Illuminating Hidden Diversity: Light-driven plasticity in cryptic coral lineages

Adrian S. Cheh[1], Meara Aberle[1], Natalie Prince[1], Cora Skaggs[1], Jeric P. Da-Anoy[1], Sarah W. Davies[1]

Abstract:

The long-term persistence of coral reefs - the fundamental structure of biodiverse marine ecosystems - depends on the ability of corals to adjust to environmental change. Coral species often display cryptic divergence (genetically distinct, but visually indistinguishable) lineages that differ in morphology, physiology, stress tolerance, and ecological distribution. In the Bocas del Toro Reef Complex, Panama (BTRC), two cryptic lineages of *Siderastrea siderea* exist in unique abiotic environments that differ in depth, light, and daily temperature variability and show differences in corallite morphology and symbiont photochemical efficiency. However, it's unclear whether differences among these lineages arise primarily from genetic divergence or from plastic responses to environmental conditions. Here, we show that *S. siderea* lineages originating from different light environments exhibit distinct patterns of phenotypic plasticity when experimentally exposed to contrasting light conditions. Using a controlled light experiment with two cryptic *S. siderea* lineages from BTRC, we found that under high-light exposure, L2 corals showed a significant increase in red-channel intensity over time, suggesting increased bleaching sensitivity in shallow reef conditions, while L1 corals remained stable in tissue coloration. Photosynthetic efficiency (F_v/F_m) increased over the experimental period for both lineages; higher values were consistently seen under the low-light treatments. Despite the more bleached response from L2, they maintained a higher F_v/F_m than L1 across treatments, indicating differences in symbiont photosynthetic performance. Together, these results demonstrate that lineage identity strongly shapes coral responses to light and that environmental history influences the degree of plasticity expressed. These findings advance our understanding of how genetic and environmental factors interact to determine coral resilience. By clarifying the contributions of plasticity and lineage divergence, this work provides insight into which coral populations may be better equipped to cope with rapid environmental change and informs strategies for conservation and restoration.

Introduction

Coral communities are vital ecosystems that serve as essential habitats for many marine species, yet are under serious threat from climate change (Rhoades et al., 2023). Although they only cover <0.1% of the Earth's surface, they are estimated to provide habitat to about 25% of the world's marine species (Spalding et al. 2001, Reaka et al.1997). Not only are reef communities fundamental structures for many marine organisms, but they also provide coastal protection, support ecotourism in many regions, and can be a potential source for integrative medicine (Cooper et al. 2014). Corals' ability to build the reef depends heavily on their complex relationship with photosynthetic algal symbionts (Family Symbiodiniaceae) and many other diverse microorganisms (Ge et al. 2021). The Symbiodiniaceae reside within coral cells, where they perform photosynthesis, using sunlight to fix carbon into glucose, and these nutrients are translocated to the coral host to provide energy (Rosset et al. 2021). Because this relationship is reliant on sunlight, light availability is a fundamental limiting factor for coral species, as it is necessary for photosymbiosis and most reef production (Rosset et al. 2021).

Understanding how coral symbiosis is shaped by light is critical for further predicting and improving coral reef resilience under future climate change conditions. Global climate change threatens coral reef survival, largely due to increasing sea temperatures, which drive increases in the frequency and severity of marine heatwaves (Mallon et al. 2022). Sea-surface temperatures have increased steadily since the 1950s (Su et al. 2017). Of the approximately 0.88°C of warming above pre-industrial levels, roughly 0.6 °C has taken place from 1960 to 2020 (Venegas et al. 2023). Sea surface temperatures are projected to rise another 0.6 to 2.0 °C before 2100 (Venegas et al. 2023). In addition to overall rising temperatures, marine heatwave events (anomalous spikes in sea temperature for a prolonged duration) have been getting longer and more intense (Oliver et al. 2018, Hughes et al. 2018). Marine heatwave conditions are projected to be near constant in the Caribbean Sea by the end of the century (Bustos Usta et al. 2024).

Increasing temperatures can lead to coral bleaching, which occurs when algal symbionts are expelled, resulting in the loss of color, nutrients, and overall photosynthetic capability (Dawson, Jarvie, and Reitsma, 2009). The bleaching process is driven mainly by ecological stressors such as temperature anomalies, salinity changes, pollution, ocean acidification, and light, and these stressors have been intensified by climate change (Riegl et al. 2019). Once bleached, corals become highly susceptible to disease and are unable to photosynthesize effectively (Riegl et al. 2019). Continued bleaching hinders their ability to recover and can

eventually lead to coral death, which has immense impacts on marine ecosystems due to their role in providing critical habitat and resources for marine life. (Glynn et al. 2018; Dawson, Jarvie, and Reitsma, 2009). However, coral responses to climate change depend on how environmental stressors interact with the biological complexity of the coral holobiont. Interactions between genotype and environment (GxE) can cause variation in coral thermal tolerance and susceptibility to stress. For example, some coral species, such as *Porites*, can maintain photosynthetic performance under moderate heat stress, whereas more sensitive species, such as *Acropora*, bleach rapidly as temperatures rise (Loya et al. 2001). Studies have also demonstrated that different populations of corals from different reefs can also show variation in thermal tolerance (Dixon et al. 2015). For example, populations of *Porites astreoides* from a more thermally variable reef show higher thermal tolerance and greater plasticity than conspecifics from a more stable offshore site (Kenkel et al. 2013; Kenkel et al. 2016). Together, this work highlights how thermal tolerance in corals is shaped not only by species identity but also by population-level environmental history, setting the stage for understanding how hidden genetic structure may further influence stress resilience.

