THE PENNSYLVANIA STATE UNIVERSITY
SCHREYER HONORS COLLEGE

DEPARTMENT OF BIOLOGY

THE THERMOTOLERANCE OF DINOFLAGELLATE ENDOSYMBIONT ALGAE IN CULTURE

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SPRING 2023

A thesis
submitted in partial fulfillment
of the requirements
for a baccalaureate degree
in Biology
with honors in Biology

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ABSTRACT

Most reef-building corals form intracellular mutualisms with dinoflagellate endosymbiont algae in the family Symbiodiniaceae, which fulfill a majority of their energetic budget and partly define their response to environmental change. Warming ocean temperatures disrupt coral-symbiont mutualisms during coral bleaching events, triggering mass mortality in reefs and depriving humans of an economically and ecologically significant resource. This investigation monitors the population growth and photochemical efficiency of five cultured species of Symbiodiniaceae, spanning three genera, under ambient and elevated temperatures to derive thermotolerance ratios. Here, I confirm the thermal tolerance of *Symbiodinium microadriaticum* and the thermal sensitivity of *Symbiodinium tridacnidorum*, as established in prior literature; yet, I characterize *Durusdinium trenchii* as thermally susceptible, challenging its status as an extremophile. Significantly, our results suggest that *Breviolum aenigmatum* and *Breviolum pseudominutum* – largely understudied species – exhibit thermal sensitivity and moderate thermal tolerance, respectively. This study provides insight into the within- and between-genera differences in symbionts' susceptibility to heat stress to characterize their potential capacity to confer tolerance to a symbiotic host in the face of environmental change.

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INTRODUCTION

Endosymbionts Sustain Ecologically Essential Coral Hosts

Healthy coral reefs are a cornerstone for marine and human life alike. Coral reefs host nearly a quarter of all fish while supporting one billion people with essential ecosystem services (Knowlton et al., 2010; Resource Watch). Most reef-building corals form an intracellular mutualism with zooxanthellae, microscopic dinoflagellate endosymbiotic algae in the family Symbiodiniaceae. Symbionts photosynthesize to provide food (e.g. carbohydrates) and amino acids to the coral host and, in return, are afforded a protective, nutrient-rich environment to live in. This mutualism is integral in sustaining healthy reefs, as it supplies corals with most of their energy (Sotka & Thacker, 2005).

Warming ocean temperatures disrupt coral-symbiont mutualisms during coral bleaching events, causing the expulsion of symbionts (Hoegh-Guldberg, 1999). Sea temperatures are rising at approximately 1-2°C every century, a rapid rate of environmental change that is likely to exceed the thermal capacity of reef-building corals (Hoegh-Guldberg, 1999). Since the first recorded global coral bleaching event in 1998, such phenomena have increased in expanse and severity, with the most recent – and likely the most damaging – occurring in 2017 (Hoegh-Guldberg, 1999; NOAA Coral Reef Watch, 2019). The symbiont types and densities within a coral host define its growth, reproduction, and mortality by changing its ability to acquire nutrients and respond to environmental change. For instance, cnidarian hosts can form symbiotic associations with non-homologous, thermally tolerant *Durusdinium trenchii* to compensate for declines in its homologous symbiont population, permitting it to better adapt to environmental change (Chen et al., 2020). Evidently, symbiont types and densities play a key role in determining the regional health and diversity of coral reefs (Baskett et al., 2010).

Symbiodiniaceae Diversity and Ecology

Symbiodiniaceae, once classified as a panmictic species, is now understood to be comprised of multiple genera, as substantiated by genetic, eco-physiological, and morphological data (LaJeunesse et

al., 2018). The focal genus of this investigation, *Breviolum,* is divided into two phylogenetic groups: B19, which radiated during the Pliocene, and B1, which radiated during the Pleistocene (LaJeunesse, 2005). *B. pseudominutum* and *B. aenigmatum,* constituents of the B1 and B19 groups respectively, are considered "ecologically cryptic," meaning they can be nonsymbiotic (i.e. free-living) and are only present in hosts at low or undetectable background concentrations (Parkinson et al., 2015; Parkinson et al., 2016). *B. aenigmatum* has been detected once in the wild in the scleractinian mustard hill coral, *Porites astreoides*. However, *B. pseudominutum* has been detected in 11 independent cultures from its wild host, *Oculina varicose,* or the ivory bush coral (Parkinson et al., 2015). These species may occur at low concentrations due to the presence of competitively dominant symbionts that restrict their population size to numbers under the standard thresholds of detection; alternatively, *B. aenigmatum* and *B. pseudominutum* may be free-living or commensal with their hosts (Parkinson et al., 2015; Schoenberg & Trench, 1980). Although their natural ecologies are largely uncharacterized, species sourced from the Greater Caribbean can survive in culture and colonize *Exaiptasia pallida* and *Cassiopea xamachana* under experimental conditions (LaJeunesse et al., 2018).

Other Symbiodiniaceae genera utilized in this investigation adopt a range of life strategies. For instance, *Symbiodinium* spp. can be free-living or symbiotic, and form specialized associations with shallow water hosts in every ocean basin (LaJeunesse et al., 2018; LaJeunesse et al., 2008). *S. microadriaticum* is the homologous endosymbiont of *Cassiopea xamachana*, the upside-down jelly. *S. tridacnidorum* also colonizes jellies of the genus *Cassiopea,* in addition to giant clams in the Pacific, despite being rare in the region (Lee et al., 2015). *Durusdinium* spp. are opportunistic, generalist symbionts capable of horizontal transfer with many hosts, permitting its spread across broad geographic ranges; yet, its diversity is centered in the Indo-West Pacific (LaJeunesse et al., 2018).

Symbiodiniaceae Thermotolerance Ex Hospite

Although not all symbionts can be maintained ex hospite (in culture or via isolation), those that can provide insight into the eco-physiological responses of species to thermal stress within and across

genera. For instance, ex hospite *Breviolum* spp. of the B1 radiation may exhibit a greater or unchanged capacity to acquire inorganic carbon in elevated water temperatures, as evidenced by their declining or constant half-saturation constants of photosynthesis (Oakley et al., 2014). Another *Breviolum* spp. representative of the B1 radiation expressed a significant decrease in F_v/F_m (maximum quantum efficiency of Photosystem II) in high temperature, low light conditions, indicating a decline in the rate of photosynthesis, and eventually ceased growth at 32° C (Robison & Warner, 2006). A member of the B19 delineation, *B. aenigmaticum,* displays a significantly higher thylakoid membrane melting point relative to *B. pseudominutum* (B1), suggesting that *B. aenigmaticum* has more stable photosynthetic membranes under heat stress and may be more thermally tolerant (Parkinson et al., 2016). Additionally, *S. aenigmaticum* has more potential for phenotypic plasticity in response to elevated temperatures, affirming evidence of genotypic differences in heat acclimation amongst the selected *Breviolum* spp. (Parkinson et al., 2016; Mansour et al., 2018).

Symbiodinium spp. are adapted to potentially stressful light conditions, as evidenced by their capacity to produce mycosporine-like amino acids that adsorb UV radiation (Banaszak et al., 2000). Compared to B1 *Breviolum* spp. in (Robison & Warner, 2006), *S. microadriaticum* exhibited a less rapid initial decline in photosystem function, followed by no further significant loss in 32°C temperatures. Further affirming its thermal tolerance, cultured *S. microadriaticum* remained physiologically active under elevated temperatures (Díaz-Almeyda et al., 2017). Another known thermally tolerant genera, *Durusdinium,* contains species adapted to highly variable temperatures and turbidity characteristic of shallow seas, establishing them as bleaching-resistant extremophiles (LaJeunesse et al., 2018). This endosymbiont's thermotolerance facilitated its successful introduction into the tropical Atlantic via human activity (LaJeunesse et al., 2018, Pettay et al., 2015).

In Hospite vs. Ex Hospite Symbiont Thermotolerance

The eco-physiological responses of symbionts in and ex hospite differ across genera. Isolated *Symbiodinium* spp. retained higher net photosynthesis under elevated temperatures compared to when it is

associated with its host, *Aiptasia pallida*, a sea anemone model system for coral research. In contrast, *Breviolum* spp. exhibited opposite trends: symbiotic *Breviolum* spp. exhibited higher net photosynthesis than isolated ones (Goulet et al., 2005). Similar to *Symbiodinium* spp., the photosynthetic apparatus of *Durusdinium trenchii* was shown to be more thermally susceptible in hospite compared to its free-living state, as evidenced by no notable changes in the expression of photosynthesis-related gene ontologies (Bellantuono et al., 2019).

