

Variable photosystem II thermal stress responses of reef-building corals *Pocillopora indiania* and *Heliopora coerulea* across latitudes from the Mascarene Plateau, Indian Ocean



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ABSTRACT

The persistence of remote reef sites invariably depends on the ability of their corals to better respond and adapt to a continuing global environmental change, by way of their protection from additional and direct stressors as a result of their remoteness; such reefs are generally referred to as coral refugia. This study investigated the latitudinal thermal thresholds of two commonly occurring corals from reefs both remote from and close to human population centres, in the understudied Mascarene Plateau (MP), Central Indian Ocean. Thermal experimental trials at 26, 29 and 32 °C for a period of 22h focused on reef-building conspecifics: the regionally-endemic hard coral *Pocillopora indiania*, and heat-tolerant photo-physiologically understudied and threatened octocoral *Heliopora coerulea* from three sites of varying degrees of remoteness and human impact (Saya de Malha (SDM), St Brandon (SB) and Mauritius Island (MAU)), each with varying mean sea surface temperature (SST). Imaging Pulse-Amplitude-Modulation (Imaging-PAM) fluorometry was used to determine how the photosynthetic performances at the Photosystem II (PSII), in terms of effective quantum yield (Φ_{PSII}), of the conspecifics responded after exposure to these different temperature regimes. SST anomaly over the past 28 years showed an increment of 1.2 °C with no significant latitudinal variation within the MP. Moreover, the experimental results displayed significant differences in intra- and interspecific Φ_{PSII} when corals were exposed to 32 °C ($p < 0.0001$); *P. indiania* from MAU suffered severe bleaching (over 90% surface area), with the highest degree of tissue sloughing leading to coral mortality, while conspecifics from SDM and SB exhibited better thermal threshold by being photosynthetically active, with 23% and 33% Φ_{PSII} , respectively. In contrast, *H. coerulea* from MAU thrived through the experiment indicating site-specific thermal threshold by displaying the lowest Φ_{PSII} (24%) as compared to conspecific from SDM (48%) and SB (58%). Although limited to Photosystem II responses, this study provides a first insight on the latitudinal variability in thermal vulnerability of conspecific corals from the MP and suggesting that corals from SDM and SB might be more resilient to the impacts of future warming events than corals at other sites.

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1. Introduction

Elevated thermal anomalies, considered to be one of the major environmental stressors, are critically threatening the persistence of global coral reefs (Klepac and Barshis, 2022). These threats are further exacerbated by ongoing local anthropogenic stresses (McClanahan and Muthiga, 2021; Bieg et al., 2024), for instance, human overpopulation (Gove et al., 2023), overfishing (Lemrabott et al., 2024) and coastal urbanisation and unsustainable tourism (Keen et al., 2022). As such, the outlook of global reefs is poor due to the increasing severity and frequency of marine heatwaves (Smith et al., 2023), leading to further intensification of global coral bleaching (Reimer et al., 2024).

Subsequently, coral reefs are under continuing threat of biodiversity loss and reduction in reef functional integrity (Quigley and Baird, 2024). However, the persistence of reef functions (McClanahan et al., 2024a,b) depends on the ability of corals to better respond to the warming environment by naturally increasing their thermal thresholds over repetitive bleaching events (Humanes et al., 2022). These recurrent events give rise to selective reef resilience, resulting in the dominance of thermally-resistant taxa with corals having higher thermal threshold (Lachs et al., 2023). For instance, some corals exhibit genetic adaptation (Humanes et al., 2022), while others employ phenotypic adaptations by stimulating adaptive traits in response to environmental changes (Drury et al., 2022). This is exemplified by empirical observations of variable coral bleaching responses in 2009 (Mattan-Moorgawa et al., 2018), and experimental observations that *Galaxea fascicularis* and the massive *Porites lutea* were found to be more thermally resistant to elevated temperature than tabular *Acropora* and branching *Porites* from MAU (Munbodhe et al., 2023).