Many coral species contain cryptic genetic lineages, genetically distinct groups that appear morphologically similar yet differ in physiology, symbiotic associations, and stress tolerance (Grupstra et al., 2024). Many cryptic lineages are often distributed across distinct light environments. These hidden genetic divisions can also influence thermal resilience and contribute to response diversity within a species (Aichelman et al., 2025). Cryptic diversity has been increasingly documented across coral taxa and is associated with functional differences relevant to adaptation (Starko et al. 2023; Aichelman et al., 2025). Lineage-level variation may arise through environmental selection on physiological and morphological traits, resulting in differential thermal tolerance and stress responses (Chevin et al. 2010; Aichelman et al. 2025). Accounting for cryptic diversity is also essential for conservation and restoration, as overlooking hidden genetic structure can lead to inaccurate assessments of biodiversity, population size, and adaptive potential (Riginos et al. 2024). Many coral lineages are distributed across distinct light environments, suggesting that light availability can act as a selective agent shaping diversification and lineage-specific ecological strategies. Incorporating cryptic lineages into restoration strategies can improve lineage environment matching, reproductive compatibility, and ecological outcomes (Riginos et al. 2024; Shaver et al. 2020). However, many lineages remain

undescribed or poorly characterized, and understanding how they respond to different light environments will be critical as restoration practitioners increasingly employ assisted gene flow and selective propagation.

As the symbiosis between the coral host and endosymbiotic algae is fundamentally light-dependent (Mallon et al. 2022), variation in light availability and intensity across environments can directly impact the amount of fixed carbon available to the coral host (Rodrigues and Grottoli 2007). Plasticity due to variation in light availability has also been documented in both morphology and trophic strategy. One lineage of *Siderastrea siderea* (L2) from Bocas del Toro, Panama, has a significantly larger corallite area compared to L1; this difference in morphology also increases the ability of symbionts to enhance the light field (LEF) for photosynthesis (Aichelman et al. 2025). As the coral host receives up to 90% of energy from photosynthetically fixed carbon, light availability can drive strong changes in coral metabolism. Furthermore, management interventions such as coral transplantation can modify the light environment experienced by corals, underscoring the need to understand how plasticity in light acclimation affects coral resilience and bleaching susceptibility (Lohr et al. 2019). Plasticity in trophic strategy is important because corals must balance energy gained from autotrophy and heterotrophy. As light availability and intensity vary across environments, shifting between these modes allows corals to maintain metabolic demands when warming, nutrient variation, or symbiont loss disrupts photosynthesis (Solomon et al. 2025). Variation in thermal tolerance, morphology, and trophic strategies highlights how GxE shapes coral persistence.

In the Bocas del Toro Reef Complex, Panama (BTRC), three cryptic lineages (L1–3) of *Siderastrea siderea* have been identified that exist along a gradient of depth, light, and daily temperature variability (DTV) across two sites (Aichelman et al. 2025). Lineage 1 (L1) is found exclusively in shallow, high-light and temperature environments, while lineages 2 and 3 (L2, L3) prefer deeper environments (Aichelman et al. 2025; Swank et al., unpublished). L2 corals that live in deeper environments have a larger corallite area and an increased ability to enhance the light field for photosynthesis (Aichelman et al. 2025). While baseline differences in spatial distribution, phenomes, and morphology of cryptic lineages of *S. siderea* in BTRC have been defined, it is unknown how environmental differences in depth and light influence the potential for plasticity in these lineages. The goal of this study is to determine if lineages differ in their phenotypic plasticity and if living in abiotically variable environments increases the potential for

plasticity. To accomplish this, two cryptic lineages of *S. siderea* (L1 and L2) from BRTC were used to determine the influence of light on the potential for plasticity in coral physiology. A two-week common garden mesocosm experiment tested whether high thermal variability and light intensity would increase the potential for plasticity in light-acclimation and trophic strategy in cryptic *S. siderea* lineages. We hypothesize that lineages of *S. siderea* are light-acclimated to different environments, but lineages that live in more abiotically variable environments (L1) may be more plastic than those that live in more stable environments (L2). Differences in growth rate and symbiont photochemical efficiency (F_v/F_m) between *S. siderea* fragments of the same cryptic lineage placed in different treatments will inform how light-acclimation differs between lineages.

Methods

In August 2025, *Siderastrea siderea* coral fragments from two sites (Punta Donato (PD); Cristobal Island (CI)) that differ in their depth distributions, light availability, and daily thermal variability were collected in Bocas del Toro, Panama (Table 1). Four colonies of previously identified *S. siderea* lineage 1 (L1) were collected from PD, and nine colonies of *S. siderea* lineage 2 (L2) were collected from CI. Colonies were live transported to Boston University and maintained at 25ºC with constant water flow, and light was maintained on an 8-hour light:16-hour dark cycle. Following recovery, coral fragments were further fragmented, and two ramets per genotype were glued to ceramic plugs (n = 26 ramets). On October 29th, all colonies were moved into light-acclimation tanks: L1 colonies were placed under 550 µmol photon m^2 s^{-1} and L1 colonies under 220 µmol photon m^2 s^{-1}, mimicking the light intensity of the sites at which the colonies were collected. On December 1st, following roughly 1-month of light-acclimation, baseline F_v/F_m, buoyant weight measurements, and photographs of each nubbin were taken prior to one nubbin from each genotype being randomly assigned to either a high- (550 µmol photon m^2 s^{-1}) or low-light (220 µmol photon m^2 s^{-1}) treatment (n = 2 tanks per treatment) for a two-week common garden experiment. Coral placement among the tanks was randomized using an online randomizer to avoid placement bias. Light levels were maintained on a 12-hour dark:12-hour light cycle (10:30 – 22:30). During this period, corals were fed twice during our experimental process (on days 3 and 9), with each tank receiving 0.0625 g/mL of frozen brine shrimp mixed into seawater. To ensure consistency, the same individual conducted both feedings.

