INDO PAC J OCEAN LIFE
Volume 9, Number 2, December 2025
Pages: 111-123

P-ISSN: 2775-1961
E-ISSN: 2775-1953
DOI: 10.13057/oceanlife/o090204

Photo-physiological thermal stress responses of *Echinopora forskaliana* from shaded and light-exposed environments around Rodrigues Island, Western Indian Ocean

SRUTI JEETUN[1,♥], MELANIE RICOT[1], SHAKEEL YAVAN JOGEE[1], NAWSHEEN TALEB-HOSSENKHAN[1], SUNDY RAMAH[1], JEAN SYLVIO PERRINE[1], DEEPEEKA KAULLYSING[1,2], RANJEET BHAGOOLI[1,2,3,4,5,6]

[1]Department of Biosciences and Ocean Studies, Faculty of Science & Pole of Research Excellence in Sustainable Marine Biodiversity, University of Mauritius. Réduit 80837, Republic of Mauritius. Tel.: +230-4037916, ♥email: sruti.jeetun@gmail.com
[2]The Biodiversity and Environment Institute. Réduit, Republic of Mauritius
[3]Department of Marine Science, Faculty of Fisheries and Marine Science, Universitas Diponegoro. Jl. Prof. Soedarto SH, Semarang 50275, Central Java, Indonesia
[4]University of Mauritius & Odysseo Marine Station, Oceanarium (Mauritius) Ltd. Les Salines Harbour Waterfront, Port Louis, Republic of Mauritius
[5]Institute of Oceanography and Environment (INOS), University Malaysia Terengganu. 21030 Kuala Nerus Terengganu, Malaysia
[6]The Society of Biology (Mauritius). Réduit, Republic of Mauritius

Manuscript received: 11 February 2025. Revision accepted: 29 September 2025.

Abstract. *Jeetun S, Ricot M, Jogee SY, Taleb-Hossenkhan N, Ramah S, Perrine JS, Kaullysing D, Bhagooli R. 2025. Photo-physiological thermal stress responses of* Echinopora forskaliana *from shaded and light-exposed environments around Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 111-123.* Corals in shaded and exposed habitats experience variable heat and light stresses, impacting their photosynthetic performance and resilience to thermal stress. This study examined bleaching, photosynthetic performance, and growth patterns of *Echinopora forskaliana* (Milne Edwards & Haime, 1849) in shaded and exposed environments at St. François, Rodrigues Island. Bleaching prevalence and colony sizes were recorded using three belt transects. Field observations in 2018 revealed healthy-looking colonies in shaded habitats, while colonies in exposed habitats showed bleaching. Responses of healthy-looking *E. forskaliana* colonies from both habitats were assessed under exposure to 29 and 32°C. Effective quantum yield at Photosystem II (Φ_{PSII}), maximum relative electron transport rate ($rETR_{max}$), and maximum non-photochemical quenching (NPQ_{max}) were measured at the start, and after 3 and 12 hours of exposure. Field bleaching surveys showed that 93.3% of exposed colonies were pale/bleached, while shaded ones remained unaffected and were significantly larger (42.1±9.0 cm). Thermal stress at 32°C and 206.5±27.0 Lux caused steep declines in Φ_{PSII} (99.7%), $rETR_{max}$ (93.5%), and NPQ_{max} (97.37%) in exposed colonies after 12 hours, while shaded colonies maintained their photosynthetic performance. These findings suggest that shaded habitats may act as refugia for corals under climate-induced thermal stress, highlighting the need for adaptive conservation and management approaches. The urgency of adaptive conservation and management approaches is underscored, as these findings highlight the need for immediate action to protect these crucial habitats.

Keywords: Bleaching susceptibility, climate change, coral, *Echinopora forskaliana*, PAM, Rodrigues, thermal stress

Abbreviations: Φ_{PSII}: Effective Quantum Yield at Photosystem II; $rETR_{max}$: Maximum Relative Electron Transport Rate; NPQ_{max}: Maximum Non-Photochemical Quenching; SST: Sea Surface Temperature; ROS: Reactive Oxygen Species; WIO: Western Indian Ocean

INTRODUCTION

Coral reefs are highly vulnerable to rising sea temperatures, which have increased the frequency and severity of coral bleaching episodes (Hughes et al. 2017; Lough et al. 2018; Sully et al. 2019). These occurrences contribute to reduced coral development and increased mortality (Hughes et al. 2018; Brown et al. 2019; Matsuda et al. 2020). Coral bleaching, induced by environmental stressors such as high sea surface temperatures (SST) and sun radiation, disturbs the coral Symbiodiniaceae symbiosis, essential for coral metabolism (Bieri et al. 2016; Goulet and Goulet 2021). Heat stress affects coral metabolism and lowers the photosynthetic efficiency of their symbiotic microalgae, limiting energy for growth, reproduction, and calcification (Allen-Waller and Barott 2023; Bouwmeester et al. 2023).

Light availability plays a crucial role in coral health, growth, and overall ecological functioning, influencing physiological processes such as photosynthesis, calcification, and symbiont density (Ross et al. 2022). Both excessive low and high light levels can be damaging to corals. While high ultraviolet (UV) radiation exposure can induce photoinhibition and coral tissue damage, insufficient illumination lowers photosynthesis (Falkowski et al. 1993). Especially during midday, exposure to intense light on shallow reefs causes oxidative stress, generates reactive oxygen species (ROS), and leads to photoinhibition (Helgoe et al. 2024; Lesser 2024), resulting in coral bleaching through symbiont loss or damage (Ainsworth and Brown 2021). High irradiance also worsens

heat stress effects, making corals more vulnerable to rising temperatures. (Hughes et al. 2017; Courtial et al. 2017; Rosic et al. 2020). Prolonged exposure to elevated SST and intense light can compromise coral defense mechanisms, causing tissue loss, increased disease susceptibility, and eventual mortality, driving reef degradation and biodiversity loss (Riegl and Purkis 2015; Elliot et al. 2018; Muller et al. 2018; McClanahan and Muthiga 2021).

Shading reduces light availability and mitigates bleaching under high temperatures (Baker et al. 2008; Berg et al. 2020; Butcherine et al. 2023). Reduced light environments, such as turbid waters (Cacciapaglia and van Woesik 2015; Morgan et al. 2017; Sully and van Woesik 2020; Rosedy et al. 2023), cloud cover (Gonzalez-Espinosa and Donner 2021), mangrove shading (Stewart et al. 2021), and deeper or sheltered reef zones (Smith et al. 2016; Cowburn et al. 2019), help mitigate stress by providing more moderate lighting conditions. In shaded environments, corals sustain stable photosynthetic rates, lowering oxidative stress and enhancing resistance to UV rays and high temperatures (Ellis et al. 2024). They are less likely to depend on photoprotective processes like non-photochemical quenching (NPQ), enabling them to sustain higher symbiont densities and better growth rates than corals in high light environments (Butcherine et al. 2023). Shaded reefs, especially in deeper or more sheltered areas, act as refuges from thermal and light stress, promoting healthier coral colonies (Stewart et al. 2021). The size and structure of coral colonies can influence how much light they receive and their susceptibility to bleaching. Smaller colonies in exposed areas may experience greater stress and limited growth, while shaded or sheltered corals often show higher survival and resilience (Glynn and D'Croz 1990; Fabricius 2006; Enríquez et al. 2017). Recent work has also examined how varying light conditions, including artificial shading, affect coral physiology and bleaching susceptibility, highlighting the potential of shading technologies for conservation (Tagliafico et al. 2022). In contrast, other studies have also reported potential drawbacks of reduced light availability, noting that increased turbidity can adversely impact coral health (Smith et al. 2016; Fisher et al. 2019; Juhi et al. 2021; López-Londoño et al. 2021; Diaz et al. 2023).

Previous studies from the Western Indian Ocean (WIO) have highlighted the role of thermal refugia in the potential for coral survival. In Mauritius, spatial thermal variability affected bleaching patterns, with bleaching primarily occurring in lagoonal and reef flat areas. At the same time, nearshore colonies exhibited greater thermal resilience despite experiencing higher maximum seawater temperatures. (Bhagooli and Taleb-Hossenkhan 2012). This pattern aligns with studies on *Acropora muricata* (Linnaeus, 1758), demonstrating enhanced photo-physiological responses and antioxidant activity in nearshore environments compared to the lagoon and reef, suggesting a greater thermal stress resilience (Louis et al. 2016, 2020). Other chlorophyll stress studies have indicated variations and stress responses in photo-physiology of corals (Ghoora et al. 2018; Mattan-Moorgawa et al. 2018, 2020; Bhagooli et al. 2021b; Munbodhe et al. 2023, 2025; Jeetun et al. 2023, 2025; Ricot et al. 2023) and other marine symbiotic organisms (Ramah et al. 2023) and seaplants (Bhagooli et al. 2021c; Narrain et al. 2023).

The reefs of the Western Indian Ocean (WIO) region have experienced repeated bleaching events over the years. Variations in thermal regimes have also influenced bleaching patterns, with Mauritius experiencing higher bleaching in 2019 compared to 2016, affecting multiple test species (Jeetun et al. 2025). Rodrigues, another key study site in the WIO, has also experienced repeated bleaching events, first recorded in 2005 (Hardman et al. 2007), and additional stressors, including sedimentation, coral diseases, and destructive fishing practices, have further contributed to reef degradation (Hardman et al. 2004, 2013; Jogee et al. 2023). However, the potential influence of shaded environments on thermal bleaching responses remains unexplored in the WIO.

Despite evidence of the significance of shaded habitats, studies comparing coral responses between shaded and exposed environments in the waters of the Republic of Mauritius remain limited. This study aims to investigate the photo-physiological responses and growth patterns of *Echinopora forskaliana* (Milne Edwards & Haime, 1849) in both shaded and light-exposed environments at St. François, Rodrigues Island. Using pulse-amplitude modulation (PAM) fluorometry, photo-physiological parameters such as effective quantum yield, relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) were examined. In addition, the effects of thermal stress on corals from both environments were evaluated to understand their resilience mechanisms better. By integrating in situ and ex situ assessments, this study is critical for understanding the environmental factors that impact coral functioning and informing conservation strategies for WIO reefs amid climate change.