Reefs exposed to recurrent prolonged thermal stresses may result in selective thermal species-specific resilience on account of both geophysical and oceanographic conditions (Skirving et al., 2017; Gonzalez-Espinosa and Donner, 2021) favouring heat dissipation along with enhanced genetic (Kenkel and Matz, 2016) and phenotypic plasticity (Grottoli et al., 2006) leading to local acclimation of certain corals. Such reefs known as coral refugia continue to persist and sustain higher coral cover, diversity and reef functions despite increasing severity and frequency of SST anomalies on these reefs (McClanahan et al., 2024). More often than not, these coral refugia sites are remote from human population centres, and examples of these have been highlighted by a number of initiatives such as The Ocean Agency's "50 Reefs" (<https://www.50reefs.org/>) and Mission Blue's "Hope Spots" (<https://missionblue.org/hope-spots/>). Nevertheless, local stressors have been found to significantly reduce the post-bleaching recovery rate (Metzel et al., 2024) and further suppress the adaptive capacity of corals, rendering anthropogenically-disturbed reefs prone to ongoing structural changes (Doorga et al., 2023). In recent decades, local stressors (compounded by recurrent and prolonged marine heatwaves) have led to a 40% reduction in functional coral reefs, which have been transformed from coral-to algal-dominated assemblages (McClanahan and Muthiga, 2021). This transformation also accounts for considerable changes in habitat complexity, with consequent loss of coral biodiversity (Guyvenchy et al., 2023) causing reduction in diversity and abundance of coral reef fishes and other associated marine organisms (McClanahan et al., 2024a,b).

Recently, latitudinal heat stress tolerances have been shown to vary among and within shallow reef colonies in the Great Barrier Reef (GBR) (Denis et al., 2024), suggesting that photo-physiological performances were highest in those corals inhabiting geographic regions with upper thermal threshold limits. Evensen et al. (2022) shed light on the variability in the thermal thresholds of four coral species over a wider geographical range from the Red Sea, while Ulstrup et al. (2011) highlighted that geographical variation in the Symbiodiniaceae-type considerably influenced the thermal tolerance of conspecific corals in the GBR. Further studies on coral photo-physiology from the Red Sea showed that corals from higher latitudes are better adapted to ongoing ocean warming (Banc-Prandi et al., 2022). However, Drury et al. (2022)

observed differential intraspecific photo-physiological performances which gave rise to a greater adaptability in individuals exhibiting phenotypic plasticity. For instance, corals which were capable of switching from photosynthetic dependence to heterotrophy (Levas et al., 2016) were able to enhance their adaptive capacity from severe bleaching in reefs dominated by dissipating waves and high-energy waters (Page et al., 2021), resulting in low water residence time (Reid et al., 2020) under nutrient-rich conditions.

The Indian Ocean comprises approximately 30% of global coral reefs (Wafar et al., 2011), of which approximately 10% of coral species are considered endemic and regionally-endemic (McClanahan et al., 2021) are continuously exposed to the deleterious impacts of climate change (Ummenhofer et al., 2024). These primarily include genera such as *Montipora*, *Acropora*, *Stylophora*, as well as *Pocillopora indiana* (Obura, 2016) from the Central Indian Ocean. The Mascarene Plateau (MP) here plays a vital role in sustaining a unique shallow marine biodiversity (Payet, 2005), including coral reefs and seagrass meadows within its lagoons and several shallow banks ranging from 20 m to 300 m deep, sloping to 2000 m–4000 m (New et al., 2005).

In the 1960s, limited information was available on the geomorphology and biological diversity on the MP owing to the few oceanographic research expeditions (for example, the International Indian Ocean Expedition (IIOE) (Wyrtyk et al., 1971) followed by the Indian Ocean Experiment in the 1970s and the World Ocean Circulation Experiment (WOCE) in the 1990s (Vianello, 2015)) that were carried out in the region. In the 2000's, major oceanographic studies were conducted, focusing primarily on oceanic circulation (New et al., 2007), primary productivity, large marine ecosystems and geomorphology (Payet, 2005), whereas 2008 ASCLME Survey No. 3 supplemented data on marine ecosystems of the MP (Strømme et al., 2008). Recent oceanographic studies (facilitated by the FAO EAF-Nansen Programme and the RV Dr Fridtjof Nansen) have updated empirical data to bridge the gaps in some of the more data-deficient areas, for instance, the macro- and megafauna of the SDM (Bergstad et al., 2021), photo-physiology of corals, seagrasses and macroalgae (Bhagooli et al., 2021a; c), pelagic and demersal fish diversity (Caussey et al., 2021), and benthic habitats and invertebrates (Ramah et al. 2021a, 2021b, 2021c) of SDM. Historically, the shipboard facilities and space required for in-depth, real-time and *ex-situ* studies on corals from SDM and SB corals have been limiting. In 2022 however, during the Indian Ocean Expedition facilitated by Monaco Explorations, the RV SA Agulhas II offered researchers the opportunity to perform *ex-situ* experimental stress trials on corals.