The survival of symbiotic cnidarians in changing environmental conditions is dictated by the synergistic adaptive capacity of themselves and their symbionts. For instance, a host may potentially help prevent the photoinhibition of its symbionts by producing fluorescent pigments, mycosporine-like amino acids, and heat-shock proteins, by altering its antioxidant systems, or by adopting a heterotrophic feeding strategy (Baird et al., 2009). On the other hand, symbionts may be limited in their capacity to photosynthesize due to self-shading and screening by the host (Lesser & Shick, 1989).

Here, I utilize cultured symbionts, since strictly studying symbionts in hospite limits our understanding of their physiological responses to stress, independent of their symbiotic partner (Goulet et al., 2005). Although some investigations use symbionts freshly isolated from host tissues; working with cultured symbionts, in contrast, may help to minimize residual host effects on the photic regimes they experience (Lesser & Shick, 1989). This investigation monitors cell density and F_v/F_m as proxies for growth and photochemical efficiency, respectively, in five cultured symbiont species under thermal stress to characterize the differences in thermal susceptibility within and between symbiont genera. Of particular interest are *B. pseudominutum* and *B. aenigmatum*, as they are ecologically cryptic species with understudied in hospite physiologies; thus isolated cultures are essential in predicting their natural ecologies. It is essential to identify thermally tolerant and intolerant symbionts to predict their capacity to confer resilience to a symbiotic host in a rapidly changing environment.

MATERIALS AND METHODS

Symbiodiniaceae Cultures

Symbiodiniaceae species were sourced from Dr. Todd LaJeunesse's collection at the Pennsylvania State University. The original cultivators of each algal culture are listed in Table 1. *Symbiodinium microadriaticum* (KB8), *Symbiodinium tridacnidorum* (RT362), *Breviolum pseudominutum* (RT147), *Breviolum aenigmatum* (MACO4-180), and *Durusdinium trenchii* (CCMP2408) were utilized in this investigation (Table 1). The thermal susceptibilities of three species were previously characterized in literature (Table 1) utilizing field observations of ecological distribution and experimental measurements of cell count, F_v/F_m, and mycosporine-like amino acid secretions (LaJeunesse et al., 2018; Díaz-Almeyda et al., 2017).

***Table 1*:** Culture Name, Species Name, and Thermal Sensitivity of Symbiodiniaceae spp.

Culture Name	**Species Name**	**Thermal Sensitivity**
KB8	*Symbiodinium microadriaticum*	Tolerant (LaJeunesse et al., 2018)
RT362	*Symbiodinium tridacnidorum*	Sensitive (Díaz-Almeyda et al., 2017)
RT147	*Breviolum pseudominutum*	Unresolved
MAC04-180	*Breviolum aenigmatum*	Unresolved
CCMP2408	*Durusdinium trenchii*	Tolerant (LaJeunesse et al., 2018)

Control and Experimental Growth Conditions of Symbiodiniaceae Cultures

Algal cultures were inoculated with $1x10^6$ cells mL^{-1} in 15 ml tubes containing 8 ml ASP-8A medium (Díaz-Almeyda et al., 2017). Each of the five cultures had three replicates, totaling n=15. Cultures were grown in an incubator at 26°C (ambient temperature conditions) with a 12:12 (light: dark) photoperiod at 100-150 µmol/m^2/s light intensity. Cell counts and photochemical efficiency were measured for all replicates in each culture at ambient temperature (26°C) during the Spring 2021 and Fall 2021 semesters. These metrics were also measured for all replicates in each culture under thermal stress

(32°C) following an acclimation period during the Fall 2022 semester. During the acclimation period, the temperature of the incubator was increased by 1°C every 12 hours from 26°C (ambient temperature) to 32°C (thermal stress temperature) to avoid heat shocking the cultures.

Population Growth

Using a hemocytometer, algal cells were counted as a proxy for culture population growth. *Ambient temperature (26°C):* Algal cells were counted once to twice weekly during the Spring 2021 semester (Days 4, 7, 11, 14, 18, 21, 25, 28, 32), for all replicates in each culture (n_{total} = 135, $n_{reps/species}$ = 27). This trial was repeated during the Fall 2021 semester (Days 4, 18, 21, 28, 33, 35, 39, 44, 46), for all replicates in culture (n_{total} = 90, $n_{reps/species}$ = 18) due to the death of *S. tridacnidorum* in the Spring 2021 trial. *Thermal stress (32°C):* Algal cells were counted once to twice weekly during the Fall 2022 semester (Days 7, 12, 15, 22, 25, 32, 37, 42), for all replicates in each culture (n_{total} = 120, $n_{reps/species}$ = 24).

Photochemical Efficiency

A Mini Pulse Amplitude Modulated (MiniPAM, Walz) Fluorometer was utilized to measure F_v/F_m, the maximum quantum yield of charge separation in photosystem II, a proxy for photochemical efficiency (Díaz-Almeyda et al., 2017). F_v/F_m was measured in both light and dark conditions and analyzed separately to capture the culture's daily range in photochemical efficiency under the experimental light settings. After measuring light F_v/F_m, the cultures were placed in a light-blocking box for 30 minutes before measuring dark F_v/F_m. *Ambient temperature (26°C):* Photochemical efficiency was measured two to three times weekly during the Spring 2021 semester (Days 4, 5, 7, 9, 11, 12, 14, 16, 18, 19, 21, 23, 25, 26, 28, 30, 32), for all replicates in culture (n_{total} = 255, $n_{reps/species}$ = 51). This trial was repeated during the Fall 2021 semester (Days 17, 19, 21, 23, 24, 25, 26, 28, 30, 31, 33, 35, 37, 40, 44, 45, 47), for all replicates in culture (n_{total} = 170, $n_{reps/species}$ = 34) due to the death of *S. tridacnidorum* in the Spring 2021 trial. *Thermal stress (32°C):* Photochemical efficiency was measured two to three times weekly during the Fall 2022 semester (Days 8, 12, 13, 15, 17, 22, 23, 25, 28, 30, 32, 35, 37, 42), for all replicates in each culture (n_{total} = 210, $n_{reps/species}$ = 42).

Statistical Analysis

Three analyses were conducted: Analysis One tested combined ambient data (Spring 2021 and Fall 2021 semesters) against thermal stress data (Fall 2022 data); Analysis Two tested Fall 2021 ambient data against Fall 2022 thermal stress data; Analysis Three tested Spring 2021 ambient data against Fall 2022 thermal stress data. Analyses One through Three were conducted for both cell count and F_v/F_m data.

The lm function in the stats package in R was utilized to test for significant differences (via t-test) between cell counts or F_v/F_m against temperature regime, days elapsed, the interaction between temperature and days elapsed, and replicates (Stats (Version 3.6.2); R Core Team, 2022). Temperature and day were inputted into the linear model as fixed effects. Replicates were inputted as a random effect, permitting differences in the number of replicates of cell count and F_v/F_m measurements to vary randomly between temperature regimes and over time. Plots were created using the ggplot2 package (v3.3.3; Wickham, 2016). m_1 indicates the slope of plots in Analysis One; m_2 indicates the slope in Analysis Two; m_3 indicates the slope in Analysis Three.

Thermotolerance ratios were calculated by averaging the cell count and photochemical efficiency data under ambient temperatures (Spring 2021 and Fall 2021 trials) and pairing them with the same data under heat stress conditions (Fall 2022 trial), according to days elapsed since culture inoculation. This produced a dataset consisting of 13 time points (cell counts) and a dataset of 14 time points (F_v/F_m) across a period of approximately six weeks. *Population growth:* the cell counts were logged under ambient and thermal stress temperatures, and a thermotolerance ratio was calculated by dividing the logged cell counts under ambient temperatures by the logged cell counts under thermal stress (Díaz-Almeyda et al., 2017). *Photochemical efficiency:* F_v/F_m values in ambient and heat stress temperatures were divided by the maximum value, and a thermotolerance ratio was obtained.

RESULTS

The Effects of Thermal Stress (32°C) on Growth (Proxied by Cell Count)

There is a significant difference among replicates in Analysis One across all species, indicating that the ambient temperature datasets collected during the Fall 2021 and Spring 2021 trials exhibited notably different associations with the Fall 2022 elevated temperature data (Table 2). Thus, both ambient datasets were also separately tested and plotted against the elevated temperature data for each species.

