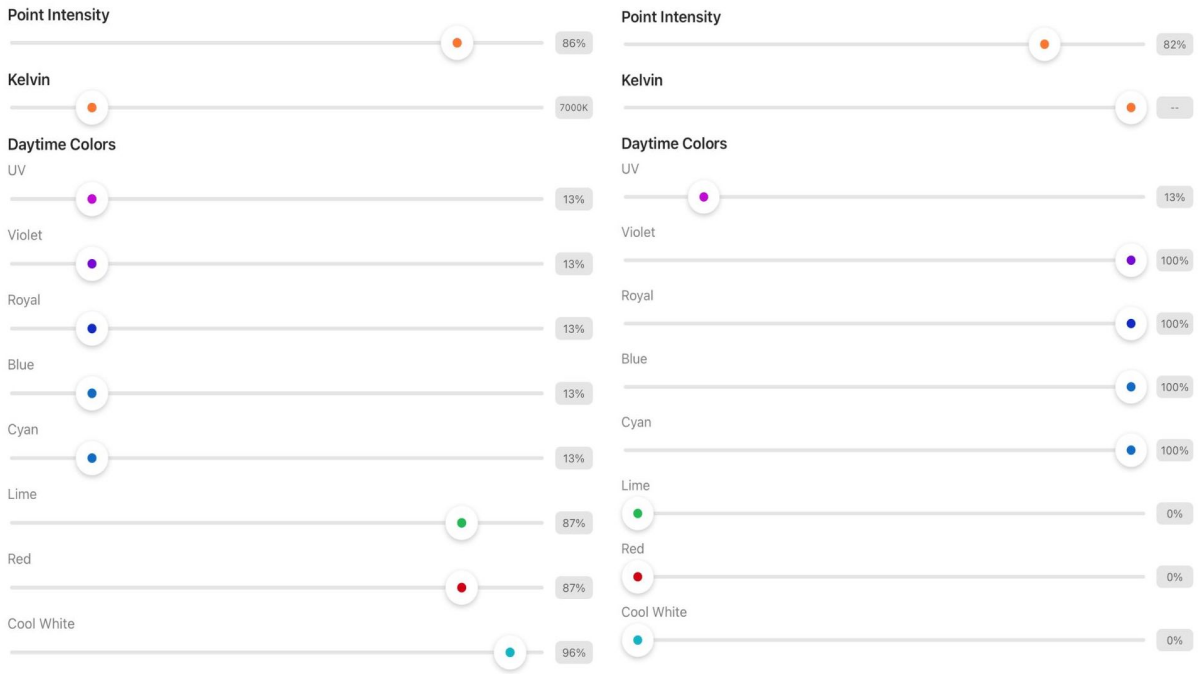

Figure S2. Ecotech Radion XR30 Mobius app settings use to create 60 PAR.
Light spectrum settings for LED treatments, reef-depth (left) and blue-shifted (right), at 5 weeks post-settlement.