MATERIALS AND METHODS

Study area

The study was conducted in 2018 at St. François (19°41'56.4"S 63°30'00.5"E), on the east coast of Rodrigues Island, which hosts the most extensive and well-developed reefs in the Mascarenes (Bhagooli and Kaullysing 2019), located in the WIO (Figure 1). A combination of shallow, exposed reef flats and shaded habitats within a natural channel characterizes this site. In the shallow reef flat, at depths of 1 to 1.5 m, *E. forskaliana* corals experience high light intensity and ultraviolet (UV) radiation. Conversely, the natural channel at St. François provides shaded conditions along its vertical walls, where corals are located at depths ranging from 1.5 to 8 m (Figure 2). These shaded habitats are distinguished by lower light intensity due to overhangs and channel structure, which results in lower temperatures compared to the reef flat, as the channel's depth and structure limit direct sunlight and reduce heat exposure.

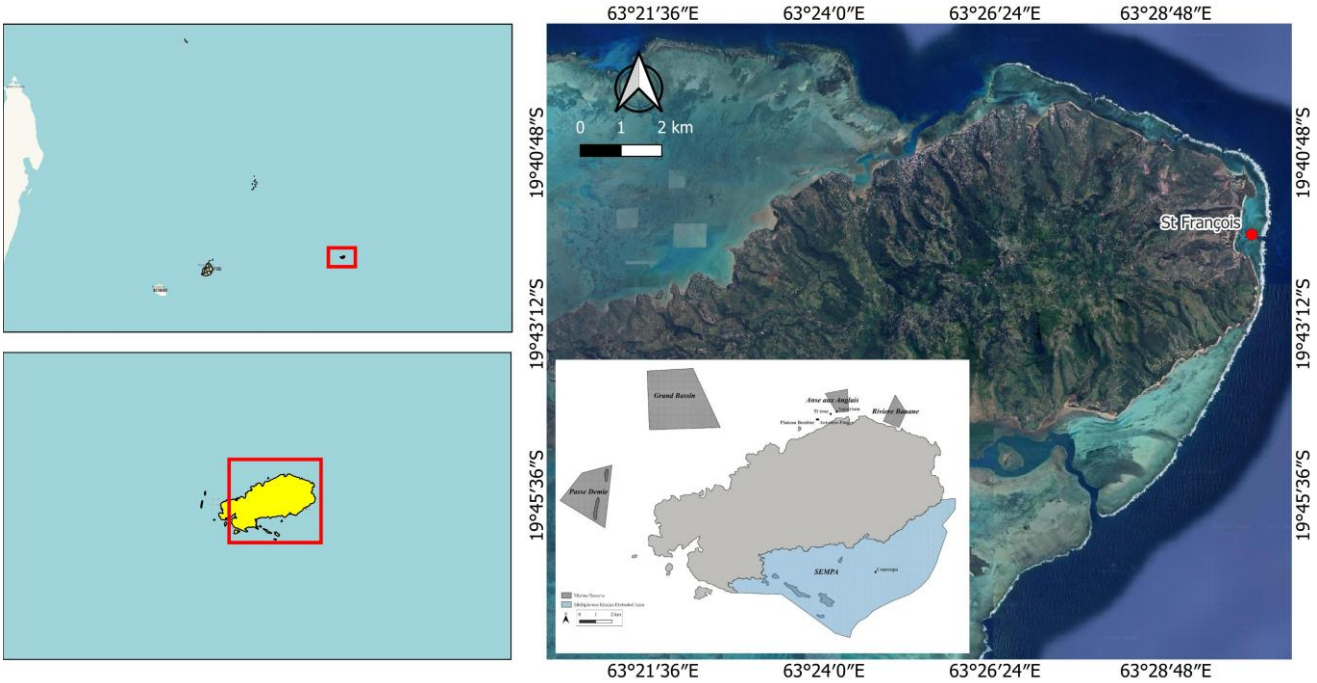

Figure 1. The study site, St. François, is situated on the east coast of Rodrigues Island. The study site features shallow and exposed reef flats and shaded habitats along a natural channel

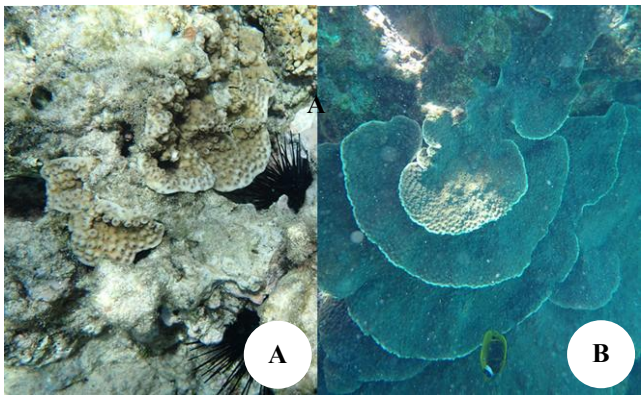

Figure 2. *Echinopora forskaliana* at St. François, Rodrigues Island. A. Exposed to light conditions on the reef flat at a depth of 1- 1.5 m; and B. Shaded from light on the walls of the channel at a depth of 1.5-8 m

This area provides a gradient of both thermal and light exposure that enables a comparative analysis of coral photo-physiological responses and growth patterns under contrasting light and temperature. Temperature and light intensity were measured every 15 minutes in both exposed and shaded areas using HOBO Pendant® Temperature/Light sensors, which were deployed at 1.5 m depth in the exposed reef flat and at 3 m depth along the shaded channel wall. Measurements were recorded continuously during the warm season in April 2018. Light intensity measurements recorded in lux were converted to photosynthetically active radiation (PAR) units of µmol photons m^{-2} s^{-1} using a standard sunlight calibration factor of 0.0185.

Bleaching and colony size survey

A bleaching survey was conducted at St. François, focusing on *E. forskaliana* colonies in shaded and exposed environments. Initial surveys noted pre-existing differences in pigmentation and colony morphology across reef zones, with shaded colonies generally appearing darker and larger than those in exposed environments. These baseline differences were taken into account throughout the study to avoid misclassification of natural variation as bleaching. This approach ensured that observed changes in pigmentation or morphology were attributed to thermal stress responses rather than inherent site-specific traits.

Bleaching magnitude and colony size variations were assessed during summer in 2018. Bleaching observations were carried out across three 100 m^2 (50 × 2 m) belt transects, including exposed reef flats and shaded channel walls. Along each transect, 10 randomly selected *E. forskaliana* colonies were visually assessed for bleaching condition and classified as "Healthy" and "Pale", following the CoralWatch Coral Health Chart (Siebeck et al. 2006). Colony size was measured in situ to the nearest centimeter using a flexible measuring tape. For each colony, the maximum diameter and two perpendicular diameters were recorded to account for irregular shapes and provide a more accurate size estimate.

Chlorophyll fluorescence parameters

To assess the photosynthetic performance and stress responses of *in situ* zooxanthellae, a Diving Pulse-

Amplitude Modulated (D-PAM; WALZ, Germany) fluorometer was used to measure chlorophyll *a* fluorescence, quantum yield (Φ_{PSII}), relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) (Bhagooli et al. 2021a). These parameters are derived from base (F or F_t) and maximum (F_m or F_m') fluorescence measured using a D-PAM fluorometer. The $rETR_{max}$ and NPQ_{max} were derived from the rapid light curves (RLCs) generated by the D-PAM.

The effective quantum yield at PSII, Φ_{PSII} (Genty et al. 1989), quantifies the quantity of light utilized by chlorophyll molecules in photochemistry in the PSII. The following equation was used to determine this parameter:

$$\text{Effective Quantum yield at PSII, } \Phi_{PSII} = \frac{\Delta F}{F_m'} = \frac{F_m' - F_t}{F_m'}$$

Where F_m' is the maximum fluorescence in light-adapted conditions, and F_t is the steady-state fluorescence value prior to the saturating pulse.

The relative electron transport rate (rETR) is a light-adapted parameter that measures the gross photosynthetic activity in vivo (Genty et al. 1989). This is determined as follows:

$$rETR = \Phi_{PSII} \times PAR \times 0.5$$

Where Φ_{PSII} is the effective quantum yield of PSII, PAR is the photosynthetic active radiation (µmol photons m^{-2} s^{-1}), and 0.5 is a partitioning factor which accounts for the energy distribution between PSI and PSII.

Non-photochemical quenching (NPQ) is the mechanism through which photosynthetic organisms convert and dissipate the excess excitation energy into heat at PSII to guard themselves against the negative effects of intense lighting. NPQ is quantified using the following equation:

$$NPQ = \frac{F_m - F_m'}{F_m'}$$

Initial measurements included shaded corals and healthy-looking and bleached corals from the exposed habitat. The experiment focused on shaded corals and healthy-looking exposed corals, comparing their responses under controlled temperature treatments.

Field sampling and initial photo-physiological measurements

Field observations indicated differences in coral condition between habitats, which determined fragment selection for subsequent measurements and experiments. To assess initial *in situ* photo-physiological variability, fragments were collected as follows: from shaded habitats, only healthy colonies were sampled; from exposed habitats, both healthy-looking and bleached colonies were sampled. For each condition (shaded healthy, exposed healthy, exposed bleached), three fragments of approximately 2 cm were collected from each of three parent colonies (n=3 per treatment, for each habitat) to assess Φ_{PSII}, $rETR_{max}$, and NPQ_{max}. Coral fragments were collected by snorkeling using pliers and immediately transferred into a bucket of aerated seawater for transport. Samples were then brought to the laboratory for subsequent experimental trials.

***Ex situ* thermal stress experiment**

For the thermal stress experiment, only healthy-looking *E. forskaliana* fragments were selected from the exposed habitat to ensure uniform health conditions and minimize initial stress, maintaining experimental consistency. Fragments of *E. forskaliana* collected from shaded and exposed reef habitats were placed in separate closed aerated tanks (80 × 60 × 42.5 cm) filled with natural seawater. Coral fragments were acclimated at 29°C for 48 hours prior to the experiment. Water movement was maintained using circulation pumps, and temperature was regulated using thermostats. Salinity was monitored at regular intervals with a refractometer, and any slight increases were adjusted by gradually adding small volumes of distilled water.