Breviolum aenigmatum

B. aenigmatum showed a significant reduction in cell count at 32°C relative to 26°C in Analysis Two (p-value = 0.0358, t-test); no other analyses indicated significant differences (Table 2). There is a significant association between cell count and days elapsed in Analysis Three (p-value = 0.00768, t-test), suggesting notably different growth patterns in each temperature regime. This is corroborated by the trendlines in Fig. 3, which show positive growth (m_3 = 0.019871, p-value = 0.00071, t-test) in ambient temperatures (26°C) and negative growth (m_3 = -0.009366, p-value = 0.00378, t-test) in elevated temperatures (32°C). Variation in cell count was best described by temperature and day in Analysis Three, which yielded the largest R^2 value (R^2 = 0.7034, p-value = 2.405e-05, t-test). The noticeable declines in cell count are substantiated by the cell count thermotolerance ratio of *B. aenigmatum*, -0.4500605615, which indicates thermal intolerance at 32°C relative to 26°C (Fig. 7).

Breviolum pseudominutum

B. pseudominutum exhibited no statistically significant reductions in cell count under elevated temperatures (32°C) across all analyses (Table 2). Analyses Two and Three showed significant associations between days elapsed and cell count, suggesting a difference in growth patterns among temperature treatments (p-value = 0.0117 and 0.00129, respectively; t-test). *B. pseudominutum* exhibits positive growth in Analyses Two and Three at 26°C (m_2 = 0.020283, p-value = 2.66e-05; m_3 = 0.01879, p-value = 5.85e-06; t-test) (Fig. 2, Fig. 3). At 32°C, Analyses Two and Three show slight positive growth

(m_2 = 0.0004893, p-value = 0.8753; m_3 = 0.0004893, p-value = 0.8753; t-test) (Fig. 2, Fig. 3). Variation in cell count was best described by temperature and day in Analysis Three, which yielded the largest R^2 value (R^2 = 0.8621, p-value = 2.4e-08, t-test). The near-zero cell count thermotolerance ratio of 0.007896069342 indicates minimal thermal tolerance at 32°C relative to 26°C (Fig. 7).

Symbiodinium microadriaticum

S. microadriaticum exhibited a significant decrease in cell count at 32°C relative to 26°C in Analysis One (p-value = 0.010289, t-test) (Table 2). Analyses Two and Three indicated a significant association between cell count and days elapsed (p-values = 0.0424 and 0.00345, respectively; t-test), suggesting *S. microadriaticum* experienced significant differences in growth patterns under each temperature treatment. In Analyses Two and Three, the slope of culture growth at 26°C (m_2 = 0.009642, p-value = 0.004392; m_3 = 0.012744, p-value = 0.00789; t-test) is larger than at 32°C (m_2 = 0.002155, p-value = 0.634), suggesting more rapid growth under ambient conditions; although, culture growth at 32°C is positive (Fig. 2, Fig. 3). Variation in cell count was best described by temperature and day in Analysis Three, which yielded the largest R^2 value (R^2 = 0.846, p-value = 2.919e-08, t-test). *S. microadriaticum* exhibited low thermal tolerance at 32°C relative to 26°C, as evidenced by a cell count thermotolerance ratio of 0.2258564362 (Fig 7).

Symbiodinium tridacnidorum

All *S. tridacnidorum* replicates died by Day 30 during the Spring 2021 trial potentially due to bacterial introduction into the cultures; therefore, external factors may have confounded the significance tests and correlation coefficients in Analyses One and Three, and the overall thermotolerance ratio. *S. tridacnidorum* showed a significant reduction in cell count at 32°C relative to 26°C in Analyses One and Three (p-values = 0.01907 and 0.00709, respectively; t-test) (Table 2). Analysis Two indicated a significant association between days elapsed and time (p-value = 0.00486, t-test), corroborating the

difference in growth patterns between temperature treatments. At 26°C, *S. tridacnidorum* exhibited positive growth (m_2 = 0.019087, p-value = 5.66e-05, t-test); at 32°C, it exhibited negative growth (m_2 = -0.006357, p-value = 0.091215, t-test) (Fig. 2). Variation in cell count was best described by temperature and day in Analysis Three, which yielded the largest R^2 value (R^2 = 0.7948, p-value = 1.185e-06, t-test). The significant reduction in cell count at 32°C in Analyses One and Three are substantiated by the cell count thermotolerance ratio of -0.2965737444, indicating thermal intolerance to elevated temperatures (32°C) (Fig. 7).

Durusdinium trenchii

D. trenchii exhibits no significant differences in cell count at 32°C relative to 26°C across all analyses (Table 2). There is a significant association between days elapsed and cell count in Analysis Three (p-value = 0.000389, t-test), which is corroborated by the culture's noticeably different growth patterns between temperature regimes (Fig. 3). The cultures exhibit positive growth in ambient temperatures (26°C) (m_3 = 2.249e-02, p-value = 1.5e-06, t-test) and negative growth in elevated temperatures (32°C) (m_3 = -0.003646, p-value = 0.382, t-test) (Fig. 3). Variation in cell count was best described by temperature and day in Analysis Three, which yielded the largest R^2 value (R^2 = 0.8067, p-value = 6.61e-07, t-test). The noticeable declines in cell count at 32°C are reflected in the cell count thermotolerance ratio of -0.2069397864, indicating thermal intolerance (Fig. 7).

The Effects of Thermal Stress (32°C) on Photochemical Efficiency (Proxied by F_v/F_m)

Breviolum pseudominutum

B. pseudominutum did not exhibit a significant association between F_v/F_m and temperature across all analyses, in both the light and dark measurements (Table 3). Analysis One and Three indicate a significant association between F_v/F_m and days elapsed in both the light (p-value = 1.06e-06 and 0.01234, respectively; t-test) and the dark (p-value = 0.00016 and 0.0165, respectively; t-test), suggesting differences in the changes in photochemical efficiency over time under each temperature regime. This is

substantiated in Fig. 4 and Fig. 6, which show positive or near-zero trends in F_v/F_m over time at 26°C in light (m_1 = 0.002499, p-value = 0.0684; m_3 = 0.004311, p-value = 0.100715; t-test) and dark (m_1 = -0.0004962, p-value = 0.703; m_3 = 0.003894, p-value = 0.0911; t-test) conditions, and a decline in F_v/F_m over time at 32°C in light (m_1 = -0.016754, p-value = 2.83e-05; m_3 = -0.016754, p-value = 2.83e-05; t-test) and dark (m_1 = -0.015599, p-value = 0.000105; m_3 = -0.015599, p-value = 0.000105; t-test) conditions. Variation in cell count was best described by temperature and day in Analysis Two, which yielded the largest R^2 values in the light (R^2 = 0.6532, p-value = 5.008e-07, t-test) and in the dark (R^2 = 0.6331, p-value = 7.465e-07, t-test). Considering light and dark values together, *B. pseudominutum* yields a F_v/F_m thermotolerance ratio of 0.647800993, indicating moderate thermal tolerance (Fig. 7).

Symbiodinium microadriaticum

S. microadriaticum exhibits a significant decrease in F_v/F_m at 32°C relative to 26°C in Analysis One, in light and dark conditions (p-value = 9.57e-05 and 3.41e-08, respectively; t-test) (Table 3). Analysis Three of the dark measurements indicate a significant decrease in F_v/F_m at 32°C (p-value = 0.000381, t-test). Analysis One shows a signification association between days elapsed and F_v/F_m in the light and the dark, suggesting notable changes in F_v/F_m over time among temperature regimes (p-value = 0.04766 and 0.0359, respectively; t-test). Fig. 4 substantiates this association, as there is a noticeable decline in F_v/F_m over time at 26°C in the light (m_1 = -0.007801, p-value = 6.07e-06, t-test) and the dark (m_1 = -0.005030, p-value = 0.00464, t-test), but a near-zero trend in F_v/F_m over time at 32°C in light (m_1 = -0.0005188, p-value = 0.9282, t-test) and dark (m_1 = -0.0003458, p-value = 0.936, t-test) conditions. Variation in cell count was best described by temperature and day in Analysis Three, which yielded the largest R^2 values in the light (R^2 = 0.364, p-value = 0.0006452, t-test) and in the dark (R^2 = 0.6432, p-value = 5.799e-09, t-test). Upon compiling the light and dark F_v/F_m measurements, *S. microadriaticum* yields a F_v/F_m thermotolerance ratio of 0.6941560486, indicating moderate thermal tolerance and corroborating its near-zero change in F_v/F_m over time at 32°C (Fig. 7).

Symbiodinium tridacnidorum

S. tridacnidorum did not exhibit a significant association between F_v/F_m and temperature across all analyses, in both the light and dark measurements (Table 3). There is a signification association between days elapsed and F_v/F_m in Analysis One of the light measurements (p-value = 0.0176, t-test), indicating a difference in the changes in F_v/F_m over time among temperature treatments. This is substantiated by the larger decline in F_v/F_m at 32°C (m_1 = -0.013449, p-value = 0.000548, t-test) relative to the decline in F_v/F_m at 26°C (m_1 = -0.001904, p-value = 0.559, t-test) over time in Fig. 4. Variation in cell count was best described by temperature and day in Analysis Two, which yielded the largest R^2 values in the light (R^2 = 0.5919, p-value = 6.208e-06, t-test) and in the dark (R^2 = 0.7613, p-value = 7.384e-10, t-test). Considering light and dark measurements together, *S. tridacnidorum* exhibits a moderate thermal tolerance of 0.551908782 (Fig. 7).

