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Research Article
Physiological Response to Thermal Stress of the Caribbean Corals *Orbicella annularis* and *Porites astreoides*

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Abstract

Background and Objective: The physiological response of corals to ocean warming is an essential component of their overall resiliency to climate change. It is important to understand how increasing sea surface temperature will affect the mutualistic relationship between corals and their endosymbionts dinoflagellates (*Symbiodinium* spp.). This study focused on the effects of temperature stress on the photophysiology of two Caribbean corals differing in life history strategies: *Orbicella annularis* (*O. annularis*) and *Porites astreoides* (*P. astreoides*). **Materials and Methods:** A total of 12 fragments of each species were collected from the Puerto Morelos, Mexico shoreline. Six fragments of each species were placed under ambient light and a water temperature of 28°C and the other six under ambient light and an elevated temperature of 32°C for 10 days. Maximum pressure over photosytem II (Qm) was estimated daily while chlorophyll content and *Symbiodinium* densities were measured at the end of the experiment. **Results:** Qm values were considerably higher in *O. annularis* at 32°C when compared to *O. annularis* at 28°C. In contrast, Qm values for *P. astreoides* did not differ significantly between treatments. Interestingly, Qm values of *P. astreoides* at 32°C was similar to that of *O. annularis* at 28°C. *Orbicella annularis* showed higher *Symbiodinium* densities and significantly higher concentrations of chlorophyll a at 28°C than at 32°C. In *P. astreoides*, no differences on chlorophyll content and *Symbiodinium* densities were found between temperature treatments. *Porites astreoides* showed higher chlorophyll a content and *Symbiodinium* densities than *O. annularis* under high temperature stress. **Conclusion:** Low Qm values but high chlorophyll concentrations and *Symbiodinium* densities within *P. astreoides* after induced temperature stress provides a physiological basis of the opportunistic strategy of this species. However, the significant increase in Qm, lower chlorophyll a concentration and reduced *Symbiodinium* densities observed in *O. annularis* at 32°C highlights its vulnerability to ocean warming. If *O. annularis*, which is considered one of the main builders of Caribbean coral reefs, disappears and is replaced by relatively small and weedy *P. astreoides*, the structural heterogeneity of Caribbean coral reefs will be reduced.

Key words: Resiliency, photo acclimation, *Symbiodinium* densities, algal dinoflagellates, photosystem II

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Corals are particularly vulnerable to climate change because they live near their physiological thermal tolerance, making them susceptible to small but rapid changes in sea surface temperature[1]. Nonetheless, the observed effects of increasing sea surface temperature on different coral species will depend on their phenotypic plasticity, genetic diversity, availability of habitats and ecological interactions within the different ecosystems[1]. Reef building corals live in mutualism with algal dinoflagellates from the genus *Symbiodinium*. The photosynthetic activity of *Symbiodinium*, which is hosted within the coral tissue, provides up to 90% of the amount of energy or quantity of carbon supplied that coral needs for functioning and the coral in turn provides protection, ammonia and phosphate that the algae assimilate[2].

Temperature is considered one of the major physical parameters that can alter the relationship between a coral and its endosymbionts. Some mechanisms on how thermal stress alters the photosynthetic performance of *Symbiodinium* include the damage of the D1 protein within the PS II reaction centers[3-5], impairment of the calvin cycle[6], damage of the rubisco site[7], thylakoid membranes deterioration[8] and the inhibition of light harvesting antennae proteins[9]. Thermal stress can also interrupt the coral/algal symbiosis by heat-induced bleaching[10], a phenomenon that refers to the reduction or loss of *Symbiodinium*. Indeed, the increase in ocean temperature has caused catastrophic mass bleaching events, such as the episode of 1998 which severely damaged 16% of coral reefs worldwide[11]. The Caribbean has also experienced these events including the bleaching event in 2005 that severely impacted the population dynamics and demography of *Orbicella annularis*, an important frame boulder coral species[12]. A reduction in the photosynthetic efficiency of corals may compromise their rates of calcification, survival and reproduction[13] increasing their susceptibility to coral diseases and lowering the capability to compete for space with macroalgae. Current climate change scenarios project increases of between 1.2 and 2.6°C on average ocean surface temperature for the year 2100[1]. It thus becomes essential to identify which coral species will have the physiological capacity (i.e., phenotypic plasticity) to cope with the expected increases in temperature.