Table 1. ***In-situ* site metadata.** Site name, GPS coordinates for sites, colonies of *Siderastrea siderea* were collected, and coral collection depth (corals were collected at two similar depths at Cristobal Island). Mean temperature (ºC) and PAR (µmol photon m^{-2} s^{-1}) recorded at coral collection depths, averages for year 2024.

Site	GPS	Colonies collected	Collection depth	Mean temperature	Mean PAR
Punta Donato	9.35845, -82.36804	4	0.914m	30.45ºC	(µmol photon m^{-2} s^{-1})
Cristobal Island	9.26827, -82.24228	9	2.438m, 2.743m	30.22ºC	

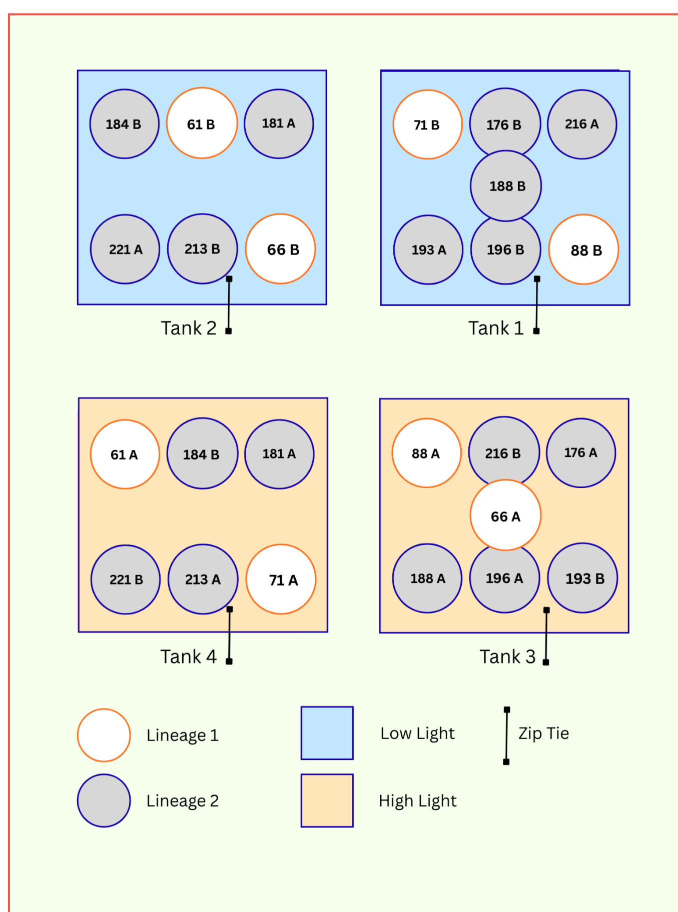

Figure 1. Experimental design to test the effects of divergent light levels. Experimental tank layout showing the placement of *Siderastrea siderea* Lineage 1 (orange) and Lineage 2 (grey) fragments across high-light (550–600 µmol photon m^{-2} s^{-1}) and low-light (220 µmol photon m^{-2} s^{-1}) treatments. Each genotype had two fragments, allowing each genotype to be represented in each treatment (e.g., 61A and 61B were placed in a low-light and a high-light 12qw tank).

Water Quality

We monitored three key environmental parameters, temperature, salinity, and light intensity, as these factors directly influence coral physiological performance and stress response. Temperature measurements were taken using two instruments: an Aqua Logic Nema 4X temperature controller for continuous monitoring and a digital thermometer for more precise point measurements. Salinity was measured using a refractometer, and light intensity was measured using an Underwater Quantum Flux instrument (MQ-510). Measurements were taken twice daily at 11-12:00 PM and 15-16:00 PM to track both consistency and potential fluctuations throughout the day.

F_v/F_m

To determine how algal symbionts are acclimating to novel light conditions, the dark-acclimated maximum photochemical efficiency of open RCIIs (F_v/F_m, Cosgrove and Borowitzka 2010) of symbionts was measured daily in darkness under red light between 9-10 am using a Junior PAM fluorometer (Walz, GmbH, Effeltrich, Germany) on dark-acclimated corals (Edmunds 2009). Measurements were made with light intensity and gain set to 6 and 1, respectively, with electronic signal dampening set at 2 and a saturation pulse width of 0.6 sec. F_v/F_m were measured using a 1.5-mm diameter PAM sensor held ~1 mm above the highest point of the nubbin, with F_v/F_m values assessed in triplicate per nubbin. These values were averaged, and mean values were used for each nubbin each day.

Red Channel Intensity

To test the extent of bleaching, color values were taken from standardized photographs of individual coral fragments. Images were taken using an iPhone 16 Pro in an evenly lit photo studio (LimoStudio) on a black background. Each fragment was placed on a CoralWatch Coral Health Chart (University of Queensland, Australia), which was used as a white-balance calibration reference. Photographs were processed using Adobe Photoshop (Adobe Inc., USA) to ensure constant exposure and color calibration. Finalized JPG images were imported into MATLAB (Version 25.2.0), where they quantified RGB color channel values using Image Processing Toolbox functions from ten points on the fragment (Ferrara et al. 2024). Mean red-channel values of all ten points were calculated and used as a proxy for tissue coloration.