These tanks corresponded to two distinct temperature treatments: 29°C, representing natural ambient conditions, and 32°C, simulating elevated thermal stress typical of bleaching events. The temperature was gradually increased at a rate of 1°C per hour until reaching 32°C. For each temperature regime, three fragments from shaded and exposed habitats were included. Temperature and light intensity were recorded at 15-minute intervals using HOBO Pendant® Temperature/Light sensors. Light intensity measurements recorded in lux were converted to photosynthetically active radiation (PAR) in µmol photons m^{-2} s^{-1} using a standard calibration factor of 0.0135, corresponding to cool white fluorescent lamps. To assess the photosynthetic performance and stress responses of the in hospite symbiont, effective quantum yield (Φ_{PSII}), relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) measurements were recorded at three time intervals to monitor the effects of thermal stress over time: before temperature exposure, after 3h, and 12 h to observe the short-term effects of thermal stress to capture the early stress signatures before the onset of visible bleaching (Bhagooli and Hidaka 2003).

Data analysis

The assumption of normality for each group (shaded and exposed conditions) was evaluated using the Shapiro-Wilk test. To assess differences in the mean diameter of coral colonies between shaded and exposed conditions, an independent t-test was conducted. The experimental data for effective quantum yield, relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) in 2018 were arcsine (square-root) transformed before Analysis of Variance (ANOVA) to ensure normality. An independent t-test was performed to compare means of effective quantum yield (Φ_{PSII}), relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) for the *in hospite* symbiont between shaded and exposed conditions. All statistical analyses were performed using IBM SPSS 21.

RESULTS AND DISCUSSION

In situ temperature variation in exposed and shaded habitats

Temperature in the exposed habitat ranged from 26.7°C to a maximum of 33.0°C, with a daily fluctuation of up to 5.2°C, and the area experienced a more pronounced temperature increase during daylight hours, peaking around midday. The shaded habitat exhibited a lower and less variable temperature range of about 2.5°C, fluctuating between 26.2°C and a maximum of 30.3°C (Figure 3.A). These temperature data were recorded continuously over two days, capturing diurnal thermal variability in both habitats.

Light intensity in the exposed habitat reached a maximum of around 203.9 µmol m^{-2} s^{-1} (11022 lux), showing significant fluctuations throughout the day and a sharp peak pattern during midday. The shaded habitat maintained a much lower light intensity of approximately a maximum of 6.99 µmol m^{-2} s^{-1} (378 lux) (Figure 3.B).

Pre-existing differences in colony morphometrics and pigmentation across reef zones

During initial field observations, noticeable differences in coral morphology and pigmentation were noted across reef zones. Colonies situated in shaded environments were typically larger and more pigmented, whereas those in exposed areas appeared smaller and paler. These characteristics were evident before any thermal stress was applied, suggesting they are characteristic of each habitat rather than signs of bleaching. These site-specific baseline differences were carefully accounted for throughout the study to ensure that natural variability was not misinterpreted as bleaching.

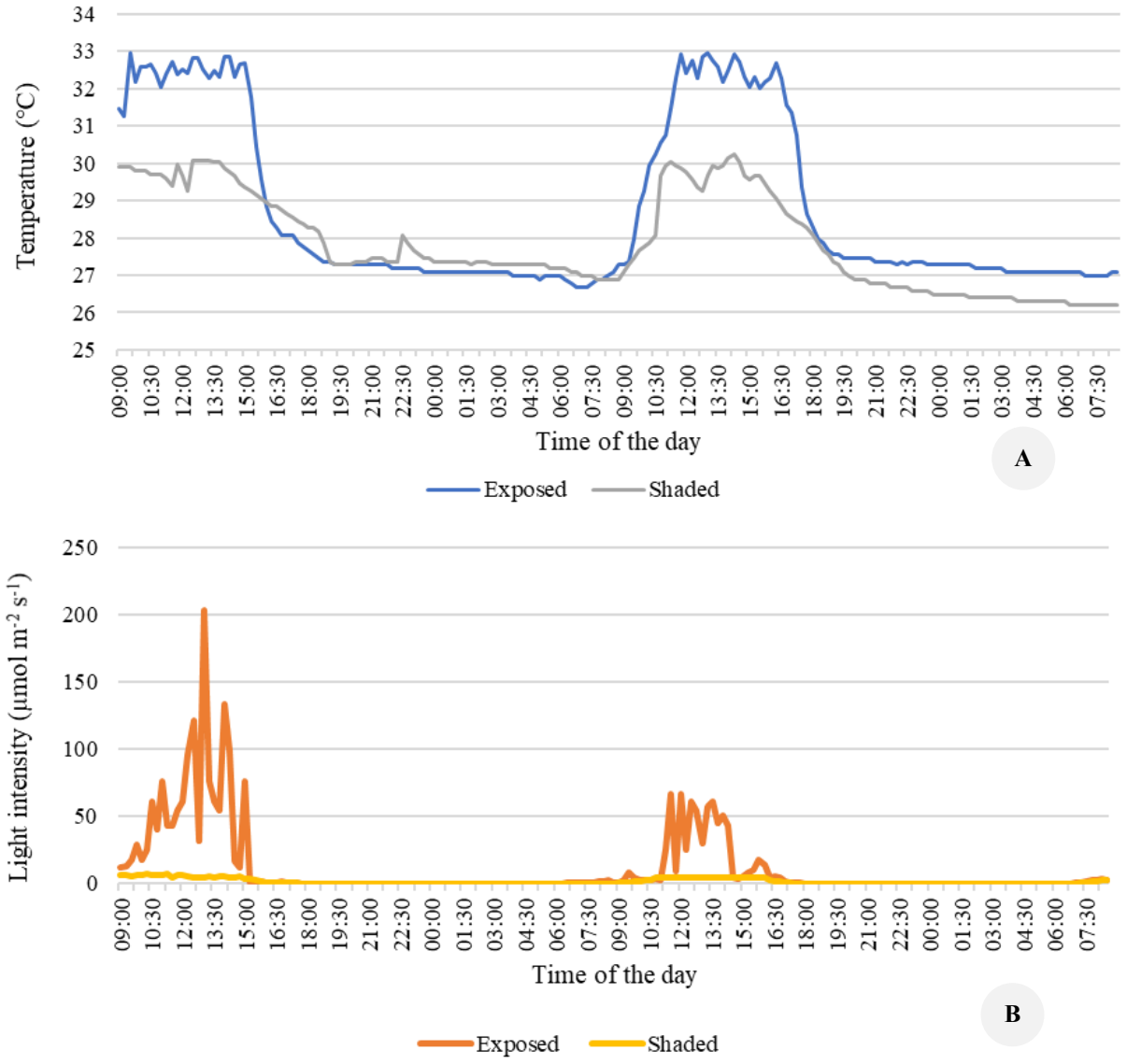

Figure 3. A. Temperature (°C); and B. light intensity (µmol m^{-2} s^{-1}) recorded from data loggers in shaded and exposed conditions at St. François, Rodrigues Island, recorded in April 2018

Bleaching and coral size survey

The bleaching survey revealed a higher percentage of pale/bleached colonies in exposed environments compared to the shaded ones (Figure 4.A). In exposed conditions, 93.3±5.8 % of the colonies displayed bleaching conditions, while no bleaching was observed in shaded colonies. Colony diameter measurements (Figure 4.B) highlighted that there was a significant difference ($p<0.05$, independent t-test) in mean colony diameter between shaded and exposed environments. Colonies in shaded environments had larger average diameters (42.±9.0 cm) compared to those in exposed environments, which were smaller (12.6±3.4 cm). Visual observations indicated a color difference between healthy-looking shaded and exposed colonies, with shaded ones appearing more pigmented than their exposed counterparts (Figure 2).

Thermal photo-physiological response of *E. forskaliana* under experimental conditions

The temperature-controlled tanks successfully maintained distinct thermal conditions, with an average temperature of 29.0±0.26°C in the 29°C treatment and 32.0±0.04°C in the 32°C treatment (Figure 5.A). While temperature remained stable within each treatment, light levels showed minor fluctuations throughout the experiment. The average light intensity in the 32°C tanks was 2.79±0.36 µmol m^{-2} s^{-1} (206.5±27.0 lux), while the 29°C tanks had a similar average light intensity of 2.80±0.030 µmol m^{-2} s^{-1} (207.7±21.9 lux) (Figure 5.B).