The objectives of this study included a comparison of the photosynthetic performance of algal symbionts of two of the most common scleractinians in Caribbean coral reefs, *Orbicella annularis* and *Porites astreoides*, under elevated temperature stress. *Porites astreoides* is characterized by high population growth rates[14], high coral cover[15], weedy life-history traits[16-17], high fecundity[18-20] and the production of brooded larvae[19-20] that normally settle at elevated densities regardless of depth[20]. *Orbicella annularis*, on the other hand, is characterized by slow growth, longer generation times, high fecundity (but low recruitment) and large corallites[17]. A comparison of *Symbiodinium* densities, chlorophyll content and photochemical efficiency based on the maximum excitation pressure over photosystem II (Qm) was done. Qm represents the interaction of photochemical and non-photochemical processes in the algal symbiont[21]. The main hypothesis was that under high thermal stress *Symbiodinium* within the weedy coral *P. astreoides* would perform better showing higher densities, higher Chl a and c content and lower Qm values. This research was a controlled experiment which explored the effects of elevated temperature on the physiology of corals. Even though the study was completed 2.5 years ago, it contributes to the advancement of knowledge because of the current increase of sea surface temperature that is affecting the mutualistic relationship between corals and their endosymbionts dinoflagellates (*Symbiodinium* spp.). Furthermore, ocean warming is predicted to continue affecting this symbiosis altering coral reef ecosystem dynamics. Therefore, the study provides essential data that can be used by coral reef managers to deal with the challenge of ocean warming.

MATERIALS AND METHODS

Sample collection: Twenty four *O. annularis* (n = 12) and *P. astreoides* (n = 12) fragments (2-4 cm^2) were collected using a hammer and a chisel at a coral nursery in Puerto Morelos, Mexico (2-4 m, 20°52' 48.9" N, 86°50' 59.34" W) in October, 2014. Fragments of each species belonged to three different parent colony (genets). The fragments were acclimated for 7 days under ambient temperature and light conditions in a seawater table at the Universidad Nacional Autónoma de México, Unidad de Sistemas Arrecifales in Puerto Morelos.

Experimental design: Six fragments of each species were placed at the center of the control seawater table (temperature range of 28.4-30.6°C), while the other six fragments were placed at the experimental seawater table with increased temperature (temperature range of 31.0-32.2°C). Fragments were placed in two rows of, 2-3 cm apart of each other and alternating species. Temperature within the experimental seawater table was maintained using a NEMA 4X Electronic Temperature Control (Ranco, Plain City,

Ohio, USA). Temperature in both seawater tables were monitored twice a day using a thermometer. These measurements were taken at different points around the two rows of fragments in each seawater table to avoid exposing the fragments to different temperature regimes. In this way, it was tried to compensate for the lack of independent temperature replication of the colonies, a limitation of that experiment. The daily irradiance exposure was 481.17±10.59 μmol photons m^{-2} sec^{-1} (Mean±SE) (data provided by the Servicio Académico de Monitoreo Meteorología y Oceanografía de la UASA del ICML de la UNAM). The experiment was run for 10 days after acclimation.

Fluorescence determinations: Fluorescence measurements were performed everyday (for 7 days) using an underwater pulse amplitude fluorometer or diving-PAM (Walz, Effeltrich, Germany). It was measured that the light-dependent reductions of the effective quantum yield of photosystem II (F/Fm') at noon and at dusk (F_v/F_m). These two values were used to calculate the maximum excitation pressure over photosystem II (Qm) or 1-[(F/F_m' at noon)/(F_v/F_m at dusk)][22].