Breviolum aenigmatum* and *Durusdinium trenchii

The F_v/F_m values of *Breviolum aenigmatum* and *Durusdinium trenchii* remained under the MiniPAM Fluorometer's threshold of detection while at 32°C; hence, I only tested for statistical significance of F_v/F_m over time at 26°C. At 26°C, *B. aenigmatum* exhibited negative growth according to the light (m = -0.0003813, p-value = 0.923, t-test) and dark (m = -0.009000, p-value = 0.010026, t-test) measurements during the Spring 2021 trial. During the Fall 2021 trial at 26°C, *B. aenigmatum* also displayed negative growth in light (m = -0.004803, p-value = 0.13, t-test) and dark (m = -0.008472, p-value = 0.0365, t-test) conditions. At 26°C in the Spring 2021 trial, *D. trenchii* exhibited positive growth in the light (m = 0.017811, p-value = 8.78e-05, t-test) and the dark (m = 0.014129, p-value = 0.000618, t-test). During the Fall 2021 trial at 26°C, *D. trenchii* displayed negative growth according to the light (m = -0.007837, p-value = 0.0119, t-test) and dark (m = -0.006854, p-value = 1.64e-05, t-test) measurements.

***Table 2*:** p-values indicating the significance of the association between the fixed (temperature, day) and random (replicate) independent factors with the dependent factor (cell count), and the R^2 value, for *Symbiodinium microadriaticum*, *Breviolum aenigmatum*, *Breviolum pseudominutum*, *Symbiodinium tridacnidorum*, and *Durusdinium trenchii*. *S. tridacnidorum* died on Day 30 during the Spring 2021 trial at 26°C, affecting Analyses One and Three (indicated in red). *** indicates a p-value of less than .001, ** indicates a p-value of less than .01, * indicates a p-value of less than .05.

		Analysis One	Analysis Two	Analysis Three
Symbiodinium microadriaticum	**Temp**	0.010289 *	0.1553	0.05218
	Day	0.392112	0.0424 *	0.00345 **
	Replicate	0.000846 ***	0.0868	0.81267
	R^2	0.3937, 1.512e-06	0.455, 0.03614	0.846, 2.919e-08
Breviolum aenigmatum	**Temp**	0.244226	0.0358 *	0.70762
	Day	0.093689.	0.1334	0.00768 **
	Replicate	0.000795 ***	0.3994	0.27436
	R^2	0.4898, 1.331e-07	0.4287, 0.2359	0.7034, 2.405e-05
Breviolum pseudominutum	**Temp**	0.084046	0.7976	0.07215
	Day	0.281857	0.0117 *	0.00129 **
	Replicate	0.000486 ***	0.4679	0.88104
	R^2	0.4757, 4.343e-08	0.8026, 7.717e-05	0.8621, 2.4e-08
Symbiodinium tridacnidorum	**Temp**	0.01907 *	0.14363	0.00709 **
	Day	0.9506	0.00486 **	0.27597
	Replicate	0.00777 **	0.91844	0.52359
	R^2	0.439, 2.418e-07	0.6416, 0.001668	0.7948, 1.185e-06
Durusdinium trenchii	**Temp**	0.16393	0.1404	0.892694
	Day	0.59569	0.0927	0.000389 ***
	Replicate	0.00437 **	0.5489	0.519512
	R^2	0.3151, 8.639e-05	0.2627, 0.302	0.8067, 6.61e-07

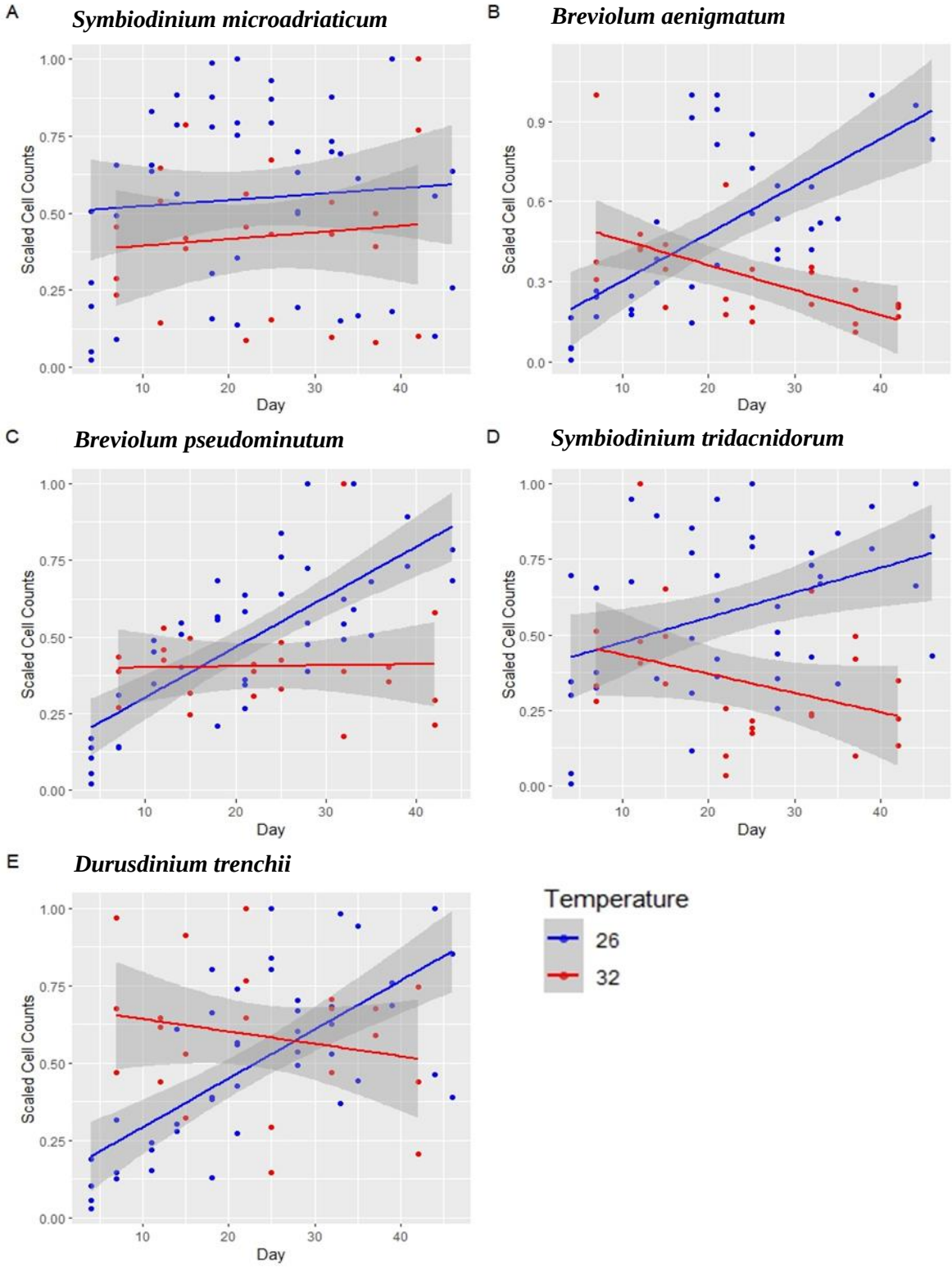

Figure 1: Analysis One. Scaled cell counts of (blue) ambient temperature trials (Spring 2021 and Fall 2021 semesters) and (red) thermal stress temperature trial (Fall 2022 semester) for *Symbiodinium microadriaticum*, *Breviolum aenigmatum*, *Breviolum pseudominutum*, *Symbiodinium tridacnidorum*, and *Durusdinium trenchii*. *S. tridacnidorum* died on Day 30 during the Spring 2021 trial at 26°C, affecting Analysis One.