Moreover, recent application of PAM have allowed the evaluation of PSII efficiency of photo-physiological responses of various corals from SDM, Nazareth Banks and MAU Island of the MP (Louis et al., 2016; Mattan-Moorgawa et al., 2018, 2020; Bhagooli et al., 2021a; Jeetun et al., 2023; Jogue et al., 2023; Munbodhe et al., 2023; Ricot et al., 2023; Jeetun et al., 2024). The effective quantum yield (Φ_{PSII}) is one of the four main and most commonly used chlorophyll fluorescence parameters in evaluating stress responses in corals (Lesser and Gorbunov, 2001; Hill et al., 2004; Ralph et al., 2015), including *in hospite* and isolated states of the microalgal symbionts (Einbinder et al., 2016), antagonism of photosynthetic performance in corals affected by pathogens (Roff et al., 2008; Jogue et al., 2023), and symbiotic marine invertebrates and seaplants (Bhagooli et al., 2021a). It is a measure of the efficiency of PSII in capturing and using light energy for photosynthesis under illuminated (or active) conditions; it quantifies the proportion of absorbed light energy that is used for photochemical versus non-photochemical processes (such as heat dissipation) in PSII (Warner et al., 1999; Jones et al., 2000).

In this study, the laboratory-based experiments were conducted onboard the RV SA Agulhas II to evaluate the implications of latitudinal thermal thresholds of two commonly occurring but morphologically-different corals of the MP using Imaging-PAM fluorometry (Bhagooli et al., 2021b). Under challenging oceanic conditions, the experiment aimed at investigating the variation in the intra- and interspecific

photosynthetic performances, i.e., Φ_{PSII} of both the regionally-endemic hard coral *P. indiana*, and the understudied and threatened octocoral *H. coerulea* (Courtney et al., 2021). These corals were sampled from the remote reefs of SDM and SB, less impacted habitats than those of MAU (McClanahan and Muthiga, 2021; Doorga et al., 2023).

2. Materials and methods

An oceanographic research expedition was undertaken by the research vessel (R/V) SA Agulhas II under the Indian Ocean Expedition 2022, coordinated by the Monaco Explorations project and endorsed by the UN Decade of Ocean Sciences for Sustainable Development 2021–2030. The research activities in SDM and SB were conducted from 11th to November 23, 2022 and the *ex-situ* laboratory-based thermal stress experiments were carried out onboard. Both the corals, *P. indiana* and *H. coerulea* were collected on SCUBA (at 15–21 m depth), and photosynthetic performance challenged at 26, 29 and 32 °C for 22 h. In January 2023, similar experiments were carried out with conspecifics from the channel inside the lagoon of Bambous Virieux (~16 m depth) in the east of Mauritius (Munbodhe et al., 2023).

2.1. Geographical location of the sites

2.1.1. The Mascarene Plateau (MP)

The MP (Fig. 1) is predominantly a submarine plateau in the Indian Ocean of about 2200 km extending southward from Seychelles (4°S, 56°E) to Mauritius (20°S, 57°E) with several shallow banks. The MP is mainly influenced by the South Equatorial Current (SEC) between latitude 8° to 20°S (New et al., 2007), bifurcating through the SDM and Nazareth Banks and between the shoals of, also known as Cargados-Carajos Bank, and Mauritius (Vianello et al., 2017). Consequently, the marine ecosystems of the shallow banks are mainly influenced by the SEC (Payet, 2005), while the coastal waters of the shoals

and the islands of the MP are dominated by the South-East Trade Winds (Bhagooli and Kauallysing, 2019). Of the major coral reef ecosystems, the MP plays a vital role in providing an extended seagrass ecosystem and a rich coral biodiversity, both in terms of abundance and diversity (Payet, 2005).

SDM Bank is a submerged oceanic shallow bank of 40,808 km² which is found in the northern tip of the MP (Betzler et al., 2021) between latitude 10–13°S and longitude 59.30–62.30°E. SB is located about 400 km from the north coast of MAU. This remote coral-reef atoll comprises approximately 19 sandbars and 24 vegetated islands with 200 km² of shallow lagoon (Van der Schyff, 2020). Several of the islets are sandy cays which are perceived to be quite dynamic in shape and position due to tidal waves and cyclonic conditions, especially since the archipelago is low-lying and is submerged frequently during harsh weather conditions (Bhagooli and Kauallysing, 2019). MAU is the main inhabited island with an overall landmass of about 1865 km² (Heezen and Tharp, 1965) and a lagoon area (relatively shallow waters) of 243 km² enclosed by approximately 150 km of fringing reefs (Bhagooli and Kauallysing, 2019). The reefs are distinctly fragmented by natural breaks giving rise to a series of lagoons that define the geomorphological characteristics such as depths, current pattern and stretches from the shore (Daby, 2006). The depth of the lagoons varies between <1 and 3 m from near-shore extending several kilometres to the reefs, with some exceptions in the southeast region where channels of <30 m depth (mainly associated with rivers or underground springs) separate the reef from the shore (Fagoonee, 1990).