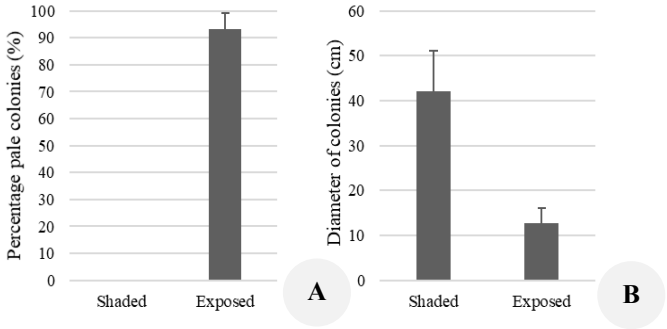

Figure 4. A. Percentage pale (bleached) colonies; and B. Diameter of colonies (out of 10 colonies for *E. forskaliana*) in shaded and exposed habitats at St. François, Rodrigues Island, recorded in 2018. Bars represent mean ± SD (n=10)

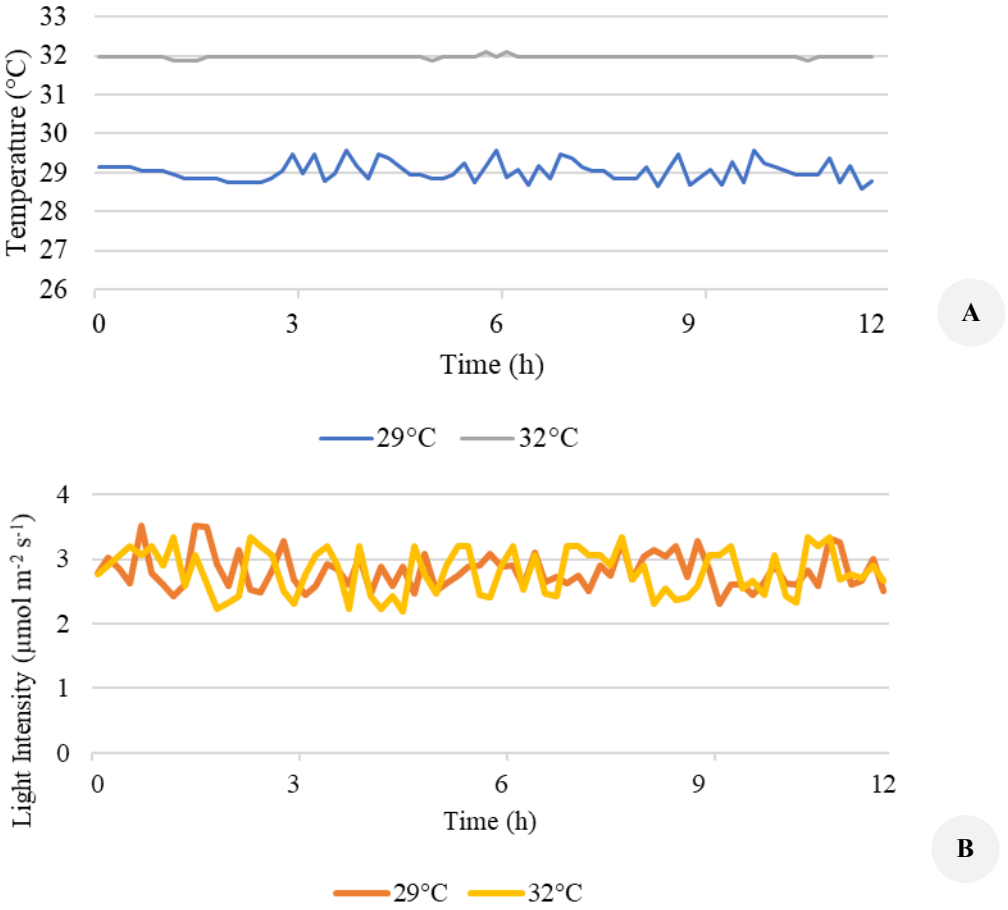

Figure 5. A. Temperature (°C); and B. light intensity (µmol m^{-2} s^{-1}) recorded from data loggers set in the experimental tanks exposed to different temperatures (29 and 32°C) and light exposures

Thermal photo-physiological responses of healthy-looking and bleached *E. forskaliana* from shaded and exposed habitats

Field-based photo-physiological assessments indicated slight but consistent differences in the responses of *E. forskaliana* colonies inhabiting shaded and exposed environments. Shaded colonies exhibited slightly higher Φ_{PSII} compared to exposed colonies in a healthy-looking state; however, no significant difference was noted (t-test, $p>0.05$). Bleached colonies, however, showed a decrease in Φ_{PSII} compared to healthy colonies, in the exposed site (Figure 6.A). The maximum relative electron transport rate ($rETR_{max}$) did not vary significantly (t-test, $p>0.05$) between shaded and exposed colonies for either healthy-looking or bleached conditions (Figure 6.B). Nonetheless, bleached colonies displayed a slight reduction in $rETR_{max}$. Non-photochemical quenching (NPQ_{max}) was significantly higher (t-test, $p<0.05$) in healthy-looking exposed colonies compared to their shaded counterparts. Conversely, exposed bleached colonies showed markedly higher NPQ_{max} than the healthy-looking shaded colonies (Figure 6.C). The healthy-looking and bleached colonies in the exposed conditions exhibited similar NPQ_{max} (0.563±0.107).

There was a significant difference ($p<0.05$) in Φ_{PSII}, $rETR_{max,}$ and NPQ_{max} between shaded and exposed habitats. Additionally, a significant difference ($p<0.05$) was found in Φ_{PSII} and NPQ_{max} due to the combined effects of shaded/exposed conditions, time of exposure, and temperature (Table 1). The Φ_{PSII} for the shaded colonies remained relatively stable across all conditions. However, the exposed colonies exhibited a significant decline at 32°C after 12 hours of exposure from 0.601 to 0.0013, representing a 99.7% reduction in Φ_{PSII} (Figure 7.A).

The shaded *E. forskaliana* colonies consistently maintained higher $rETR_{max}$ values across all conditions compared to the exposed colonies (Figure 7.B). Both shaded and exposed colonies exhibited a decline in $rETR_{max}$ at 32°C compared to initial ($p<0.05$) and 29°C conditions (shaded: $p<0.05$; exposed: $p<0.05$), with the ones from exposed conditions having even lower $rETR_{max}$ than the shaded ones ($p<0.05$). At 29°C, shaded colonies exhibited a 4.0% decrease in $rETR_{max}$ from initial values (55.9±3.4) to 3 h (53.7±4.8) and a further 2.3% decrease after 12 h (to 52.4±5.7) (significant over time, $p<0.05$). In contrast, exposed colonies experienced a larger reduction, with a 9.6% decline in $rETR_{max}$ from initial values (46.8±11.6) to 3 h (42.3±9.5) and a 5.8% decrease after 12 h (to 44.0±13.0) (not significant over time: $p>0.05$). At 32°C, shaded colonies experienced a dramatic 87.1% decline in $rETR_{max}$ after 3 h (from 55.9±3.4 to 7.2±1.4) and a 96.9% decline after 12 h (from 55.9±3.4 to 1.8±0.5) ($p<0.05$). Exposed colonies showed an even more severe decline ($p<0.05$), with a 91.4% reduction after 3 h (from 46.8±11.6 to 4.0±1.2) and a complete collapse after 12 h (from 46.8±11.6 to 0.5±0.4).

In the shaded colonies, NPQ_{max} increased moderately over time, although these changes were not statistically significant ($p>0.05$). However, in the exposed samples, NPQ_{max} were higher initially and in the 29°C treatment, though differences were not significant ($p>0.05$). In 32°C treatment, the shaded colonies had a higher NPQ_{max} compared to colonies from exposed habitats, both after 3h ($p<0.05$) and 12 h ($p<0.05$ treatments (Figure 7.C). In shaded colonies, the NPQ_{max} decreased by 38.29%, while in exposed conditions, a 97.37% decline was observed from 3h to 12 h treatment ($p<0.05$).

Discussion

With the increasing global frequency and duration of marine heatwaves, the intensity and occurrence of coral bleaching are expected to rise. However, even during extreme warming events, bleaching patterns can vary considerably across different areas of the reefscape, influenced by local environmental factors such as light exposure, water flow, and depth (Grottoli et al. 2017; Schoepf et al. 2020; van Woesik et al. 2022). The results of this study show how environmental conditions greatly impact the photo-physiological performance and thermal stress responses of *E. forskaliana* colonies from shaded and exposed habitats.

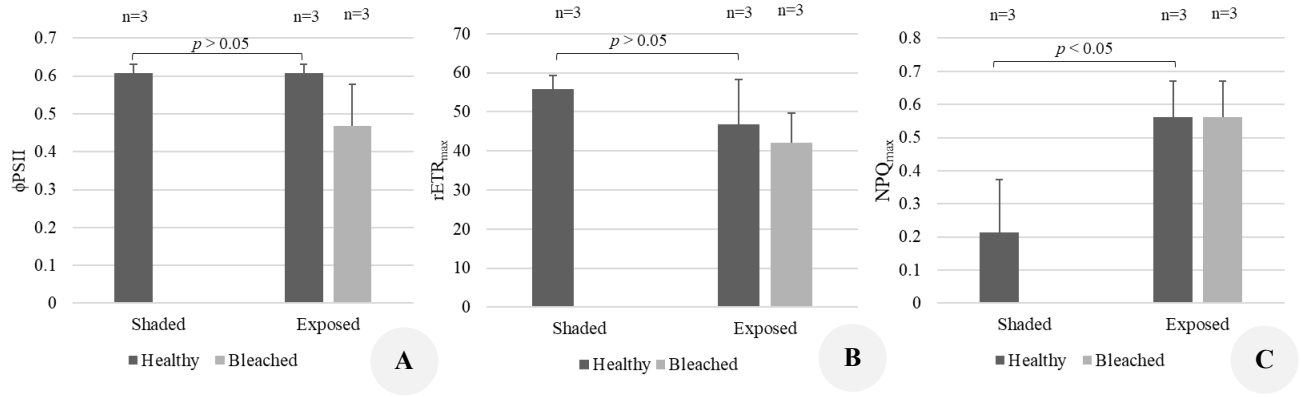

Figure 6. A. Effective quantum yield (Φ_{PSII}); B. Maximum relative electron transport rate ($rETR_{max}$); C. Non-photochemical quenching (NPQ_{max}) for in hospite zooxanthellae of the shaded and exposed colonies of healthy-looking and bleached *E. forskaliana.* Bars represent mean ± SD (n=3). Sample sizes (n) are indicated for each condition. Note that no bleached colonies were observed at the shaded site. Different letters above bars indicate statistically significant differences (t-test, $p<0.05$)

Table 1. Summary of three-way ANOVA on effects of conditions (shaded vs exposed), time of exposure, and temperature on the effective quantum yield (ΦPSII), relative maximum electron transport (rETRmax), and non-photochemical quenching (NPQ_{max}) *in hospite* zooxanthellae of *E. forskaliana*. Asterisks represent significant differences at P<0.05 *, P<0.01 **, P<0.001 ***, and NS indicates no significant difference