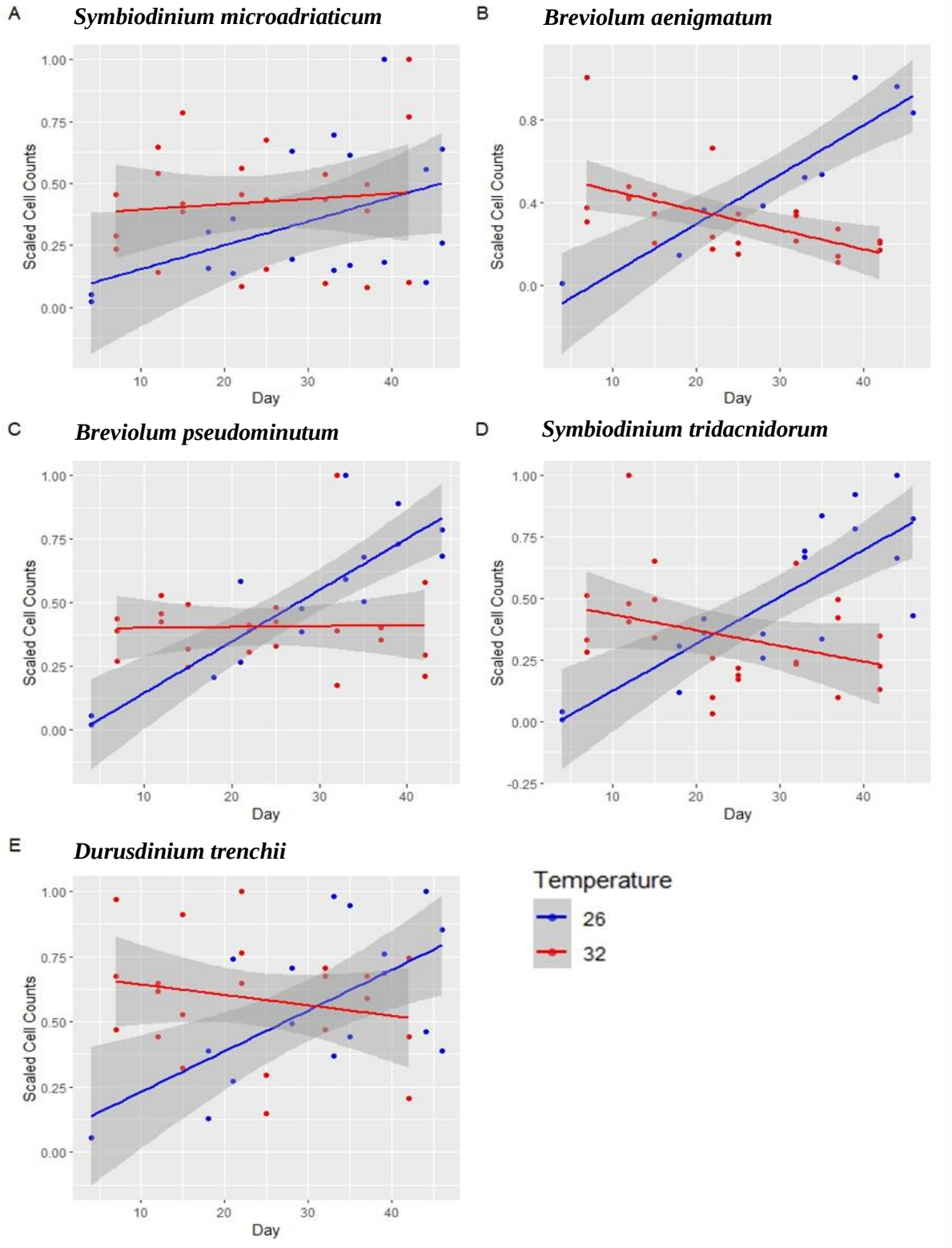

Figure 2: Analysis Two. Scaled cell counts of (blue) ambient temperature trial (Fall 2021 semester) and (red) thermal stress temperature trial (Fall 2022 semester) for *Symbiodinium microadriaticum, Breviolum aenigmatum, Breviolum pseudominutum, Symbiodinium tridacnidorum,* and *Durusdinium trenchii*.

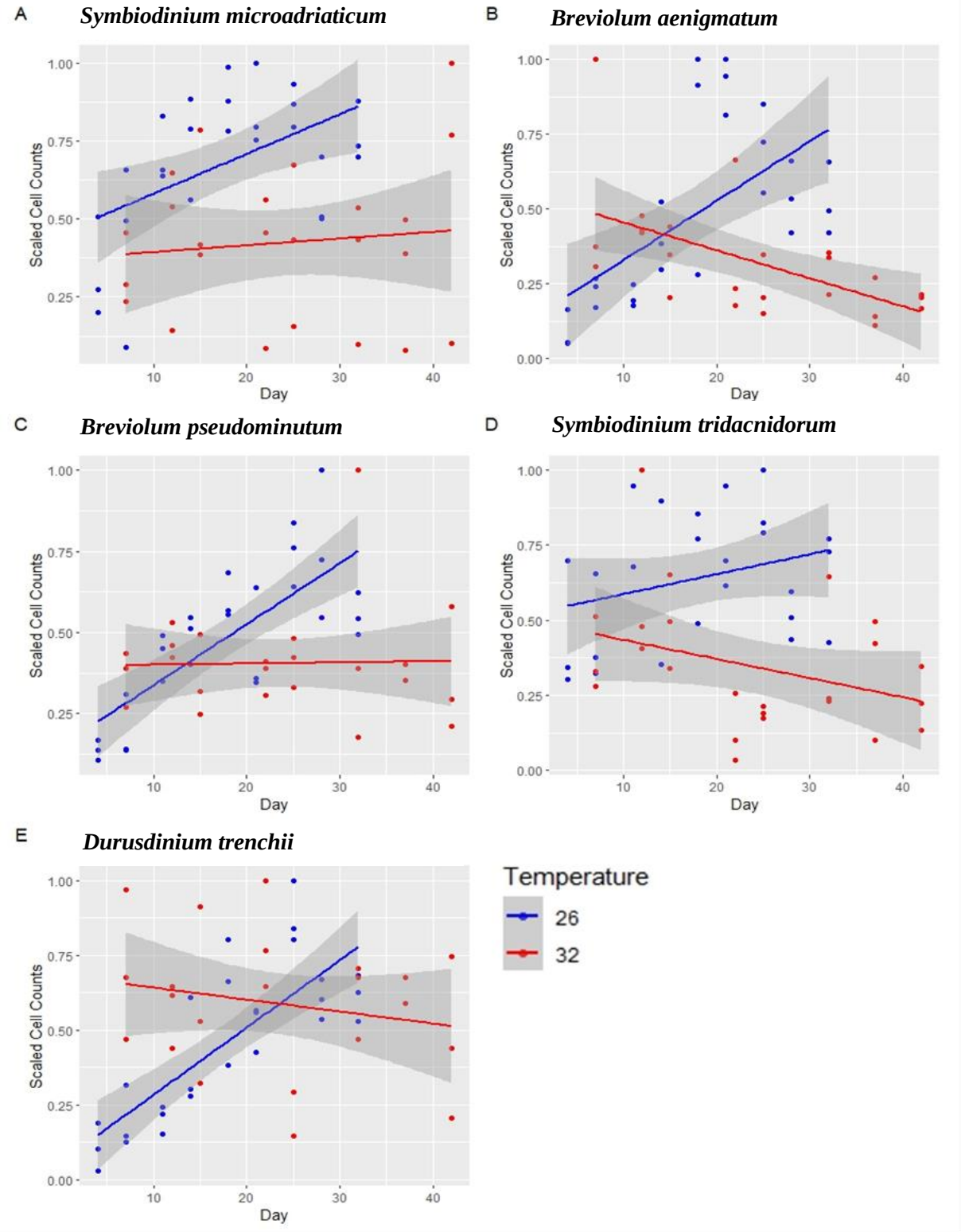

Figure 3: Analysis Three. Scaled cell counts of (blue) ambient temperature trial (Spring 2021 semester) and (red) thermal stress temperature trial (Fall 2022 semester) for *Symbiodinium microadriaticum*, *Breviolum aenigmatum*, *Breviolum pseudominutum*, *Symbiodinium tridacnidorum*, and *Durusdinium trenchii*. *S. tridacnidorum* died on Day 30 during the Spring 2021 trial at 26°C, affecting Analysis Three.