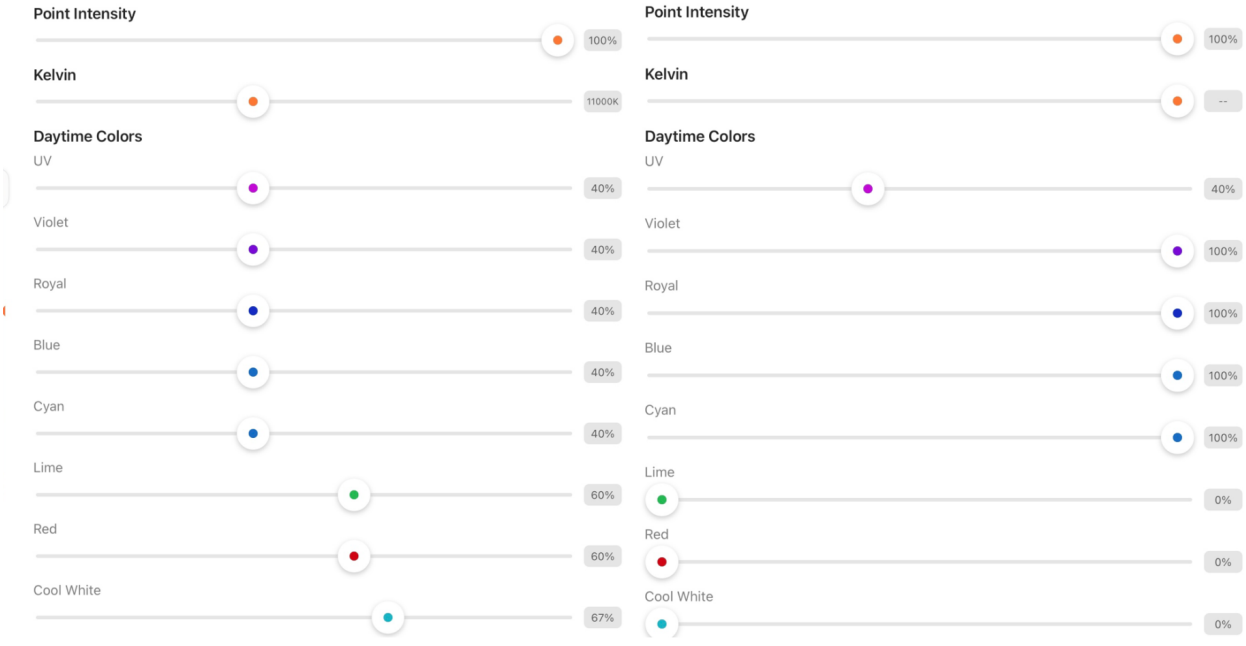

Figure S3. Ecotech Radion XR30 Mobius app settings used to create 110 PAR.
Light spectrum settings for LED treatments, reef-depth (left) and blue-shifted (right), at 14 weeks post-settlement.

Figure S4. Differential Algal growth between sunlight (left) and LED (right) light source.
Algae under LED treatment accumulated quickly compared to the area designated for the sunlight treatment.