Photo- physiological parameters	**ϕPSII**				**$rETR_{max}$**			**NPQ_{max}**		
Source of variation	**ANOVA**									
	DF	**MS**	***F***	***P***	**MS**	***F***	***P***	**MS**	***F***	***P***
Conditions	1	0.001	125.948	0.000^{***}	0.076	13.714	0.001^{**}	0.002	14.876	0.000^{***}
Time of exposure	2	0.003	446.938	0.000^{***}	0.467	83.736	0.000^{***}	0.108	1061.533	0.000^{***}
Temperature	1	0.002	394.637	0.000^{***}	1.467	263.119	0.000^{***}	0.000	1.762	0.197^{NS}
Shaded and exposed conditions × Time	2	0.001	123.971	0.000^{***}	0.000	0.002	0.998^{NS}	0.000	4.404	0.023^{*}
Shaded and exposed conditions × Temperature	1	0.001	115.807	0.000^{***}	0.000	0.060	0.809^{NS}	0.002	21.203	0.000^{***}
Time × Temperature	2	0.002	418.273	0.000^{***}	0.384	68.908	0.000^{***}	0.002	16.087	0.000^{***}
Shaded and exposed conditions × time × Temperature	2	0.001	120.978	0.000^{***}	0.001	0.107	0.899^{NS}	0.005	51.670	0.000^{***}

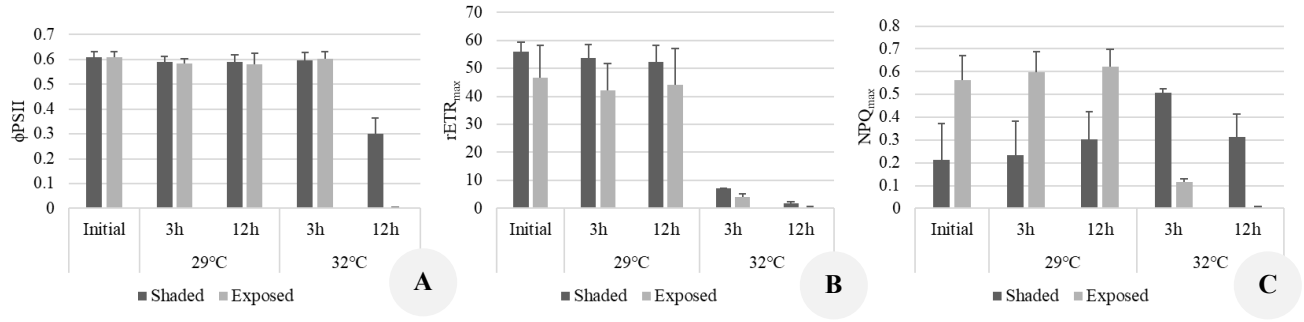

Figure 7. A. Effective quantum yield (Φ_{PSII}); B. Relative maximum electron transport rate ($rETR_{max}$); C. Non-photochemical quenching (NPQ_{max}) initially, after 3h and 12h exposure at 29 and 32°C stress exposure for *in hospite* zooxanthellae of the shaded and exposed *E. forskaliana*. Bars represent mean ± SD (n=3)

In addition to heat stress, the extent of coral bleaching is also influenced by light intensity. Therefore, providing shade to corals by blocking direct sunlight can help lessen the bleaching impact caused by higher ocean temperatures (Hoegh-Guldberg 1999; Swain et al. 2016). Bleaching surveys revealed a significant disparity between the two environments, with 93.3% of colonies in exposed habitats showing signs of bleaching, while shaded areas remained unaffected. The findings of the survey support the findings of previous studies (Baker et al. 2008; Hoogenboom et al. 2017; Muir et al. 2017; Van Woesik and McCaffrey 2017), which suggested that corals in shaded areas are less susceptible to bleaching when exposed to high-temperature stress, unlike their counterparts in more exposed environments. Conversely, some studies highlight potential drawbacks of reduced light availability, such as increased turbidity negatively affecting coral health (Fisher et al. 2019; Juhi et al. 2021; López-Londoño et al. 2021). Furthermore, experimental evidence has shown that thermal bleaching can still occur in the absence of light and photosynthesis, suggesting additional, yet unidentified, bleaching mechanisms (Tolleter et al. 2013).

Light significantly impacts coral calcification and metabolism by enhancing photosynthesis in algal symbionts, which supports coral growth (Mallon et al. 2022; Neder et al. 2022; Ross et al. 2022; Izumi et al. 2023). This aligns with the observed differences in *E. forskaliana* colonies at St. François, where those in exposed environments, receiving higher light intensities, were smaller and less pigmented compared to the larger, more pigmented colonies found in shaded areas. Similar studies have shown that artificial shading positively influences coral growth and pigmentation, with non-shaded corals exhibiting slower growth and reduced coloration (Coelho et al. 2017). Smaller colonies in exposed habitats likely reflect limited growth due to environmental stressors such as high light intensity and temperature fluctuations (Fabricius 2006). Additionally, coral colony geometry influences light availability, photoacclimation, and energy balance, shaping the light niche of symbiotic corals (Enríquez et al. 2017; López-Londoño et al. 2024). Other studies have shown that coral polyps exposed to less direct sunlight display lower levels of bleaching. This effect was especially evident in polyps located on parts of the colony that faced away from the main angle of solar exposure or were protected within crevices and fissures (Glynn and D'Croz 1990). In contrast, shaded habitats seem to reduce thermal stress, emphasizing their importance as crucial refuges for more resilient coral populations (Baker et al. 2008). Evidence from experimental and field studies indicates that certain coral taxa maintain photosynthetic performance and growth under reduced light, and that

shading responses are highly species-dependent (Rosic et al. 2020; Ellis et al. 2024). Consequently, coral responses to shading cannot be generalized and must be interpreted in the context of species-specific physiological traits and adaptive capacities.

This study observed differences in photo-physiological responses and pigmentation between corals from different light environments, suggesting habitat-linked physiological adaptations. Recent studies have also highlighted species-specific resilience patterns, emphasizing the role of local adaptation and physiological plasticity in modulating thermal stress responses (Morais et al. 2024). One possible explanation for the observed variation is the presence of different symbiont types across habitats. While symbiont genotyping was not performed in this study, previous research suggested that such photo-physiological variability could stem from differences in symbiont types within the same coral species. A study by Bhagooli (2009) revealed that *Stylophora pistillata* (Esper, 1792) (susceptible) and *Platygyra ryukyuensis* Yabe & Sugiyama, 1935 (resistant) corals, when exposed to elevated temperatures, exhibited distinct photo-physiological responses in their symbiont, with differing ITS2 genotypes showing variations in heat dissipation and electron transport rates, potentially explaining their differential susceptibility to bleaching. Tilstra et al. (2017) also highlighted the variability in physiological responses within individual *S. pistillata* corals, suggesting that differences among the spatially distinct clades of this species may contribute to this variability. Similarly, research by Winters et al. (2009) found that the composition of zooxanthellae in *S. pistillata* varies with light exposure. Deeper colonies were associated with *Cladocopium* species (clade C), while shallower colonies hosted *Symbiodinium* species (clade A), influencing their ability to tolerate thermal stress. *Symbiodinium* species (Clade A) has demonstrated the ability to dissociate antenna complexes from PSII under high light, enhancing host survival and bleaching resistance. As the most ancestral type, it has retained key protective mechanisms, which help minimize PSII damage, enhance NPQ through xanthophyll de-epoxidation, and facilitate UV protection via UV-protective mycosporine-like amino acids (MAAs) production, unlike deeper-dwelling corals with non-Clade A symbionts (Reynolds et al. 2008; Fujise et al. 2018). Similarly, darker pigmentation in corals from low-light environments may reflect higher chlorophyll concentrations, a trait associated with increased light-harvesting capacity but potentially greater vulnerability under thermal stress. These patterns align with studies that report species- and habitat-specific plasticity in coral thermal tolerance (Kenkel et al. 2015; Mizerek et al. 2018; Kuanui et al. 2020; Dobson et al. 2021; Morais et al. 2024; Ellis et al. 2024). These findings suggest that coral symbiont composition and pigmentation adjust in response to changes in light intensity, which significantly affects coral health and their ability to withstand environmental stressors. Understanding these adaptive responses is vital for predicting how corals will cope with climate change and for creating targeted conservation strategies.

The observed differences in Φ_{PSII}, $rETR_{max}$, and NPQ_{max} between shaded and exposed *E. forskaliana* colonies can be attributed to variations in light exposure and thermal stress tolerance. The significant decline in Φ_{PSII} in exposed colonies at 32°C suggests severe photoinhibition and damage to the photosynthetic apparatus, likely due to excessive light stress and impaired repair mechanisms (Lesser 2021). This aligns with the findings of Jones et al. (1998), which suggested that heat stress in *S. pistillata* initially impacts the Calvin cycle, with photoinhibition of PSII as a secondary effect, exacerbated by light. It is noteworthy that Bhagooli (2013) showed that in *S. pistillata*, bleaching occurred due to interruption of the Calvin-Benson cycle, associated with increased photoinhibition through suppression of repair of the protein synthesis at PSII. Further research by Bhagooli and Hidaka (2003, 2004) demonstrated that thermal stress reduces the light intensity threshold for photoinhibition differently in these coral species, leading to increased bleaching and mortality in *S. pistillata*, but no mortality in *P. ryukyuensis*, with zooxanthellae from different corals showing varying stress tolerances. In contrast, shaded colonies maintained more stable Φ_{PSII}, indicating better photoprotection and sustained photosynthetic efficiency. Similarly, the greater decline in $rETR_{max}$ in exposed colonies compared to shaded ones highlights their reduced ability to maintain electron transport under high temperatures, potentially due to increased oxidative stress and damage to Photosystem II (Yakovleva and Hidaka 2004). The contrasting NPQ_{max} responses further support this explanation; shaded colonies exhibited a more controlled increase in NPQ_{max} at 32°C, suggesting an adaptive photoprotective response to dissipate excess energy, whereas exposed colonies showed a sharp decline, indicating a breakdown in their capacity for non-photochemical quenching. The inability of exposed colonies to regulate excess energy dissipation likely exacerbated photodamage, ultimately leading to higher susceptibility to bleaching.