Coral tissue extraction and processing: Coral tissue was removed using an airbrush and filtered sea water. The resulting slurry containing coral tissue and symbiotic algae was homogenized and centrifuged (Thermo Fisher Scientific, Waltham, Massachusetts, USA) at 2000 rpm for10 min. A total of 5 mL of supernatant was removed for protein analysis and stored samples in freezer. Afterwards, discarded the remaining supernatant. The pellet was re-suspended in 5 mL filtered seawater and removed 0.5 mL for cell counts. Samples were preserved in 200 μL iodine. Finally, we removed 3 replicates of 0.3 mL subsamples for chlorophyll analysis.

Pigment analysis and *Symbiodinium* densities: Three replicates of the 0.3 mL subsamples were placed into 3 Eppendorf tubes (300 μL each), centrifuged at 13,000 rpm for 1 min. After this, samples were processed in the dark at 4°C. Then added 50 μL DMSO and vortex the samples. Then, added 950 μL Acetone and vortex once again. Tubes were wrapped in aluminum foil and stored them at 4°C for 12 h. After the 12 h, we centrifuged at maximum speed for 5 min and read absorption (630, 663 and 750 nm) in 1 mL glass cuvettes. Chlorophyll a and c concentrations were determined by using the equations of Jeffrey and Humphrey[23]. *Symbiodinium* densities were determined with triplicate counts in a hemacytometer (LW Scientific, Lawrenceville, Georgia, USA).

Estimated absorbance (D_e) calculations based on reflectance measurements: Reflectance measurements were done following Enríquez *et al.*[24]. The reflectance spectra of corals were measured between 400 and 750 nm using a fiber optic attached to an USB4000 Spectrometer (Ocean Optics, Winter Park, Florida, USA). Coral samples were submerged in seawater in a small glass container with a black bottom. Uniform lighting was provided by an incandescent light source placed 25 cm above the coral surface (see Enriquez *et al.*[24] for further details). The fiber optic was placed underwater, 1 cm away from the sample. Reflectance measurements were expressed as the ratio of the radiance measured from the coral surface relative to the radiance obtained from a reference white coral skeleton[24]. These data were used to calculate the absorbance (D_e) which was expressed as $D_e = LOG_{10}$ (1/Reflectance). Chl a specific absorption coefficient was calculated by relating:

$$a^{*}chl\ a = \ln 10 \left(\frac{De}{\rho}\right)$$

Where:

ρ = Pigment content per surface area (mg cm^{-2})

D_e = Estimated absorbance described above but using only values at 675 nm[24-25]

At this wavelength, the reflectance of the skeleton is closer to one and it reduces the intrusion of accessory algal and animal pigments[24-25].

Statistical analyses: Fluorescence data were analyzed using a two-way repeated measures ANOVA, followed by Holm-Sidak multiple comparison tests. Factors included type of species, temperature treatments and number of days. Chlorophyll a and c and *Symbiodinium* densities were analyzed using a two-way ANOVA followed by Holm-Sidak multiple comparison tests. Factors included type of species and temperature treatments ($p<0.05$).

RESULTS

Fluorescence measurements: The mean maximum pressure over photosystem II (Qm) in *O. annularis* was significantly lower ($p<0.05$) between the 28°C (mean 0.145±0.029 SE) and 32°C (mean 0.277±0.041 SE) water temperature treatments during the 7 days that these measurements were taken (Fig. 1, Table 1). There was also a significant temporal heterogeneity in Qm, with significantly lower values in *P. astreoides*) and 28°C treatment on days 2-3 and 5-7. No significant differences were found in Qm of *P. astreoides* colonies at 28°C and those at 32°C (Fig. 2).

Chlorophyll a content: *Porites astreoides* at 28°C had significantly more chlorophyll a (19.23 mg cm^{-2}±1.18 SE) than at 32°C (11.83 mg cm^{-2}±1.15 SE). *Orbicella annularis* exhibited the same pattern, with significantly higher concentrations of chlorophyll a at 28°C (10.82 mg cm^{-2}± 0.88 SE) than at 32°C (3.28 mg cm^{-2}±0.27 SE) (Fig. 3, Table 2). Also, chlorophyll a content in *P. astreoides* at 32°C and *O. annularis* at 28°C were significantly higher ($p<0.05$) than *O. annularis* at 32°C. However, no significant differences in chlorophyll a content were found between *P. astreoides* at 32°C and *O. annularis* at 28°C.