Bleaching was then scored on a scale of 0-255, where higher red-channel values indicate more bleached. Significance was calculated through a series of paired t-tests.

Buoyant Weight

Buoyant weight was measured to assess coral growth over the course of this experiment (Spencer Davies 1989). To confirm the design's accuracy and establish a baseline for the calculations, we measured the buoyant weight of an object with known mass. All measurements were done with a digital Ohaus Scou balance scale fitted with a suspension hook and a submerged hanging platform placed in a tank of seawater. Prior to weighing, the scale was zeroed with the platform in place. The known object and corals were placed on the platform one at a time, making sure they weren't touching the sides or bottom of the tank. Because buoyant weight is dependent on the density of the fluid, temperature and salinity were kept constant between measurements, 21.3°C and 33ppm, respectively. Buoyant weights were recorded at the start and end of the experiment and used as a proxy for estimating the percent change in weights. To characterize differences in percent buoyant weight change, the percent change was graphed in a boxplot using the equation below.

$$\%Change = \frac{(final - initial)}{initial}.$$

Statistical analyses

All statistical analyses were run in R version 12.1 (R Core Team 2024). Differences in light treatments were compared using a two-sample Welch's t-test. Changes in F_v/F_m over the course of the experiment were analyzed using a repeated-measures linear random mixed effects model ("lmerTest" package, version 3.1-3 Kuznetsova et al. 2017). Lineage, treatment, and date were included as fixed effects, and genotype was included as a random effect. Growth rate and red-light intensity were compared before and after the experiment using a two-way ANOVA, with lineage, treatment, and date included as fixed effects.

<u>Results</u>

Across the 12-day experimental period, low light tanks were held at an average of 192.16 µmol photon m^2 s^{-1} and high light tanks at 510.66 µmol photon m^2 s^{-1} (Figure 3a). A two-sample Welch's t-test shows that these light treatments were significantly different ($t = 32.27$, $df = 44.50$,

$p < 0.001$). Temperature (24.33ºC) and salinity (34.74ppt) were held constant as seawater from all tanks was circulated through one system (Fig. 3b, c).

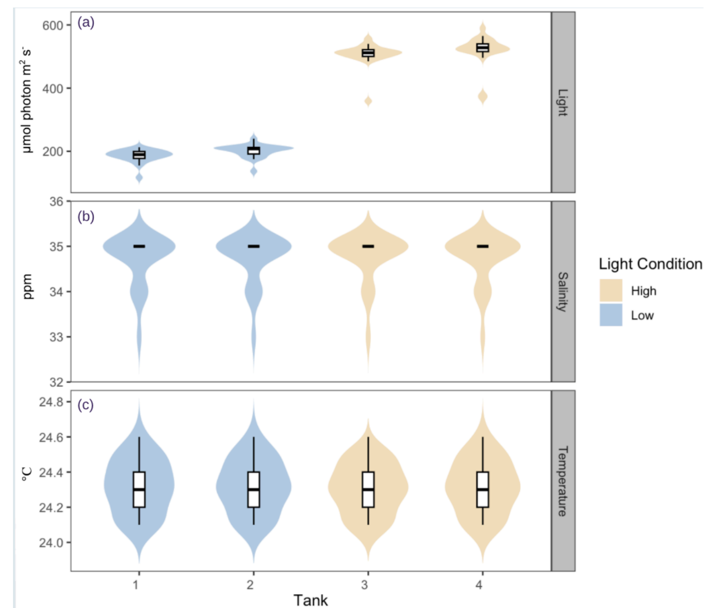

Figure 2. The only variable manipulated was light treatment; salinity and temperature remained constant. Environmental conditions across all four experimental tanks under different light treatments, high light treatment shown in orange and low shown in blue. The top panel shows light intensity (μmol photons m^{-2} s^{-1}), the middle panel depicts salinity (ppm) measurements, and the bottom panel shows temperature (°C). The only variable manipulated was high vs. Low light treatments.

Corals kept under low-light treatment conditions exhibited significantly higher dark-acclimated maximum photochemical efficiency of open PSII centers (F_v/F_m) than corals in the high-light treatment (Fig. 3; RM-ANOVA, $P < 0.0001$). F_v/F_m also varied significantly across sampling dates, and a significant date × treatment interaction was detected (Fig. 3; RM-ANOVA, $P = 0.0213$), indicating a non-constant effect of light treatment across the experiment dates. No significant effect of lineage or lineage-by-time interactions was observed. Visualization of individual genotype trajectories further revealed substantial within-genotype variability in Fv/Fm across the experimental period (Fig. 4).