This study highlights the significance of microhabitats as natural refuges against climate stress, offering corals in shaded or structurally intricate reef environments a buffer from extreme heat and light exposure. These protective areas, including mesophotic reefs, deeper slopes, and overhangs, are associated with higher coral survival during major bleaching episodes. However, recovery in turbid environments can be slower due to recurring disturbances (Evans et al. 2020). Light naturally diminishes with depth (Kahng et al. 2019), while temperature variations are less predictable (Bongaerts et al. 2010). In some instances, deeper reef areas experience lower temperatures (Prasetia et al. 2016), which may contribute to reduced bleaching and mortality rates at greater depths (Glynn 1996). During the 2016 bleaching of the northern Great Barrier Reef, coral bleaching prevalence declined with depth, likely due to reduced light exposure (Baird et al. 2018; Frade et al. 2018). However, it's important to note that species-specific variability indicates that depth-mediated thermal refugia are not universally effective. This variability should caution us against generalizing the protective effects of microhabitats. Overall, these findings highlight the

protective role of shaded habitats in mitigating light and thermal stress on corals. By understanding the mechanisms underlying coral resilience, conservation efforts can prioritize the preservation of these microhabitats to enhance reef survival in an era of climate change.

In conclusion, this study highlights the significant impact of habitat conditions, exposure duration, and temperature on the photo-physiological performance and thermal stress responses of *Echinopora forskaliana* colonies in both shaded and exposed environments. The results emphasize the protective advantages of shaded habitats, where corals showed increased resilience to bleaching and thermal stress experiments. Shaded colonies showed larger sizes, more stable photo-physiological metrics (Φ_{PSII}, $rETR_{max}$, and NPQ_{max}), and higher thermal tolerance compared to exposed colonies. Conversely, exposed colonies experienced notable declines in these metrics, especially at higher temperatures, indicating their greater vulnerability to thermal stress and bleaching. These results underscore the importance of habitat structure in coral health, with shaded areas offering a potential refuge for corals amid climate change-driven ocean warming. Focusing conservation efforts on these shaded microhabitats could enhance coral resilience, which may be vital for the long-term survival of coral reefs as sea temperatures continue to rise.

ACKNOWLEDGEMENTS

RB and DK are thankful to the Higher Education Commission (Mauritius) for funding (T0721) to work on corals/coral reefs. SJ is grateful to the University of Mauritius for MPhil/PhD partial research grant and the then Ministry of Blue Economy, Marine Resources, Fisheries and Shipping; the Rodrigues Regional Assembly (RRA); the Outer Islands Development Cooperation; and the Department for Continental Shelf, Maritime Zone Administration & Exploration at the Prime Minister's Office for granting permission to conduct coral reefs studies. RB and DK are thankful to Mitsui O.S.K. Lines (MOL) Ltd for funding to further coral reefs research in Rodrigues.

REFERENCES

Ainsworth TD, Brown BE. 2021. Coral bleaching. Curr Bio 31 (1): R5-R6. DOI: 10.1016/j.cub.2020.10.048.

Allen-Waller L, Barott KL. 2023. Symbiotic dinoflagellates divert energy away from mutualism during coral bleaching recovery. Symbiosis 89: 173-186. DOI: 10.1007/s13199-023-00901-3.

Baird AH, Madin JS, Álvarez-Noriega M, Fontoura L, Kerry JT, Kuo CY, Precoda K, Torres-Pulliza D, Woods RM, Zawada KJ, Hughes TP. 2018. A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. Mar Ecol Prog Ser 603: 257-264. DOI: 10.3354/meps12732.

Baker AC, Glynn PW, Riegl B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80 (4): 435-471. DOI: 10.1016/j.ecss.2008.09.003.

Berg JT, David CM, Gabriel MM, Bentlage B. 2020. Fluorescence signatures of persistent photosystem damage in the staghorn coral *Acropora* cf. *pulchra* (Anthozoa: Scleractinia) during bleaching and recovery. Mar Biol Res 16 (8-9): 643-655. DOI: 10.1080/17451000.2021.1875245.

Bhagooli R, Hidaka M. 2003. Comparison of stress susceptibility of *in hospite* and isolated zooxanthellae among five coral species. J Exp Mar Biol Ecol 291 (2): 181-197. DOI: 10.1016/S0022-0981(03)00121-7.

Bhagooli R, Hidaka M. 2004. Photoinhibition, bleaching susceptibility and mortality in two scleractinian corals, *Platygyra ryukyuensis* and *Stylophora pistillata*, in response to thermal and light stresses. Comp Biochem Physiol A Mol Integr Physiol 137 (3): 547-555. DOI: 10.1016/j.cbpb.2003.11.008.

Bhagooli R, Kaullysing D. 2019. Seas of Mauritius. In: Sheppard C (eds.). World Seas: an Environmental Evaluation Volume II: the Indian Ocean to the Pacific. Elsevier, Amsterdam. DOI: 10.1016/B978-0-08-100853-9.00016-6.

Bhagooli R, Mattan-Moorgawa S, Kaullysing D, Louis YD, Gopeechund A, Ramah S, Soondur M, Pilly SS, Beesoo R, Wijayawanti DP, Bachok ZB, Monrás VC, Casareto BE, Suzuki Y, Baker AC. 2021a. Chlorophyll fluorescence - a tool to assess photosynthetic performance and stress photophysiology in symbiotic marine invertebrates and seaplants. Mar Pollut Bull 165: 112059. DOI: 10.1016/j.marpolbul.2021.112059.

Bhagooli R, Soondur M, Ramah S, Gopeechund A, Jeetun S, Kaullysng D. 2021b. Photo-physiology of healthy and bleached corals from the Mascarene Plateau. SI - Studies on the Mascarene Plateau, Western Indian Ocean J Mar Sci (2/2021): 109-120. DOI: 10.4314/wiojms.si2021.2.8.

Bhagooli R, Soondur M, Ramah S, Gopeechund A, Kaullysing D. 2021c. Variable photo-physiological performance of macroalgae and seagrasses from Saya de Malha and Nazareth Banks, Mascarene Plateau. SI - Studies on the Mascarene Plateau, Western Indian Ocean J Mar Sci (2/2021): 95-108. DOI: 10.4314/wiojms.si2021.2.7.

Bhagooli R, Taleb-Hossenkhan N. 2012. Thermal spatial heterogeneityand coral bleaching: Implications for habitat refuges. Proceedings of the 12th International Coral Reef Symposium 2012, Cairns, Australia.

Bhagooli R. 2009. Symbiont Dependent Thermal Bleaching Susceptiblity in Two Reef-building Corals, *Stylophora pistillata* and *Platygyra ryukyuensis*. Univ Mauritius Res J 15 (1): 607-626.

Bhagooli R. 2013 Inhibition of Calvin-Benson cycle suppresses the repair of photosystem II in *Symbiodinium*: Implications for coral bleaching. Hydrobiologia 714: 183-190. DOI: 10.1007/s10750-013-1535-4.

Bieri T, Onishi M, Xiang T, Grossman AR, Pringle JR. 2016. Relative contributions of various cellular mechanisms to loss of algae during cnidarian bleaching. PLoS One 11 (4): e0152693. DOI: 10.1371/journal.pone.0152693.

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O. 2010. Assessing the 'deep reef refugia' hypothesis: Focus on Caribbean reefs. Coral reefs 29: 309-327. DOI: 10.1007/s00338-009-0581-x.

Bouwmeester J, Daly J, Zuchowicz N, Lager C, Henley EM, Quinn M, Hagedorn M. 2023. Solar radiation, temperature and the reproductive biology of the coral *Lobactis scutaria* in a changing climate. Sci Rep 13 (1): 246. DOI: 10.1038/s41598-022-27207-6.

Brown BE, Dunne RP, Somerfield PJ, Edwards AJ, Simons WJ, Phongsuwan N, Putchim L, Anderson L, Naeije MC. 2019. Long-term impacts of rising sea temperature and sea level on shallow water coral communities over a~ 40 year period. Sci Rep 9 (1): 8826. DOI: 10.1038/s41598-019-45188-x.

Butcherine P, Tagliafico A, Ellis SL, Kelaher BP, Hendrickson C, Harrison D. 2023. Intermittent shading can moderate coral bleaching on shallow reefs. Front Mar Sci 10: 1162896. DOI: 10.3389/fmars.2023.1162896.

Cacciapaglia C, van Woesik R. 2016. Climate-change refugia: Shading reef corals by turbidity. Glob Chang Biol 22 (3): 1145-1154. DOI: 10.1111/gcb.13166.

Coelho VR, Fenner D, Caruso C, Bayles BR, Huang Y, Birkeland C. 2017. Shading as a mitigation tool for coral bleaching in three common Indo-Pacific species. J Exp Mar Biol Ecol 497: 152-163. DOI: 10.1016/j.jembe.2017.09.016.

Courtial L, Roberty S, Shick JM, Houlbrèque F, Ferrier-Pagès C. 2017. Interactive effects of ultraviolet radiation and thermal stress on two reef-building corals. Limnol Oceanogr 62 (3): 1000-1013. DOI: 10.1002/lno.10481.

Cowburn B, Moritz C, Grimsditch G, Solandt JL. 2019. Evidence of coral bleaching avoidance, resistance and recovery in the Maldives during the 2016 mass-bleaching event. Mar Ecol Prog Ser 626: 53-67. DOI: 10.3354/meps13044.

Diaz C, Foster NL, Attrill MJ, Bolton A, Ganderton P, Howell KL, Robinson E, Hosegood P. 2023. Mesophotic coral bleaching associated with changes in thermocline depth. Nat Commun 14 (1): 6528. DOI: 10.1038/s41467-023-42279-2.

Dobson KL, Ferrier-Pagès C, Saup CM, Grottoli AG. 2021. The effects of temperature, light, and feeding on the physiology of *Pocillopora damicornis*, *Stylophora pistillata*, and *Turbinaria reniformis* corals. Water 13 (15): 2048. DOI: 10.3390/w13152048.

Elliott JA, Patterson MR, Staub CG, Koonjul M, Elliott SM. 2018. Decline in coral cover and flattening of the reefs around Mauritius (1998-2010). PeerJ 6: e6014. DOI: 10.7717/peerj.6014.