Chlorophyll a specific absorption coefficient: Results on the Chl a specific absorption coefficient showed the highest absorption coefficient in *O. annularis* at 32°C (0.460 cm^2 mg^{-1} Chl a) and the lowest absorption coefficient in *P. astreoides* 28°C (0.076 cm^2 mg^{-1} Chl a) while *P. astreoides* at 32°C and *O. annularis* at 28°C showed similar values (0.140 and 0.130 cm^2 mg^{-1} Chl a, respectively) (Table 3).

Chlorophyll c content: *Porites astreoides* had significantly more ($p<0.05$) chlorophyll c at 28°C (9.35 mg cm^{-2}±0.48 SE) than at 32°C (5.72 mg cm^{-2}±0.60 SE). *Orbicella annularis* followed the same pattern, with more chlorophyll a at 28°C (4.59 mg cm^{-2}±0.52 SE) than at 32°C (2.24 mg cm^{-2}±0.63 SE) (Fig. 4, Table 4). The results of the effect of temperature on chlorophyll c content were similar to those of chlorophyll a, in *P. astreoides* and *O. annularis*. However, no significant differences in chlorophyll c content were found between *P. astreoides* at 32°C and *O. annularis* at 28°C.

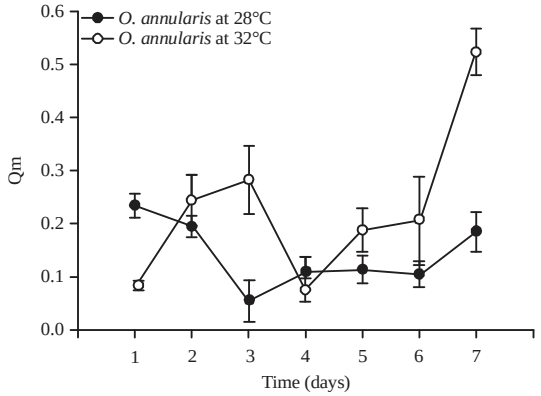

Fig. 1: Qm (±SE) values for *O. annularis*

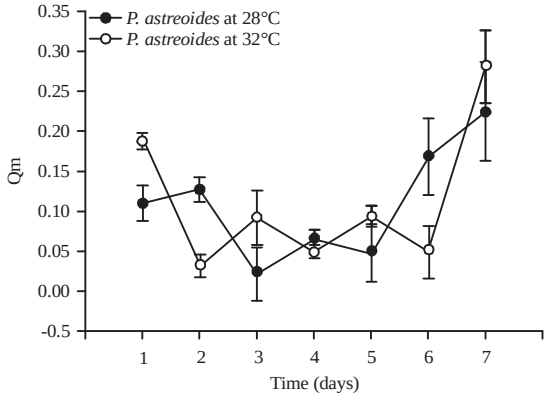

Fig. 2: Qm (±SE) values for *P. astreoides*

Table 1: Two way-repeated measures ANOVA results for the fluorescence data (statistical analyses only for 7 days)

Source of variation	DF	SS	MS	F	p-value
Species+Temperature	3	0.377	0.126	7.855	0.001
Subject* (Species+Temperature)	21	0.336	0.016		
Time	6	0.545	0.0909	12.038	<0.001
(Species+Temperature)×Time	18	0.662	0.0368	4.874	<0.001
Residual	126	0.951	0.00755		
Total	174	2.867	0.0165		

*Subject: Number of fragments

Table 2: Results for the two-way ANOVA analysis for chlorophyll a data

Source of variation	DF	SS	MS	F	p-value
Species	1	1087.147	1087.147	84.6300	<0.001
Temperature (°C)	1	775.114	775.114	60.3390	<0.001
Species×Temperature	1	1.200	1.200	0.0935	0.761
Residual	44	565.219	12.846		
Total	47	2428.681	51.674		