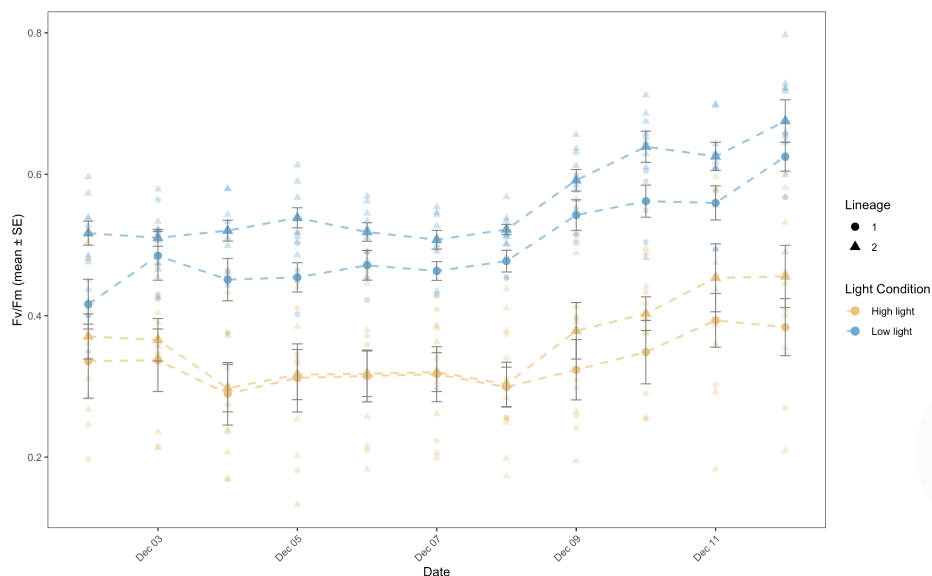

Figure 3. Maximum quantum yield of photosystem II (Fv/Fm) in *Siderastrea siderea* lineages measured over time under contrasting light conditions. Fv/Fm values are shown for coral fragments from two genetic lineages of *S. siderea* - Lineage 1 (light-acclimated) and Lineage 2 (dark-acclimated) - collected from Bocas del Toro, Panama, and maintained in either high light or low light treatments (L1: N=4, L2: N=9). Semi-transparent points represent individual fragment measurements, while larger points and dashed lines indicate treatment-by-lineage means (± standard error (SE)) across sampling dates. Colors indicate experimental light treatment, and shapes denote lineage identity. Mean Fv/Fm was measured using a pulse-amplitude-modulated (PAM) fluorometer. Repeated-measures ANOVA detected significant effects of light treatment (P < 0.0001), sampling date (P < 0.0001), and their interaction (P = 0.021).

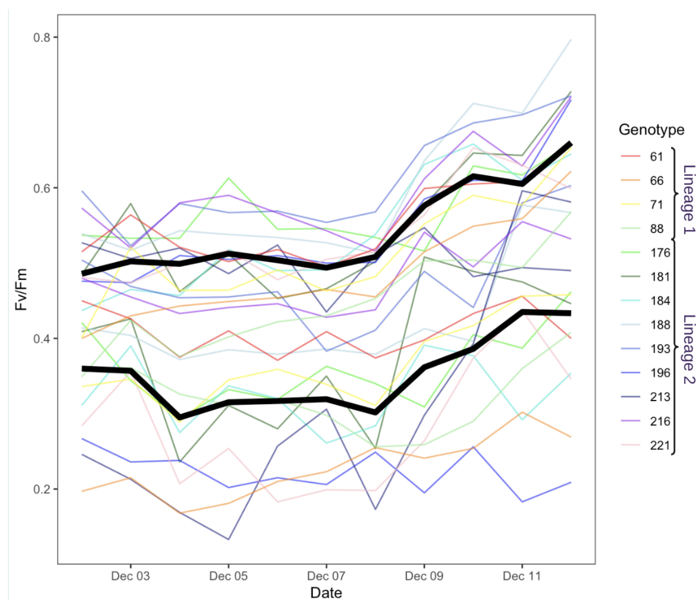

Figure 4. Temporal variation in maximum quantum yield of photosystem II (Fv/Fm) for individual *Siderastrea siderea* genotypes measured across the experimental period. Coral fragments were collected from Bocas del Toro, Panama, and placed into either high-light (N = 13) or low-light (N = 13) treatment conditions. Thin colored lines represent repeated Fv/Fm measurements from individual coral fragments, with colors indicating genotype identity, while thick black lines denote mean Fv/Fm across fragments within each light treatment at each sampling date. Measurements were obtained using a pulse-amplitude-modulated (PAM) fluorometer. This figure highlights within-genotype variability and treatment-level trends in PSII efficiency through time.

Change in coral bleaching, which was quantified as mean red-channel intensity, was found to vary by lineage and light treatment. Through a linear model, we were able to identify the significance of treatment on red channel intensity values. (df= 1, f value= 7.8280, p value= 0.0076). Post hoc pairwise tests were performed to compare red-channel intensity between sampling dates within each lineage and varying light treatments. We were able to identify that Lineage 2 corals demonstrated significantly increased mean red-channel intensity values over time when exposed to high-light treatments, with values increasing from 1/12/2025 to 12/12/2025 ($p = 0.0205$) (Fig. 5). In contrast, Lineage 1 corals in the high-light treatment showed no significant change in red-channel intensity during the experimental period ($p = 0.9099$). Under low light conditions, neither Lineage 1 ($p = 0.2206$) nor Lineage 2 ($p = 0.7692$) showed significant changes in red-channel intensity over time (Fig. 5). Comparisons between lineages within each light treatment and sampling date showed no significant differences in red-channel intensity (all $p > 0.22$). There was no significant effect of treatment ($p = 0.38$) or lineage ($p = 0.74$) on percent change in buoyant weight.