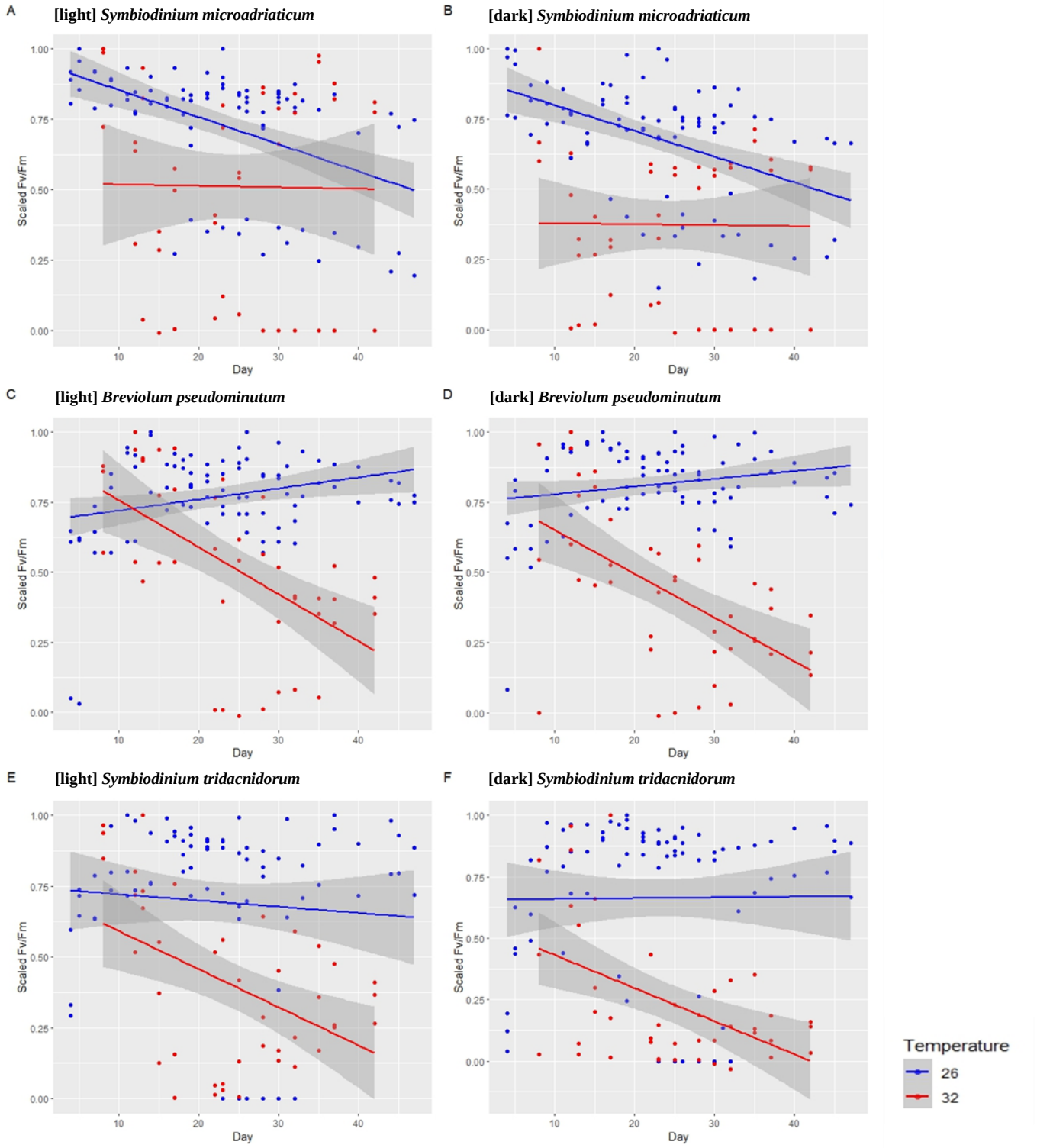

Figure 4: Analysis One. Scaled F_v/F_m of (blue) ambient temperature trials (Spring 2021 and Fall 2021 semesters) and (red) heat stress temperature trial (Fall 2022 semester) in light and dark conditions for *Symbiodinium microadriaticum*, *Breviolum pseudominutum*, and *Symbiodinium tridacnidorum. Breviolum aenigmatum* and *Durusdinium trenchii* did not produce detectable F_v/F_m values at 32°C; thus, they were omitted.

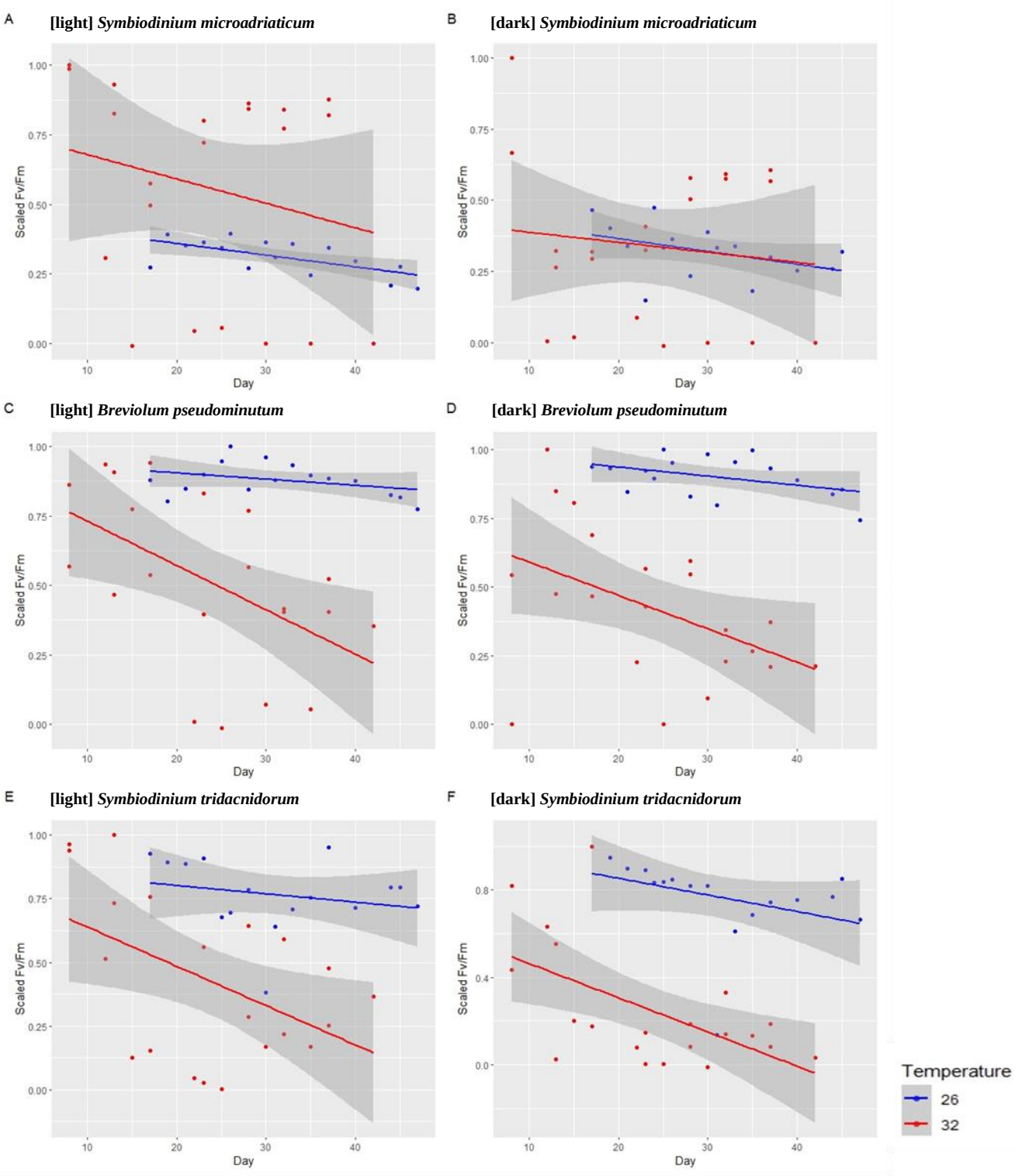

Figure 5: Analysis Two. Scaled F_v/F_m of (blue) ambient temperature trial (Fall 2021 semester) and (red) heat stress temperature trial (Fall 2022 semester) in light and dark conditions for *Symbiodinium microadriaticum*, *Breviolum pseudominutum*, and *Symbiodinium tridacnidorum*. *Breviolum aenigmatum* and *Durusdinium trenchii* did not produce detectable F_v/F_m values at 32°C; thus, they were omitted.