Table 3: Chl a specific absorption coefficient values for each treatment

Species+Treatment	Chlorophyll a density (mg cm^{-2})	De LOG ($1/R_{675}$)	a* Chlorophyll a (cm^2 mg^{-1})
P. astreoides at 28°C	19.2	0.68	0.076
P. astreoides at 32°C	11.8	0.75	0.140
O. annularis at 28°C	10.8	0.61	0.130
O. annularis at 32°C	3.3	0.66	0.460

***Symbiodinium* densities:** *Porites astreoides* colonies at 28°C had significantly higher ($p<0.05$) *Symbiodinium* densities cm^{-2} ($3.07\times10^6\pm5.64\times10^5$ SE) than at 32°C ($1.51\times10^6\pm3.44\times10^5$ SE). *Orbicella annularis* followed the same pattern, with higher *Symbiodinium* densities at 28°C ($1.49\times10^6\pm3.18\times10^5$ SE) than at 32°C ($3.64\times10^5\pm1.02\times10^5$ SE) (Fig. 5, Table 5).

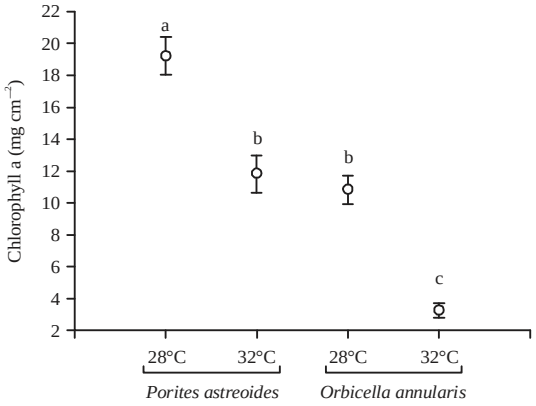

Fig. 3: Chlorophyll a content (mg cm^{-2}) (±SE) for both species and treatments
Different letters denote statistical difference ($p<0.05$)

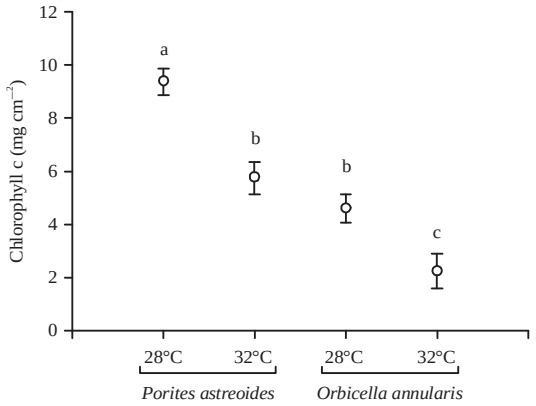

Fig. 4: Chlorophyll c (mg cm^{-2}) (±SE) for both species and treatments
Different letters denote statistical difference ($p<0.05$)

DISCUSSION

Algal symbionts within *O. annularis* exposed to the elevated temperature (32°C) showed the highest maximum pressure over photosystem II (Qm) in comparison to symbionts in *O. annularis* exposed to normal temperature conditions, while *P. astreoides* exposed to both temperature treatments did not differ significantly in Qm. Differences in Qm values have been used to explain the vertical distribution of corals in the Pacific[22]. As Qm approaches 1.0, a higher fraction of PS II reaction centers are closed, causing photoinhibition[22]. Warner *et al.*[21] found similar patterns in Belize when comparing symbionts within the same species. In that study pressure over PS II or Qm in *P. astreoides* was significantly lower than in *O. annularis* colonies at 8 m without any thermal