Ellis SL, Butcherine P, Tagliafico A, Hendrickson C, Kelaher BP, Schulz KG, Harrison DP. 2024. Shading responses are species-specific in thermally stressed corals. Front Mar Sci 11: 1333806. DOI: 10.3389/fmars.2024.1333806.

Enríquez S, Méndez ER, Hoegh-Guldberg O, Iglesias-Prieto R. 2017. Key functional role of the optical properties of coral skeletons in coral ecology and evolution. Proc R Soc B: Biol Sci 284 (1853): 20161667. DOI: 10.1098/rspb.2016.1667.

Evans RD, Wilson SK, Fisher R, Ryan NM, Babcock R, Blakeway D, Bond T, Dorji P, Dufois F, Fearns P, Lowe RJ. 2020. Early recovery dynamics of turbid coral reefs after recurring bleaching events. J Environ Manag 268: 110666. DOI: 10.1016/j.jenvman.2020.110666.

Fabricius KE. 2006. Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: Implications for coral bleaching? Limnol Oceanogr 51 (1): 30-37. DOI: 10.1098/rsif.2011.0144.

Falkowski PG, Dubinsky Z, Muscatine L, McCloskey L. 1993. Population control in symbiotic corals. Bioscience 43 (9): 606-611. DOI: 10.2307/1312147.

Fisher R, Bessell-Browne P, Jones R. 2019. Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. Nat Commun 10 (1): 2346. DOI: 10.1038/s41467-019-10288-9.

Frade PR, Bongaerts P, Englebert N, Rogers A, Gonzalez-Rivero M, Hoegh-Guldberg O. 2018. Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. Nat Commun 9 (1): 3447. DOI: 10.1038/s41467-018-05741-0.

Fujise L, Nitschke MR, Frommlet JC, Serôdio J, Woodcock S, Ralph PJ, Suggett DJ. 2018. Cell cycle dynamics of cultured coral endosymbiotic microalgae (*Symbiodinium*) across different types (species) under alternate light and temperature conditions. J Eukaryot Microbiol 65 (4): 505-517. DOI: 10.1111/jeu.12497.

Genty B, Briantais JM, Baker NR. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta Gen Subj 990 (1): 87-92. DOI: 10.1016/S0304-4165(89)80016-9.

Ghoora MD, Pilly SS, Chumun PK, Jawaheer SJ, Bhagooli R .2018. Short-term effects of heavy metal and temperature stresses on the photo-physiology of *Symbiodinium* isolated from the coral *Fungia repanda*. Ocean Life 2 (1): 11-20. DOI: 10.13057/oceanlife/o020102.

Glynn PW, D'croz L. 1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 8: 181-191. DOI: 10.1007/BF00265009.

Glynn PW. 1996. Coral reef bleaching: Facts, hypotheses and implications. Glob Change Biol 2 (6): 495-509. DOI: 10.1111/j.1365-2486.1996.tb00063.x.

Gonzalez-Espinosa PC, Donner SD. 2021. Cloudiness reduces the bleaching response of coral reefs exposed to heat stress. Glob Chang Biol 27 (15): 3474-3486. DOI: 10.1111/gcb.15676.

Goulet TL, Goulet D.2021. Climate change leads to a reduction in symbiotic derived cnidarian biodiversity on coral reefs. Front Ecol Evol 9: 636279. DOI: 10.3389/fevo.2021.636279.

Grottoli AG, Tchernov D, Winters G. 2017. Physiological and biogeochemical responses of super-corals to thermal stress from the Northern Gulf of Aqaba, Red Sea. Front Mar Sci 4: 215. DOI: 10.3389/fmars.2017.00215.

Hardman ER, Edwards AJ, Raffin JS. 2013. The seine-net fishery of Rodrigues Island, western Indian Ocean: Is it sustainable or in terminal decline? Fish Res 139: 35-42. DOI: 10.1016/j.fishres.2012.10.013.

Hardman ER, Sabrina Meunier M, Turner JR, Lynch TL, Taylor M, Klaus R. 2004. The extent of coral bleaching in Rodrigues. J Nat Hist 38 (23-24): 3077-3089. DOI: 10.1080/00222930410001695051.

Hardman ER, Stampfli NS, Hunt L, Perrine S, Perry A, Raffin JS. 2007. The impacts of coral bleaching in Rodrigues, Western Indian Ocean. Atoll Res Bull 555: 1-10. DOI: 10.5479/si.00775630.555.1.

Helgoe J, Davy SK, Weis VM, Rodriguez-Lanetty M. 2024. Triggers, cascades, and endpoints: connecting the dots of coral bleaching mechanisms. Biol Rev Camb Philos Soc 99 (3): 715-752. DOI: 10.1111/brv.13042.

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshwater Res 50 (8): 839-866. DOI: 10.1071/MF99078.

Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S, Álvarez-Noriega M, Peterson K, Critchell K, Berry KL, Nicolet KJ, Ramsby B, Paley AS. 2017. Environmental drivers of variation in bleaching severity of *Acropora* species during an extreme thermal anomaly. Front Mar Sci 4: 376. DOI: 10.3389/fmars.2017.00376.

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC. 2017. Global warming and recurrent mass bleaching of corals. Nature 543 (7645): 373-377. DOI: 10.1038/nature21707.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ. 2018. Global warming transforms coral reef assemblages. Nature 556 (7702): 492-496. DOI: 10.1038/s41586-018-0041-2.

Izumi R, Tan ES, Higa H, Shi Z, Takeuchi Y, Isomura N, Takemura A. 2023. Effects of light intensity and spectral composition on the growth and physiological adaptation of Acroporid corals. Coral Reefs 42 (2): 385-398. DOI: 10.1007/s00338-023-02348-w.

Jeetun S, Ricot M, Taleb-Hossenkhan N, Kaullysing D, Flot J-F, Bhagooli R. 2023. Differential responses of effective quantum yield to acute thermal stress in scleractinian corals including pre- and post-transplanted *Acropora muricata*. Indo Pac J Ocean Life 7 (1): 54-63. DOI: 10.13057/oceanlife/o070106.

Jeetun S, Ricot M, Jogee SY, Kaullysing D, Taleb-Hossenkhan N, LaJeunesse TC, Philippart G, Collard O, Flot JF, Wijayanti DP, Yucharoen M. 2025. Morphological and genetic characterization of *Stylophora madagascarensis*, *Pocillopora acuta*, and *Pocillopora verrucosa* in Mauritius and their thermal photophysiological stress responses. Bull Mar Sci 101 (1): 247-269. DOI: 10.5343/bms.2023.0124.

Jogee SY, Gopalsing S, Jeetun S, Ricot M, Taleb-Hossenkhan N, Mattan-Moorgawa S, Kaullysing D, Wijayanti DP, Casareto BE, Suzuki Y, Bhagooli R. 2023. First report of diseases and compromised health conditions on hard corals around Rodrigues Island, Southwest Indian Ocean. Diversity 15 (10): 1086. DOI: 10.3390/d15101086.

Jones RJ, Hoegh-Guldberg O, Larkum AW, Schreiber U. 1998. Temperature-induced bleaching of corals begins with impairment of the CO_2 fixation mechanism in zooxanthellae. Plant Cell Environ 21 (12): 1219-1230. DOI: 10.1046/j.1365-3040.1998.00345.x.

Juhi ZS, Mubin NA, Jonik MG, Salleh S, Mohammad M. 2021. Impact of short-term light variability on the photobiology of turbid water corals. J Sea Res 175: 102088. DOI: 10.1016/j.seares.2021.102088.

Kahng SE, Akkaynak D, Shlesinger T, Hochberg EJ, Wiedenmann J, Tamir R, Tchernov D. 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. In: Loya Y, Puglise K, Bridge T (eds.). Mesophotic Coral Ecosystems. Coral Reefs of the World, vol 12. Springer, Cham. DOI: 10.1007/978-3-319-92735-0_42.

Kenkel CD, Almanza AT, Matz MV. 2015. Fine-scale environmental specialization of reef-building corals might be limiting reef recovery in the Florida Keys. Ecology 6 (12): 3197-3212. DOI: 10.1890/14-2297.1.

Kuanui P, Chavanich S, Viyakarn V, Omori M, Fujita T, Lin C. 2020. Effect of light intensity on survival and photosynthetic efficiency of cultured corals of different ages. Estuar Coast Shelf Sci 235: 106515. DOI: 10.1016/j.ecss.2019.106515.

Lesser MP. 2021. Eutrophication on coral reefs: what is the evidence for phase shifts, nutrient limitation and coral bleaching. Bioscience 71 (12): 1216-1233. DOI: 10.1093/biosci/biab101.

Lesser MP. 2024. Irradiance dependency of oxidative stress and coral bleaching. Coral Reefs 43 (5): 1393-1403. DOI: 10.1007/s00338-024-02545-1.

López-Londoño T, Enríquez S, Iglesias-Prieto R. 2024. Effects of surface geometry on light exposure, photoacclimation and photosynthetic energy acquisition in zooxanthellate corals. Plos one 19 (1): e0295283. DOI: 10.1371/journal.pone.0295283.

López-Londoño T, Galindo-Martínez CT, Gómez-Campo K, González-Guerrero LA, Roitman S, Pollock FJ, Pizarro V, López-Victoria M, Medina M, Iglesias-Prieto R. 2021. Physiological and ecological consequences of the water optical properties degradation on reef

corals. Coral Reefs 40 (4): 1243-1256. DOI: 10.1007/s00338-021-02133-7.

Lough JM, Anderson KD, Hughes TP. 2018. Increasing thermal stress for tropical coral reefs: 1871-2017. Sci Rep 8 (1): 6079. DOI: 10.1038/s41598-018-24530-9.

Louis YD, Bhagooli R, Seveso D, Maggioni D, Galli P, Vai M, Dyall SD.2020. Local acclimatization-driven differential gene and protein expression patterns of Hsp70 in *Acropora muricata*: Implications for coral tolerance to bleaching. Mol Ecol 29 (22): 4382-4394. DOI: 10.1111/mec.15642.