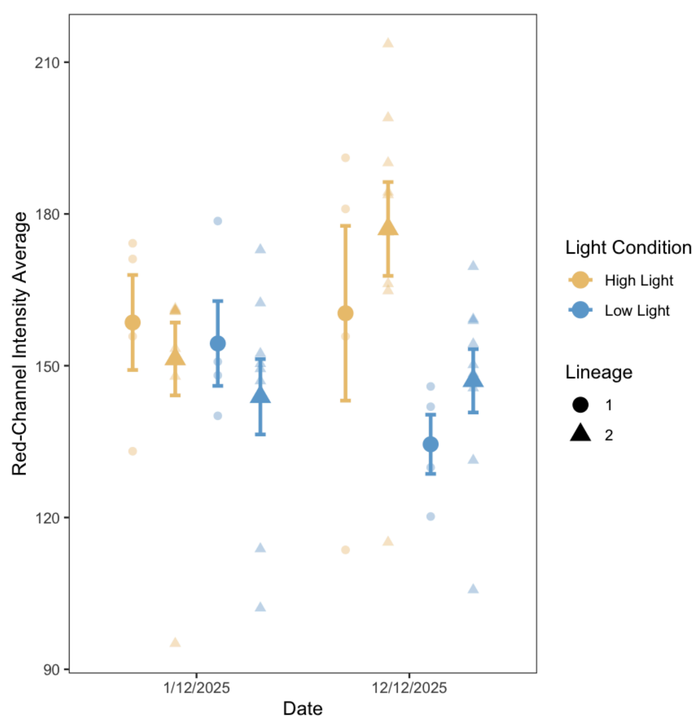

Figure 5. High-Light Treatment Lineage 2 Showed a Significant Increase in Red-Channel Intensity Over Time. Mean red-channel intensity (proxy for coral color) +/- standard error (SE) of *Siderastrea siderea* Lineage 1 and Lineage 2 coral fragments collected from high light and low light conditions at the beginning of the study. Lineage 2 corals showed significantly increased mean red-channel intensity values over time when exposed to high-light treatments; no other lineage or treatment combinations demonstrated significant changes.

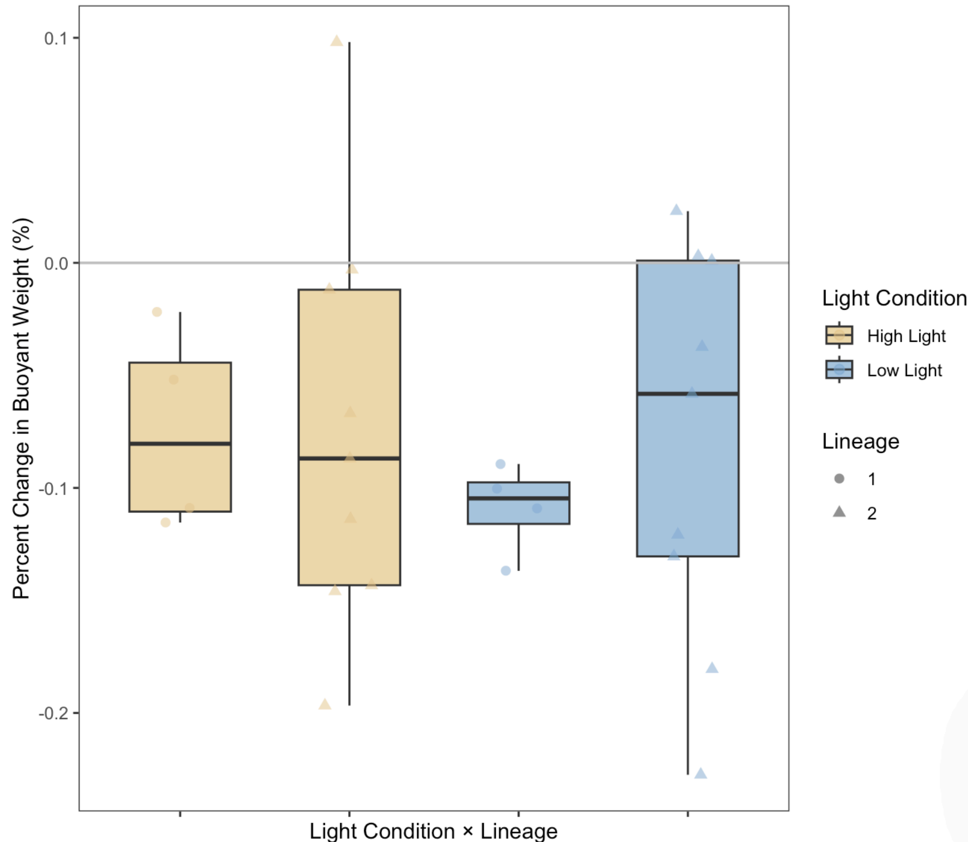

Figure 6. There was no significant effect of treatment or lineage on % of buoyant weight change. Percent change in buoyant weight across high and low light treatments and lineage (L1 and L2). Boxplots show the distribution of percent changes for each group, with individual data points overlaid. There was no significant difference between groups, indicating that buoyant weight stayed relatively consistent across treatment and lineage.