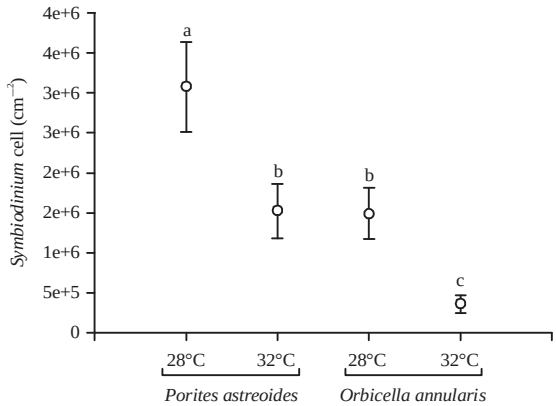

Fig. 5: *Symbiodinium* densities (±SE) for both species and treatments
Different letters denote statistical difference ($p<0.05$)

Table 4: Two-way ANOVA results for chlorophyll c content

Source of variation	DF	SS	MS	F	p-value
Species	1	244.518	244.518	49.723	<0.001
Temperature (°C)	1	141.554	141.554	28.785	<0.001
Species×Temperature	1	11.032	11.032	2.243	0.141
Residual	44	216.373	4.918		
Total	47	613.478	13.053		

Table 5: Two-way ANOVA results for *Symbiodinium* densities

Source of variation	DF	SS	MS	F	p-value
Species	1	1.25E+13	1.25E+13	15.867	0.001
Temperature	1	9.61E+12	9.61E+12	12.234	0.003
Species×Temperature	1	3.38E+11	3.38E+11	0.430	0.521
Residual	16	1.26E+13	7.85E+11		
Total	19	3.50E+13	1.84E+12		

stress. Also, when exposed briefly to elevated temperature, a higher loss in PS II activity was found in *Orbicella* colonies compared to *P. astreoides* colonies. However, Qm values from *P. astreoides* and *O. annularis* at 25 m reported by Warner *et al.*[21] were similar to values from colonies from thermal induced stress study which were collected at much shallower depths (2-4 m). A relationship between thermal stress and the disruption of photosystem II (based on the Qm values) especially in *Orbicella* colonies was found, which concurs with Warner *et al.*[21]. These authors also found that *P. astreoides* exposed to higher temperatures exhibited a significantly lower loss in activity of photosystem II than colonies of *Orbicella faveolata* exposed to the same conditions.

Mechanisms of photo-acclimation of *Symbiodinium* to light variability include changes of pigment concentration and the shifting of the photosynthetic response curve (e.g., P:I curve) and photosynthetic units (e.g., reaction center+ light-harvesting pigments), changes in algal densities, size and clade within the host due to spatial (depth), temporal (seasons) and nutrient concentrations within the coral reef[26-30]. Iglesias-Prieto and Trench[27] found that 3 clades of *Symbiodinium* increased their photosynthetic unit when exposed to low photon flux density levels. Colonies of *Turbinaria mesenterina* contained lower chlorophyll concentration within their dinoflagellates when exposed to levels higher than their acclimation irradiance[26]. *Symbiodinium* can also acclimatize to increased temperatures[29,31-34]. Robinson and Warner[29] found that diverse cultures of *Symbiodinium* under high light but normal temperature (26°C) conditions showed lower values of F_v/F_m than cultures under low light conditions. However, when they increased the temperature to 32°C, F_v/F_m values of some *Symbiodinium* acclimated to high light conditions showed an intense drop and the authors found that D1 protein inactivated the PS II. D1 protein degradation within the reaction centers of PS II has been proposed as the primary cause of photoinhibition[35]. The results by Robinson and Warner[29] concur with the hypothesis that increased temperature causes photoinactivation within the reaction centers of the PS II due to a low capacity of D1 repair when corals suffer from bleaching[5]. Non-photochemical quenching (e.g., dissipation of excess of light as heat) is another way of photoprotection of the PS II when thermal stress occurs because when the F_v/F_m decreases, an increase in the non-photochemical pathways occur while the net photosynthesis remains high[36]. Symbionts in *O. annularis* appear to have less physiological plasticity to warming. This is supported by the non-significant results in Qm, Chl a aborption coefficient and algal densities between *P. astreoides* under normal conditions (28°C) and *P. astreoides* under elevated temperature stress (32°C) found in this study and the significant differences between temperature treatments found in *O. annularis.* Perhaps the efficiency of the D1 repair of the PS II of *Symbiodinium* within *P. astreoides* during thermal stress may confer these colonies the phenotypic plasticity to cope with ocean warming.