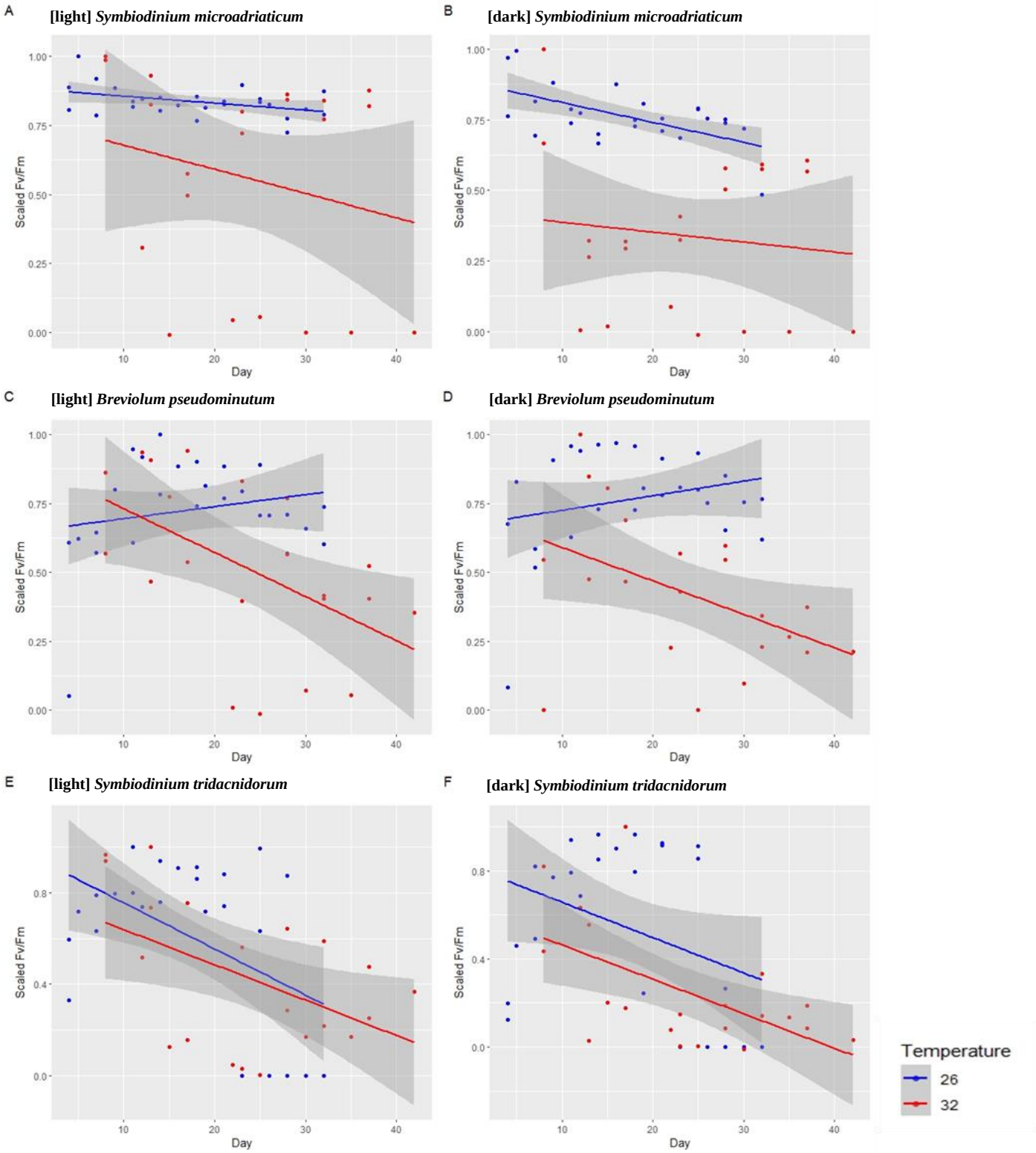

Figure 6: Analysis Three Scaled F_v/F_m of (blue) ambient temperature trial (Spring 2021 semester) and (red) heat stress temperature trial (Fall 2022 semester) in light and dark conditions for *Symbiodinium microadriaticum*, *Breviolum pseudominutum*, and *Symbiodinium tridacnidorum. Breviolum aenigmatum* and *Durusdinium trenchii* did not produce detectable F_v/F_m values at 32°C; thus, they were omitted.

***Table 3*:** p-values indicating the significance of the association between the fixed (temperature, day) and random (replicate) independent factors with the dependent factor (F_v/F_m), and the R2 value, for *Symbiodinium microadriaticum*, *Breviolum pseudominutum*, and *Symbiodinium tridacnidorum* in light and dark conditions. *Breviolum aenigmatum* and *Durusdinium trenchii* did not produce detectable F_v/F_m values at 32°C; thus, they were omitted. *** indicates a p-value of less than .001, ** indicates a p-value of less than .01, * indicates a p-value of less than .05.

		Analysis One	Analysis Two	Analysis Three
***Symbiodinium microadriaticum* (light)**	**Temp**	9.57e-05 ***	0.452	0.3043
	Day	0.04766 *	0.808	0.5641
	Replicate	0.00158 *	0.801	0.6059
	R^2	0.3386, 3.613e-10	0.1709, 0.1861	0.364, 0.0006452
***Symbiodinium microadriaticum* (dark)**	**Temp**	3.41e-08 ***	0.96	0.000381 ***
	Day	0.0359 *	0.809	0.395302
	Replicate	7.83e-05 ***	0.526	0.932681
	R^2	0.5264, < 2.2e-16	0.04123, 0.8462	0.6432, 5.799e-09
***Breviolum pseudominutum* (light)**	**Temp**	0.0832	0.2941	0.30302
	Day	1.06e-06 ***	0.0966	0.01234 *
	Replicate	0.2915	0.0126 *	0.86853
	R^2	0.4613, 2.183e-15	0.6532, 5.008e-07	0.3918, 0.0002688
***Breviolum pseudominutum* (dark)**	**Temp**	0.59497	0.311	0.8961
	Day	0.00016 ***	0.294	0.0165 *
	Replicate	0.04377 *	0.855	0.0604
	R^2	0.6137, < 2.2e-16	0.6331, 7.465e-07	0.5557, 5.051e-07
***Symbiodinium tridacnidorum* (light)**	**Temp**	0.5641	0.79436	0.765
	Day	0.0176 *	0.20263	0.509
	Replicate	0.1388	0.00567 **	0.332
	R^2	0.2191, 5.088e-06	0.5919, 6.208e-06	0.2809, 0.006786
***Symbiodinium tridacnidorum* (dark)**	**Temp**	0.478288	0.3653	0.384
	Day	0.082050	0.5447	0.709
	Replicate	0.000813 ***	0.0120 *	0.5
	R^2	0.3908, 1.839e-12	0.7613, 7.384e-10	0.3192, 0.002402