Louis YD, Kaullysing D, Gopeechund A, Mattan-Moorgawa S, Bahorun T, Dyall SD, Bhagooli R. 2016. In hospite *Symbiodinium* photophysiology and antioxidant responses in *Acropora muricata* on a coast-reef scale: Implications for variable bleaching patterns. Symbiosis 68 (1): 61-72. DOI: 10.1007/s13199-016-0380-4.

Mallon J, Cyronak T, Hall ER, Banaszak AT, Exton DA, Bass AM. 2022. Light-driven dynamics between calcification and production in functionally diverse coral reef calcifiers. Limnol Oceanogr 67 (2): 434-449. DOI: 10.1002/lno.12002.

Matsuda SB, Huffmyer AS, Lenz EA, Davidson JM, Hancock JR, Przybylowski A, Innis T, Gates RD, Barott KL. 2020. Coral bleaching susceptibility is predictive of subsequent mortality within but not between coral species. Front Ecol Evol 8: 178. DOI: 10.3389/fevo.2020.00178.

Mattan-Moorgawa S, Chumun PK, Taleb-Hossenkhan N, Rughooputh SDDV, Bhagooli R. 2020. Variable thermal and biochemical stress responses of tissue balls from *Lithophyllon repanda*, *Pocillopora damicornis* and *Acropora muricata*. Galaxea J Coral Reef Stud 22 (1): 37-50. DOI: 10.3755/galaxea.22.1_37.

Mattan-Moorgawa S, Rughooputh SDDV, Bhagooli R. 2018. Variable PSII functioning and bleaching conditions of tropical scleractinian corals pre- and post- bleaching event. Ocean Life 2 (1): 1-10. DOI: 10.13057/oceanlife/o020101.

McClanahan TR, Muthiga NA. 2021. Oceanic patterns of thermal stress and coral community degradation on the island of Mauritius. Coral Reefs 40 (1): 53-74. DOI: 10.1007/s00338-020-02015-4.

Mizerek TL, Baird AH, Madin JS. 2018. Species traits as indicators of coral bleaching. Coral Reefs 37: 791-800. DOI: 10.1007/s00338-018-1702-1.

Morais J, Tebbett SB, Morais RA, Bellwood DR. 2024. Hot spots of bleaching in massive *Porites* coral colonies. Mar Environ Res 193: 106276. DOI: 10.1016/j.marenvres.2023.106276.

Morgan KM, Perry CT, Johnson JA, Smithers SG. 2017. Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great Barrier Reef following the 2016 ocean warming event. Front Mar Sci 4: 224. DOI: 10.3389/fmars.2017.00224.

Muir PR, Marshall PA, Abdulla A, Aguirre JD. 2017. Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef? Proc Biol Sci 284 (1864): 20171551. DOI: 10.1098/rspb.2017.1551.

Muller EM, Bartels E, Baums IB. 2018. Bleaching causes loss of disease resistance within the threatened coral species *Acropora cervicornis*. eLife 7: e35066. DOI: 10.7554/eLife.35066.

Munbodhe V, Jeetun S, Ricot M, Jogee S, Kaullysing D, Bhagooli R. 2023. Photo-physiological responses and thermal tolerance of regionally endemic/rare and morphologically different corals of the Western Indian Ocean. Indo Pac J Ocean Life 7: 100-107. DOI: 10.13057/oceanlife/o070111.

Munbodhe V, Ramah S, Kaullysing D, Jogee SY, Dine M, Wilson B, Bhagooli R. 2025. Variable photosystem II thermal stress responses of reef-building corals *Pocillopora indiania* and *Heliopora coerulea* across latitudes from the Mascarene Plateau, Indian Ocean. Deep Sea Res Part II: Top Stud Oceanogr 222: 105467. DOI: 10.1016/j.dsr2.2025.105467.

Narrain D, Baulroop J, Bhagooli R, Bahorun T. 2023. Differential photosynthetic, phytochemical and antioxidative responses of three macroalgae *Ulva lactuca*, *Gracilaria salicornia* and *Turbinaria ornata* exposed to thermal and irradiance conditions. Indo Pac J Ocean Life 7 (1): 1-15. DOI: 10.13057/oceanlife/o070101

Prasetia R, Sinniger F, Harii S. 2016. Gametogenesis and fecundity of *Acropora tenella* (Brook 1892) in a mesophotic coral ecosystem in Okinawa, Japan. Coral Reefs 35: 53-62. DOI: 10.1007/s00338-015-1348-1.

Neder M, Saar R, Malik A, Antler G, Mass T. 2022. New insights on the diurnal mechanism of calcification in the stony coral, *Stylophora pistillata*. Front Mar Sci 8: 745171. DOI: 10.3389/fmars.2021.745171.

Ramah S, Kaullysing D, Soondur M, Taleb-Hossenkhan N, Bhagooli R. 2023. Differential photo-physiological responses of two giant clam species to elevated temperature stress from Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 7 (1): 64-70. DOI: 10.13057/oceanlife/o070107.

Reynolds JM, Bruns BU, Fitt WK, Schmidt GW. 2008. Enhanced photoprotection pathways in symbiotic dinoflagellates of shallow-water corals and other cnidarians. Proc Natl Acad Sci 105 (36): 13674-13678. DOI: 10.1073/pnas.0805187105

Ricot M, Jeetun S, Joggee S, Kaullysing D, Taleb-Hossenkhan N, Bhagooli R. 2023. Thermal photo-physiological responses of massive heat-resistant coral *Porites lutea* under fish predated versus non-predated conditions. Indo Pac J Ocean Life 7 (1): 38-47. DOI: 10.13057/oceanlife/o070104.

Riegl B, Purkis S. 2015. Coral population dynamics across consecutive mass mortality events. Glob Chang Biol 21 (11): 3995-4005. DOI: 10.1111/gcb.13014.

Rosedy A, Ives I, Waheed Z, Hussein MA, Sosdian S, Johnson K, Santodomingo N. 2023. Turbid reefs experience lower coral bleaching effects in NE Borneo (Sabah, Malaysia). Reg Stud Mar Sci 68: 103268. DOI: 10.1016/j.rsma.2023.103268.

Rosic N, Rémond C, Mello-Athayde MA. 2020. Differential impact of heat stress on reef-building corals under different light conditions. Mar Environ Res 158: 104947. DOI: 10.1016/j.marenvres.2020.104947.

Ross CL, Warnes A, Comeau S, Cornwall CE, Cuttler MV, Naugle M, McCulloch MT, Schoepf V. 2022. Coral calcification mechanisms in a warming ocean and the interactive effects of temperature and light. Commun Earth Environ 3 (1): 72. DOI: 10.1038/s43247-022-00396-8.

Schoepf V, Jung MU, McCulloch MT, White NE, Stat M, Thomas L. 2020. Thermally variable, macrotidal reef habitats promote rapid recovery from mass coral bleaching. Front Mar Sci 7: 245. DOI: 10.3389/fmars.2020.00702.

Siebeck UE, Marshall NJ, Klüter A, Hoegh-Guldberg O. 2006. Monitoring coral bleaching using a colour reference card. Coral Reefs 25: 453-460. DOI: 10.1007/s00338-006-0123-8.

Smith TB, Gyory J, Brandt ME, Miller WJ, Jossart J, Nemeth RS. 2016. Caribbean mesophotic coral ecosystems are unlikely climate change refugia. Glob Chang Biol 22 (8): 2756-27565. DOI: 10.1111/gcb.13175.

Stewart HA, Kline DI, Chapman LJ, Altieri AH. 2021. Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. Ecosphere 12 (3): e03413. DOI: 10.1002/ecs2.3413.

Sully S, Burkepile DE, Donovan MK, Hodgson G, Van Woesik R. 2019. A global analysis of coral bleaching over the past two decades. Nat Commun 10 (1): 1264. DOI: 10.1038/s41467-019-09238-2.

Sully S, van Woesik R. 2020. Turbid reefs moderate coral bleaching under climate-related temperature stress. Glob Chang Biol 26 (3): 1367-1373. DOI: 10.1111/gcb.14948.

Swain TD, Vega-Perkins JB, Oestreich WK, Triebold C, DuBois E, Henss J, Baird A, Siple M, Backman V, Marcelino L. 2016. Coral bleaching response index: A new tool to standardize and compare susceptibility to thermal bleaching. Glob Chang Biol 22 (7): 2475-2488. DOI: 10.1111/gcb.13276.

Tagliafico A, Baker P, Kelaher B, Ellis S, Harrison D. 2022. The effects of shade and light on corals in the context of coral bleaching and shading technologies. Front Mar Sci 9: 919382. DOI: 10.3389/fmars.2022.919382.

Tilstra A, Wijgerde T, Dini-Andreote F, Eriksson BK, Salles JF, Pen I, Osinga R, Wild C. 2017. Light induced intraspecific variability in response to thermal stress in the hard coral *Stylophora pistillata*. PeerJ 5: e3802. DOI: 10.7717/peerj.3802.

Tolleter D, Seneca FO, DeNofrio JC, Krediet CJ, Palumbi SR, Pringle JR, Grossman AR. 2013. Coral bleaching independent of photosynthetic activity. Curr Biol 23 (18): 1782-1786. DOI: 10.1016/j.cub.2013.07.041.

van Woesik R, McCaffrey KR. 2017. Repeated thermal stress, shading, and directional selection in the Florida reef tract. Front Mar Sci 4: 182. DOI: 10.3389/fmars.2017.00182.

Van Woesik R, Shlesinger T, Grottoli AG et al. 2022. Coral-bleaching responses to climate change across biological scales. Glob Chang Biol 28 (14): 4229-4250. DOI: 10.1111/gcb.16192.

Winters G, Beer S, Zvi BB, Brickner I, Loya Y. 2009. Spatial and temporal photoacclimation of *Stylophora pistillata*: zooxanthella size, pigmentation, location and clade. Mar Ecol Prog Ser 384: 107-119. DOI: 10.3354/meps08036.

Yakovleva I, Hidaka M. 2004. Differential recovery of PSII function and electron transport rate in symbiotic dinoflagellates as a possible determinant of bleaching susceptibility of corals. Mar Ecol Prog Ser 268: 43-53. DOI: 10.3354/meps268043.