As anticipated, the estimated absorbance analysis was dominated by absorption bands of Chl a and Chl c. Based on the results of the Chl a specific absorption coefficient *Symbiodinium* within *P. astreoides* at 32°C absorbed most of the incident light (0.75) with 11.8 mg cm^{-2} Chl a whereas *O. annularis* at 28°C absorbed the least (0.61) with 10.8 mg cm^{-2} Chl a. *P. astreoides* at 28°C showed 19 mg cm^{-2} Chl a with and absorbance of 0.64. Other studies have found values of 19 mg cm^{-2} Chl a associated to absorbance values closer to 1 in *Porites branneri* after a natural coral bleaching event[24]. In this context, *P. branneri* seems to be more efficient in absorbing light than *P. astreoides* but further research and comparison among both species should be done. Also, in that study, other *P. branneri* colonies showed concentration values of 3.3 mg cm^{-2} Chl a associated to approximately 0.1 of absorbance values. In the current study, 3.3 mg cm^{-2} Chl a was related to absorbance values of 0.66 in *O. annularis* at 32°C. This suggests that under thermal stress *O. annularis* colonies may be more efficient in absorbing a higher fraction of incident light than *P. branneri* with comparable Chl a concentration in both species. Results on the Chl a absorption coefficient supports this as well with the highest values found on *O. annularis* at 32°C. Increases in the light harvesting carotenoid associated to chlorophyll and peridinin enhances the light capturing capability of *Symbiodinium*[37]. This may explain differences in the absorbance values. However, this was not addressed in this study. *Porites astreoides* under thermal stress have shown no significant differences in Chl a values when compared to colonies in normal conditions[38]. It has found contrasting results since colonies at 32°C showed a significant reduction in Chl a and c in relation to control *P. astreoides*, perhaps due to a reduction in *Symbiodinium* densities at 32°C. Also, *O. annularis* at 28°C showed similar pigment values to *P. astreoides* at 32°C. The same patterns were found when comparing absorption coefficient values of control *O. annularis* showing similar values to treatment *P. astreoides.* Venn *et al.*[38] found no significant differences when comparing algal densities from *P. astreoides* under normal and stressful conditions. Significant differences were

found in the current study but we only exposed corals to thermal stress while these authors also increased irradiance, which may explain these differences.

Fitt *et al.*[39] found that typical algal symbiont densities within *O. annularis* are approximately 2×10^6 cells cm^{-2}. Similar algal densities within *O. annularis* at 28°C were found but significant reduction when exposed to elevated temperature. *Porites astreoides* at 32°C, on the other hand, showed comparable algal densities to *O. annularis* at 28°C. While *Symbiodinium*/coral symbiosis is essential for the corals' adaptations to thermal stress, host distinctiveness such as DNA, mucus production, skeletal structure and tissue biomass also matters[40]. Thornhill *et al.*[41] suggest that there is a strong and significant positive correlation between tissue biomass (e.g., tissue excluding skeleton) of *P. astreoides* and *Symbiodinium* densities. However, this correlation weakens within *O. annularis.* These authors explain that the nutritional relationship between the coral and its algal symbionts is essential to understand this correlation. That study also found that low coral tissue biomass within *O. annularis* increases its susceptibility to death following stress which is contrasting to the idea that *O. annularis* is stress-tolerant[17]. Corals with thicker tissue have been proposed to resist coral bleaching[42] and *Porites* spp. are known to have high tissue biomass[43].