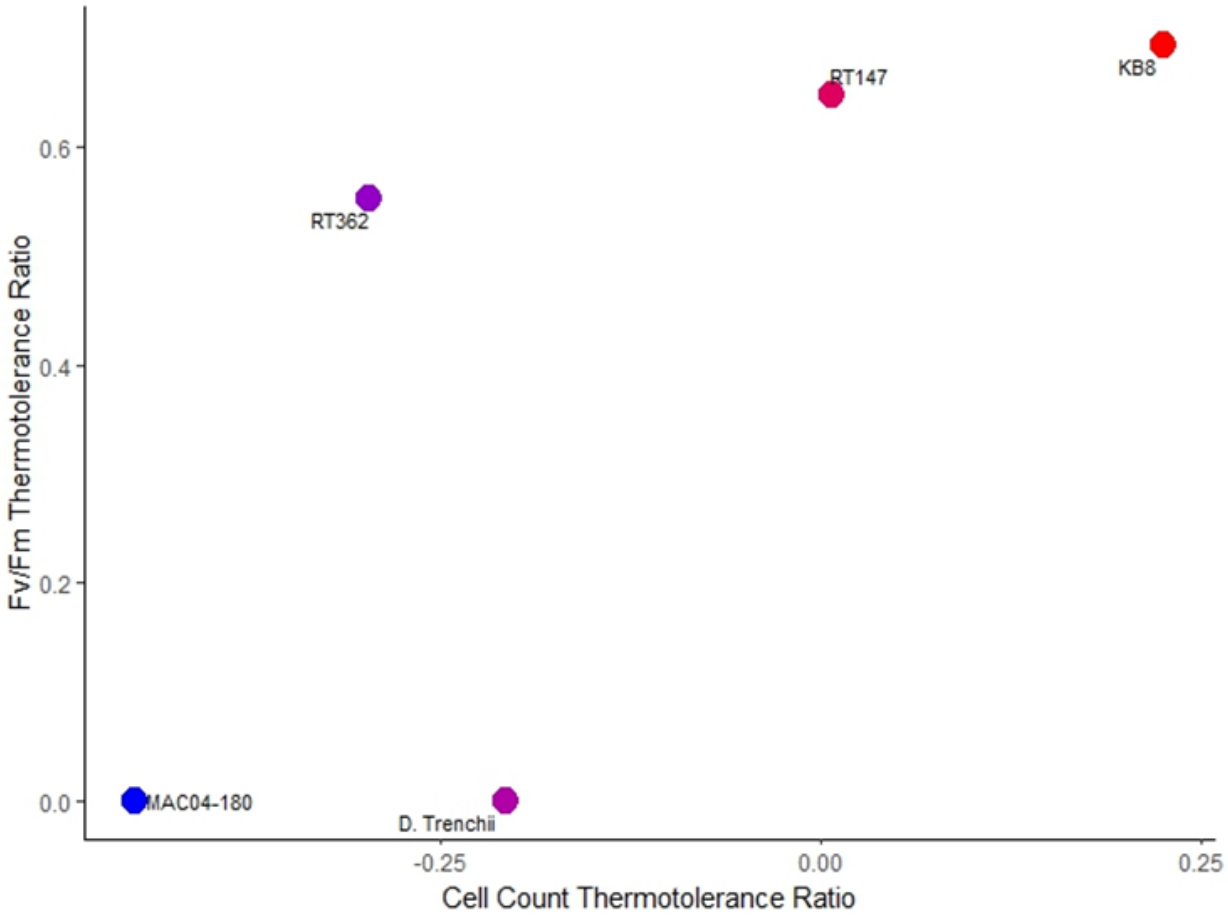

Figure 7: Cell count and F_v/F_m thermotolerance ratios for *Symbiodinium microadriaticum* (KB8), *Breviolum aenigmatum* (MAC04-180), *Breviolum pseudominutum* (RT147), *Symbiodinium tridacnidorum* (RT362), and *Durusdinium trenchii* (CCMP2408) . Red indicates thermal tolerance; blue indicates thermal sensitivity. *B. aenigmatum* and *D. trenchii* did not produce detectable F_v/F_m values at 32°C; thus, they have F_v/F_m thermotolerance ratios of 0.0.

DISCUSSION

Comparison of the Effects of Thermal Stress (32°C) on Symbiodiniaceae

Generalized thermotolerance ratios derived from averaged cell count and F_v/F_m values at 26°C and 32°C indicate the thermal tolerance of each species relative to one another (Fig. 7). *B. pseudominutum* (Culture RT147) exhibited the second-highest overall thermal tolerance, as evident by its growth trends and photochemical efficiency (Tables 2 and 3, Fig. 7). This corroborates the known ability of B1 radiation species to maintain metabolic function under elevated temperatures (Oakley et al., 2014) but refutes previously documented declines in growth and photochemical efficiency at 32°C (Robison & Warner, 2006). This reveals the diversity in responses to heat stress within the B1 radiation group and necessitates the further study of within-radiation group thermal susceptibility. Although *B. pseudominutum* occurs at low background concentrations in its natural host, the ivory bush coral, its potential thermal tolerance may allow it to persist in elevated ocean temperatures and assume a higher concentration within its symbiotic partner (Parkinson et al., 2015). *B. aenigmatum* (Culture MAC04-180) exhibited the lowest overall thermal tolerance, despite its known phenotypic plasticity in elevated temperatures (Parkinson et al., 2016). Although it retained physiological activity, as evidenced by the presence of living cells in culture; *B. aenigmatum*'s photochemical efficiency remained under the threshold of detection of the MiniPAM at 32°C, suggesting thermal intolerance. *B. aenigmatum*'s thermal sensitivity may facilitate its suppression to the low, background concentrations in hosts described by (Parkinson et al., 2015). The difference in thermal tolerance within genera and radiation groups warrants the continued characterization of the understudied eco-physiologies of *Breviolum* spp.

S. microadriaticum (Culture KB8) exhibited the highest overall thermal tolerance, substantiating its previously studied capacity to retain photosystem function and physiological activity in elevated temperature conditions (Robison & Warner, 2006; Díaz-Almeyda et al., 2017). *S. tridacnidorum* (Culture RT362) showed the third-highest overall thermal tolerance; although, there is a larger decline in cell count

relative to photochemical efficiency at 32°C, suggesting the uncoupling of growth and photosynthesis. The uncoupling of these processes has been documented previously in *S. microadriaticum* (Robison & Warner, 2006). The differences in thermal susceptibility among *Symbiodinium* spp. may be indicative of the habitat ranges of their hosts. *S. tridacnidorum* is more thermally sensitive than *S. microadriaticum*, which may be attributed to *S. tridacnidorum*'s affinity to form symbiotic associations with giant clams in colder Pacific waters (Lee et al., 2015).

D. trenchii exhibited the second lowest overall thermal tolerance, refuting its status as an extremophile resistant to highly variable temperatures (LaJeunesse et al., 2018). This culture undergoes noticeable decoupling of photosynthesis and growth, as evidenced by its higher cell count thermotolerance ratio relative to its F_v/F_m thermotolerance ratio. The unanticipated thermal intolerance of *D. trenchii* can be attributed to its previously studied biphasic growth pattern in ambient temperatures (26°C) (Klueter et al., 2017). The initial lag phase in biphasic growth may have been lengthened under thermal stress, resulting in relatively low cell counts and undetectable F_v/F_m measurements within the trial period, necessitating a longer trial run. Alternatively, the origin of the *D. trenchii* culture may influence its rate of proliferation in culture.

In conclusion, I characterized the within- and between-genera differences in symbionts' susceptibility to heat stress, notably the potential thermal tolerance of *B. pseudominutum* and thermal intolerance of *B. aenigmatum*, both ecologically cryptic species. Although cultured symbionts can provide insight into their host's eco-physiological response to environmental change, it is essential to assess their thermal tolerance both inside and outside of a symbiotic partner, as survival depends on the synergistic adaptive capacity of the symbiont and host. This investigation warrants further investigation into the intra-genera variability in thermal tolerance of Symbiodiniaceae, both in hospite and ex hospite, to better predict their capacity to confer resilience to a symbiotic host during bleaching phenomena.

ACKNOWLEDGEMENTS

This undergraduate thesis was conducted in Dr. Mónica Medina's laboratory. Thank you to Dr. Medina for her support throughout my undergraduate career and for inspiring me to pursue a career in marine science. Immense thanks to Victoria Sharp for her constant guidance in designing and executing my project, teaching me new laboratory techniques, and being willing to answer my questions. During my four years as Victoria's mentee, her breadth of knowledge and noticeable passion for research encouraged me to continually dive deeper into my studies, at and outside of Penn State. Additionally, I would like to express my gratitude for Dr. Raúl González-Pech's, Dr. Marta Mammone's, and Julia Stewart's help in analyzing and compiling my data. Finally, thank you to Dr. Todd LaJeunesse for his mentorship and willingness to lend his laboratory's cultures and facilities to my investigation.

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PROFESSIONAL AND RESEARCH EXPERIENCE

Undergraduate Research Assistant **Sept. 2019-Present**
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- Investigate the adaptive potential of *Cassiopea xamachana* jellyfish and their symbionts under heat stress
- Plot and test the significance of algal growth and photochemical efficiency curves using R
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Ernest F. Hollings Scholarship Intern **June 2022-Aug. 2022**
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- Managed daily deployment of a two-meter ring net and midwater trawl on a three-week research cruise
- Parameterized organisms' physiologies in a MATLAB ECOTRAN ecosystem model with cruise data
- Designed and executed model simulations under alternate metabolic cost and temperature regimes to predict the effect of environmental change on production rates and community composition

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- Outlined and performed an experiment to quantify how *Mnemiopsis leidyi* mucus alters oceanic food webs
- Utilized statistics to assess the individual and additive effects of stressors on *M. leidyi* mucus production

Crew Member **Dec. 2019-Jan. 2020**
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- Collaborated with seven students for a 30-page report on the effects of chemical parameters on plankton
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Snyder, JT, S Calhoun-Grosch, KL Robinson. (2022) The Effects of Mechanical Disturbance and Food Concentration on *Mnemiopsis leidyi* Mucus Production. Oral Presentation. *Joint Aquatic Sciences Meeting*, Grand Rapids, MI, USA.

Snyder, JT, S Calhoun-Grosch, KL Robinson. (2021) The Effects of Mechanical Disturbance and Food Concentration on *Mnemiopsis leidyi* Mucus Production. Poster Presentation. *Healthy Streams, Healthy Coasts Symposium*, University of Louisiana at Lafayette.

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Janice A. Jacobs Friend of the Commonwealth Award | The Pennsylvania State University	**2022**
NOAA Ernest F. Hollings Undergraduate Scholar | National Oceanic and Atmospheric Administration	**2021**
VALLEY Magazine Cover Star | The Pennsylvania State University	**2021**
The Evan Pugh Scholar Award | The Pennsylvania State University	**2021**
Nominee for Rock Ethics Institute Stand Up Award | The Pennsylvania State University	**2021**
The President's Freshman Award | The Pennsylvania State University	**2020**
Salutatorian | Lower Dauphin High School	**2019**