Discussion

Patterns in analyses of *Siderastrea siderea* red-channel intensity showed a lineage-specific response to high-light exposure over the 12-day experimental period. Although Lineage 1 and Lineage 2 corals did not differ significantly in tissue color at the beginning, only L2 corals demonstrated a significant increase in red-channel intensity over time under the high-light conditions (Fig. 5). This indicates a stronger sensitivity to high-light intensities and shallow reef conditions. The increase in red-channel intensity is consistent with prior research showing bleaching response driven by physiological stress, and can suggest the idea of loss of Symbiodiniaceae density under high light conditions (Ferrara *et al.* 2024). In contrast, Lineage 1 remained relatively stable in tissue coloration under high-light conditions, suggesting an overall better tolerance or capability for acclimation over the duration of the experiment. Additionally,

corals that remained in light treatments similar to the conditions where they were sourced showed more stable tissue coloration over time. This idea suggests that the prior light conditions may have contributed to their physiological stability throughout the experiment. Although there were no statistically significant changes to red light intensity under low-light conditions, L1 showed a non-significant trend of darker tissue coloration over time (Fig. 5). This may suggest an acclimation response to the reduced light, as L1 corals could be increasing pigmentation through increased symbiont density to enhance their ability to capture light (Aichelman et al. 2025). Although this response was not significant, it supports the idea of potential physiological plasticity that differs between L1 and L2 corals.

The F_v/F_m of L1 (high-light: 14.3%, low-light: 50.2%) and L2 corals (high-light: 22.9%, low-light: 30.7%) steadily increased over the course of the experiment, indicating that corals were still acclimating to light conditions on the last day of data collection. Corals under low light showed significantly higher F_v/F_m than corals under high light on all days of data collection. The significantly higher F_v/F_m values in both lineages under low light compared to corals under high light suggest that lineages under high light may have experienced very mild light stress. However, the increase in F_v/F_m in both L1 and L2 under high-light suggests that algal symbionts were not under ecologically meaningful light stress. Although there was a significant increase to red light intensity in L2 corals under high light, this response was not mirrored in the F_v/F_m of L2 algal symbionts. Despite showing significantly bleaching under high-light, L2 corals maintained consistently higher F_v/F_m values than L1 corals in both treatments during the experiment. These results partially match those from other studies; in Jones and Hoegh-Guldberg 2001, shade- and light-acclimated *Stylophora pistillata* were exposed to high- and low-light conditions and measured dark-adapted F_v/F_m. Under low-light, shade-acclimated *S. pistillata* maintained higher F_v/F_m than light-acclimated conspecifics, and in light-acclimated *S. pistillata* had higher F_v/F_m than shade-acclimated corals (Jones and Hoegh-Guldberg 2001). The photosynthetic response of *S. pistillata* symbionts under high-light does match the results from this study; differences in these results may be related to identity and differences in the stress tolerance of algal symbionts.

Patterns of F_v/F_m observed in this study suggest that even with significant bleaching in high light, L2 symbionts may be more efficient at photosynthesis. This is further reinforced by higher F_v/F_m values of L2 symbionts compared to L1 symbionts under low light. Studies have shown that algal symbionts can also display long-term acclimatization to unique environmental

regimes that can influence stress tolerance (Howells et al. 2012). L2 symbionts that typically live in low-light conditions may be more efficient at the capture and conversion of light to fixed carbon. Aichelman et al. (2025) found that L2 *S. siderea* have 58% larger corallite areas compared to L1 *S. siderea*, which increases the light field across the coral surface, making more light available for algal photosynthesis. The low-light morphology of L2 *S. siderea,* as well as the higher efficiency of photosynthesis in L2 symbionts, may contribute to greater plasticity across different light conditions.

This study had several limitations that should be considered while interpreting our results. First, the experimental duration lasted 12 days, which is relatively short for coral acclimation, which often occurs over weeks to months. This study likely only captured the initial phase of physiological responses from the lineages, which may explain why some traits showed directional shifts but did not reach their full statistical significance. For example, buoyant weight did not change significantly across our experiment; however, this metric is known to require longer experimental periods to detect biomass changes. Secondly, there was a large variation in the number of colonies between lineages, with fewer Lineage 1 colonies compared to Lineage 2. This imbalance potentially limited our ability to see significant effects and overall lineage comparisons. Finally, the experiment was conducted in controlled laboratory conditions where light was isolated as a single stressor, which does not capture the complexity of natural reef environments where there are multiple stressors (nutrient availability, temperature and salinity fluctuations, water flow, etc.). Lack of these environmental variables potentially could modify coral responses; therefore, in situ conditions should be considered cautiously.

Overall, these results highlight the importance of considering lineage-specific responses to varying light conditions when planning coral restoration and management. The observed differences in bleaching patterns and photosynthetic performance suggest that some lineages become more plastic in varying long-term light exposures. This has direct implications for coral restoration efforts, as it indicates that matching lineages to appropriate light conditions may improve their overall survival and photosynthetic performance for outplanting reefs. In particular, corals selected for high-light environments may benefit from a prior evaluation of their photosynthetic capabilities and bleaching response to assist with long-term success. This is particularly important as reef environments are becoming more variable due to climate change.

Through incorporating light history and lineage type into future restoration strategies, we can enhance long-term resilience and reduce further stress in restored coral populations.

Literature Cited

Aichelman, H., et al. (2025). Cryptic coral diversity is associated with symbioses, physiology, and response to thermal challenge. *Science Advances, 11*(3), Article 5237. https://doi.org/10.1126/sciadv.adr5237

Bustos Usta, D., et al. (2024). Observation and projection of marine heatwaves in the Caribbean Sea from CMIP6 models. *Remote Sensing, 16*(13), 2357. https://doi.org/10.3390/rs16132357

Chevin, L. M., et al. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLOS Biology, 8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Cooper, E. L., et al. (2014). Corals and their potential applications to integrative medicine. *Evidence-Based Complementary and Alternative Medicine, 2014*, Article 184959. https://doi.org/10.1155/2014/184959

Cosgrove, J., & Borowitzka, M. A. (2010). Chlorophyll fluorescence terminology: An introduction. In D. Suggett, O. Prášil, & M. Borowitzka (Eds.), *Chlorophyll a fluorescence in aquatic sciences: Methods and applications*, *Vol. 4.* Springer.