In the current study, *P. astreoides* under thermal stress (i.e., 32°C) showed similar values in photopigments, Chl a absorption coefficient and algal densities to *O. annularis* under normal conditions (i.e., 28°C). These results demonstrate the higher likelihood of these colonies to colonize warmer localities within reefs or of coping better to warmer episodes than *O. annularis*[17]. This supports the hypothesis that *P. astreoides* will continue to strive under ocean warming scenarios[14-15,44]. This resilience to heat stress could be either a trait of the *Porites* genus or to the relationship this coral has with *Symbiodinium* clade A[38], considered a bleaching resistant clade due to its tolerance to high light[45] and temperature[46]. However, other studies have found thermally resistant and highly derived clade C (C15) within massive *Porites* from the Pacific[47] which is transmitted vertically (e.g., obtained directly from parents) to the host[48]. This type of coral-*Symbiodinium* association creates an intrinsic mutualism within *Porites* causing a high fidelity symbiosis which helps the coral to thrive under stressful conditions[47] and this may be happening with *Porites astreoides*.

Weedy corals, such as *P. astreoides* may be better survivors and colonizers in disturbed environments than non-weedy corals due to their high reproductive output and because of the set of life history traits that weedy species exhibit in comparison to other species[17]. Colonies from the genus *Porites* are known to cope well with thermal stress events[49] and are considered "ecological winners" after coral bleaching episodes due to their specificity with their symbiotic partners[47].

The "stress tolerant" classification of *O. annularis* by Darling *et al.*[17] do not include any physiological trait and responses to elevated temperature conditions. In the case of *O. annularis*, several studies point towards a high susceptibility of this species to thermal stress and bleaching. After the massive coral bleaching event in the Eastern Caribbean in 2005, *O. annularis* species complex (*O. annularis*, *O. faveolata* and *O. franksi*) suffered a 51% cover decline in St. John[50]. In Puerto Rico, more than 90% of *O. annularis* bleached during 2005[51] and over the last 15 years bleaching and disease have reduced coral cover of this species up to 80% within two important natural reserves[52]. Edmunds and Elahi[53] found a 57% decline in the cover of *O. annularis* during 15 years in St. John and predicted a possible local extinction of this species in next 50 years. Demographic analysis and modeling indicates that the vital rates of *O. annularis* are very sensitive to bleaching and that interval of mayor events of less than 17 years will result in population reduction that will seriously compromise the viability of *O. annularis* populations[12]. The results of this study provide a physiological basis for the documented sensitivity of *O. annularis* to thermal stress. In this context, we propose that *O. annularis* should not be considered a "stress tolerant" species as categorized by Darling *et al.*[17] but a species "sensitive to thermal stress".

CONCLUSION

One of the most important findings in the current study is that under thermal stress, the photophysiology of *P. astreoides* is similar to *O. annularis* exposed to normal conditions. This advances our understanding on coral resilience and vulnerability and enlightens us about the potential community structure of Caribbean coral reefs in the future due to current climate change effects. This shows a novel comparison with results that can be used to improve coral reef management and conservation initiatives. Moreover, the overall findings of the current study support the hypothesis of future increase in *P. astreoides* and decline of *O. annularis* population under the expected global warming scenarios. If *O. annularis*, which is considered one of the main builders of Caribbean coral reefs, disappears and is replaced by relatively small and weedy *P. astreoides*, the structural heterogeneity of Caribbean coral reefs will be reduced. This will result in less habitat availability for fish and other highly

important commercial species altering species composition and dynamics within these reefs. This shift in species composition will affect directly coastal communities due to less food availability, less coastal protection from hurricanes, loss of sources for pharmaceutical products and a reduction in biodiversity. Local and global anthropogenic inputs altering coral reef habitats are and will continue to be one of the most important problems to address when managing these ecosystems.

SIGNIFICANCE STATEMENT

The results of the experiment significantly advance understanding of the photosynthetic response to elevated water temperature of the symbionts associated with this two coral hosts. In this study, results were interpreted within the context of life history strategies of corals and coral reef resilience to ocean warming. The paper should be of interest to readers in the areas of coral physiology and coral reef resilience.

One of the most important findings in the current study is that under thermal stress, the photophysiology of *P. astreoides* is similar to *O. annularis* exposed to normal conditions. This advances our understanding on coral resilience and vulnerability and enlightens us about the potential community structure of Caribbean coral reefs in the future due to current climate change effects. It is believed that RJES readers will benefit from this study because it shows a novel comparison with results that can be used to improve coral reef management and conservation initiatives.

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