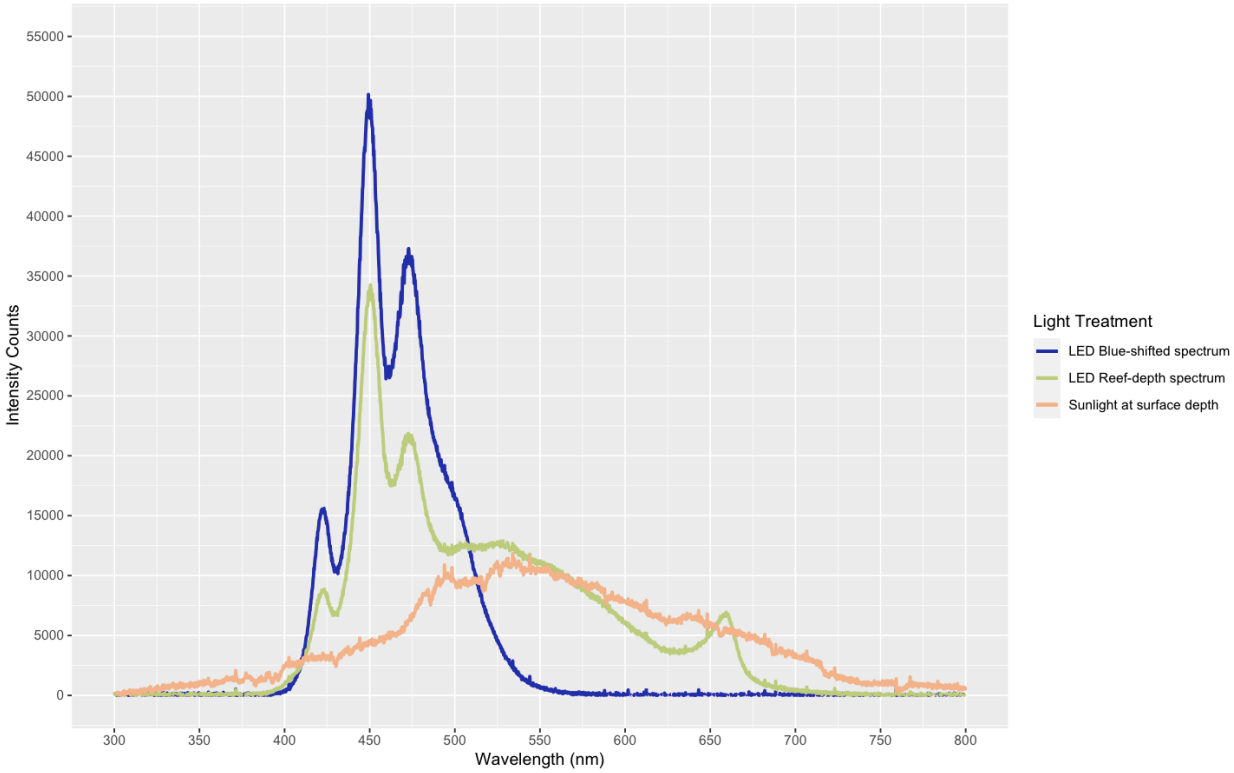

Figure S5. Spectral analysis at 60 PAR.
Spectral measurements for each light treatment at 5 weeks post-settlement. Intensity counts represent the quantity of photons detected at each wavelength.

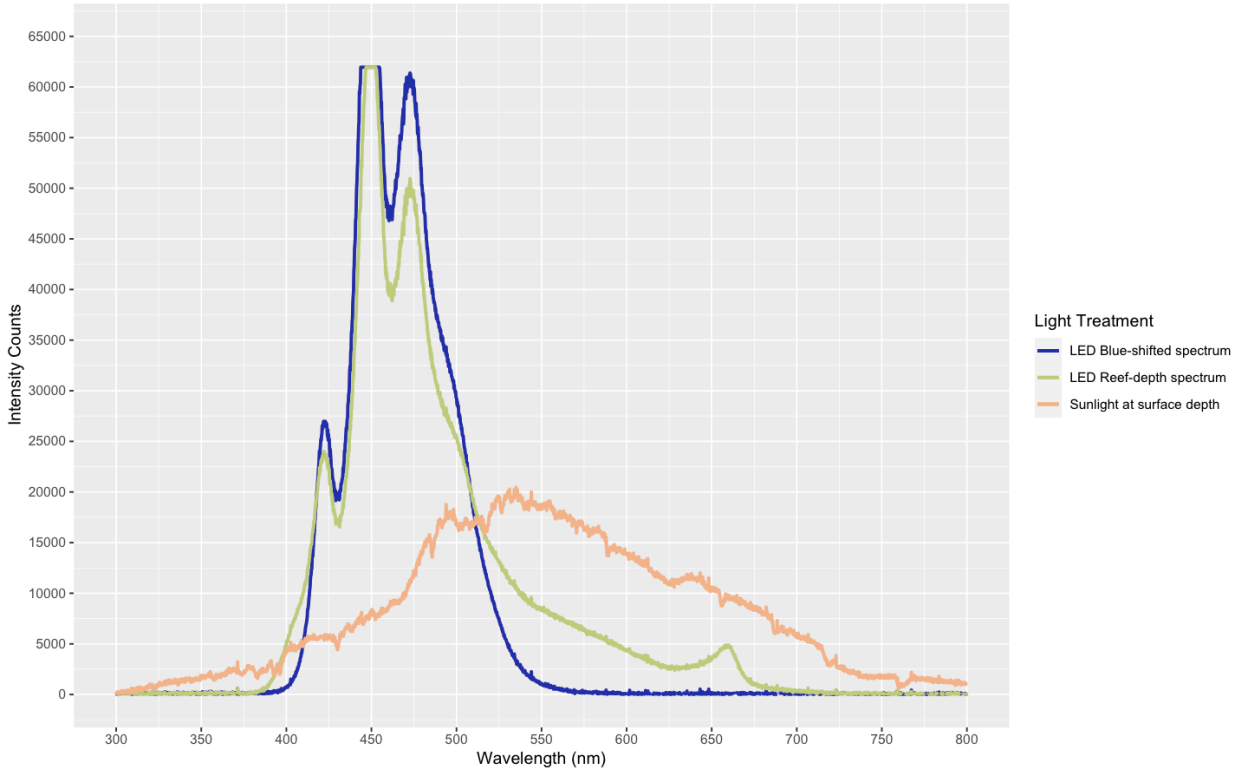

Figure S6. Spectral analysis at 110 PAR.
Spectral measurements for each light treatment at 14 weeks post-settlement. Intensity counts represent the quantity of photons detected at each wavelength.

Table S4. RPubs links

Survival	https://rpubs.com/Dayponce/CoralSurvivalCurves
Growth	https://rpubs.com/Dayponce/CoralGrowth

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