Dawson, T., Jarvie, F., & Reitsma, F. (2009). A habitat suitability model for predicting coral community and reef distributions in the Galápagos Islands. *Galapagos Research, 66*, 20–26.

Edmunds, P. J. (2009). Effect of acclimatization to low temperature and reduced light on the response of reef corals to elevated temperature. *Marine Biology, 156*, 1797–1808. https://doi.org/10.1007/s00227-009-1213-2

Ferrara, E. F., et al. (2024). RGB color indices as proxy for symbiont cell density and chlorophyll content during coral bleaching. *bioRxiv*. https://doi.org/10.1101/2024.12.20.629333

Ge, R., et al. (2021). Regulation of the coral-associated bacteria and *Symbiodiniaceae* in *Acropora valida* under ocean acidification. *Frontiers in Microbiology, 12*, 767174. https://doi.org/10.3389/fmicb.2021.767174

Glynn, P. W., et al. (2018). State of corals and coral reefs of the Galápagos Islands (Ecuador): Past, present and future. *Marine Pollution Bulletin, 133*, 717–733. https://doi.org/10.1016/j.marpolbul.2018.06.002

Grupstra, C. G., Gómez-Corrales, M., Fifer, J. E., Aichelman, H. E., Meyer-Kaiser, K. S., Prada, C., & Davies, S. W. (2024). Integrating cryptic diversity into coral evolution, symbiosis, and conservation. *Nature Ecology & Evolution, 8*(4), 622–636. https://doi.org/10.1038/s41559-023-02319-y

Howells, E. J., Beltran, V. H., Larsen, N. W., Bay, L. K., Willis, B. L., & Van Oppen, M. J. H. (2012). Coral thermal tolerance shaped by local adaptation of photosymbionts. *Nature Climate Change, 2*(2), 116–120. https://doi.org/10.1038/nclimate1330

Jones, R. J., & Hoegh-Guldberg, O. (2001). Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates of corals: Photoprotection, photoinactivation and the relationship to coral bleaching. *Plant, Cell & Environment, 24*(1), 89–99. https://doi.org/10.1046/j.1365-3040.2001.00648.x

Kenkel, C. D., Goodbody-Gringley, G., Caillaud, D., Davies, S. W., Bartels, E., & Matz, M. V. (2013). Evidence for a host role in thermotolerance divergence between populations of the mustard hill coral (*Porites astreoides*). *Molecular Ecology, 22*(16), 4335–4348. https://doi.org/10.1111/mec.12391

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software, 82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Loya, Y., et al. (2001). Coral bleaching: The winners and the losers. *Ecology Letters, 4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203

Mallon, J., et al. (2022). Light-driven dynamics between calcification and production in functionally diverse coral reef calcifiers. *Limnology and Oceanography, 67*(2), 434–449. https://doi.org/10.1002/lno.12002

Oliver, E. C. J., et al. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications, 9*(1), 1324. https://doi.org/10.1038/s41467-018-03732-9

Reaka, M. L. (1997). *The Global Biodiversity of Coral Reefs: A Comparison with Rain Forests.* In M. L. Reaka-Kudla et al. (Eds.), *Biodiversity II*. Joseph Henry Press.

Riegl, B., et al. (2019). Environmental and biological determinants of coral richness, resilience, and reef building in Galápagos (Ecuador). *Scientific Reports, 9*(1), 10322. https://doi.org/10.1038/s41598-019-46607-9

Riginos, C., et al. (2024). Cryptic species and hybridisation in corals: Challenges and opportunities for conservation and restoration. *Peer Community Journal, 4*, e106. https://doi.org/10.24072/pcjournal.492

Rodrigues, L. J., & Grottoli, A. G. (2007). Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnology and Oceanography, 52*(5), 1874–1882. https://doi.org/10.4319/lo.2007.52.5.1874

Rosset, S. L., et al. (2021). The molecular language of the cnidarian–dinoflagellate symbiosis. *Trends in Microbiology, 29*(4), 320–333. https://doi.org/10.1016/j.tim.2020.08.005

Solomon, S. L., de Goeij, J. M., Croasdale, E. M., & Schoepf, V. (2025). Seasonality modulates coral trophic plasticity in an extreme, multi-stressor environment. *Limnology and Oceanography, 70*(5), 1466–1480. https://doi.org/10.1002/lno.70046

Spalding, M. (2001). *World atlas of coral reefs*. University of California Press.

Spencer Davies, P. (1989). Short-term growth measurements of corals using an accurate buoyant weighing technique. *Marine Biology, 101*, 389–395. https://doi.org/10.1007/BF00428135

Starko, S., et al. (2023). Marine heatwaves threaten cryptic coral diversity and erode associations among coevolving partners. *Science Advances, 9*(32), eadf0954. https://doi.org/10.1126/sciadv.adf0954

Su, J., Zhang, R., & Wang, H. (2017). Consecutive record-breaking high temperatures marked the handover from hiatus to accelerated warming. *Scientific Reports, 7*(1), 43735. https://doi.org/10.1038/srep43735

Venegas, R., et al. (2023). Three decades of ocean warming impacts on marine ecosystems: A review and perspective. *Deep-Sea Research Part II: Topical Studies in Oceanography, 212*, 105318. https://doi.org/10.1016/j.dsr2.2023.105318