2.1.2. Geomorphological differences among the study sites

In addition to SST and SST anomalies used as climatic variability, population density, fishing activities and tourist arrivals per year were also considered as main cues for local stressors and to determine the influence of human activities on the corals (Table 1).

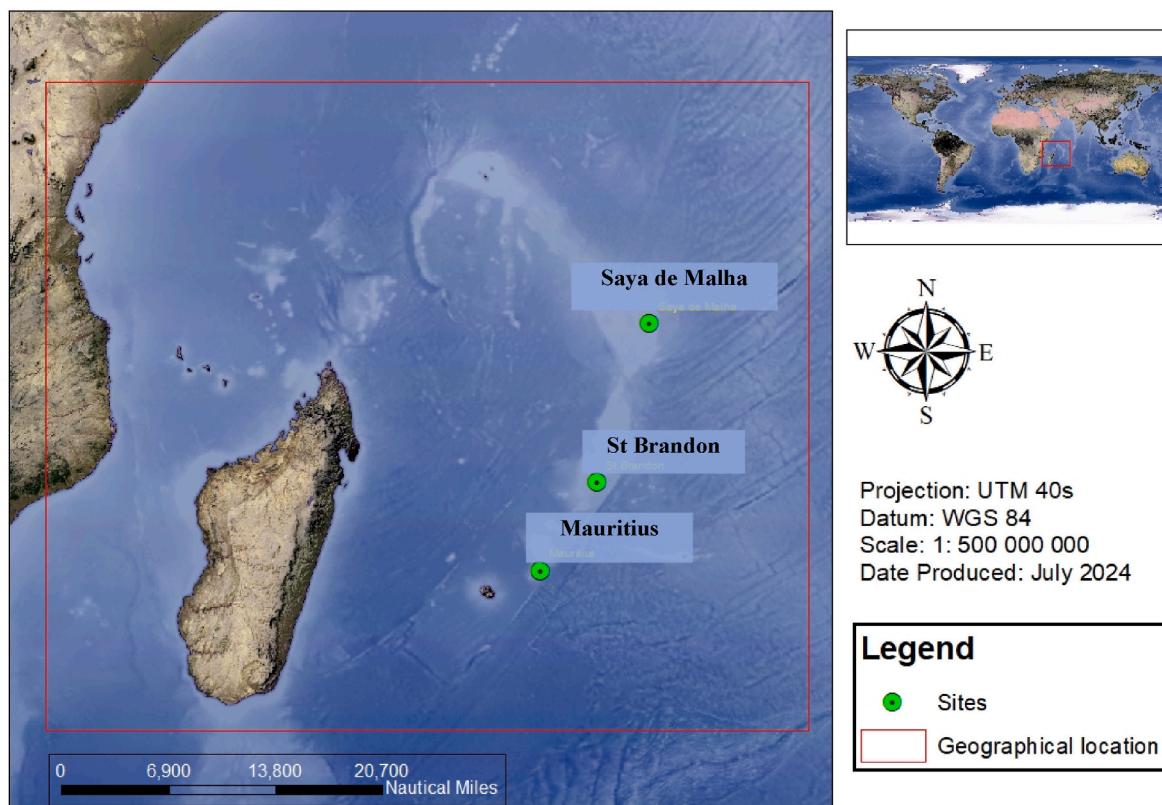


Fig. 1. Geographic location of the MP on the world map (right topmost) while the main map (left) shows the latitudinal differences among the three sites targeted for coral sampling for the thermal stress experiment.

Table 1

Main geomorphological features, demographic differences, climatic variability and major economic activities of MAU, SB and SDM of the Mascarene Plateau. <MSY denotes yearly fishing activities is less than the maximum sustainable yield (Mundodhe, 2022). ^aData obtained from Statistics Mauritius (2024), <https://statsmauritius.govmu.org/Pages/Statistics/statsbysubj.aspx>.

Geomorphological features	Mauritius Island	St Brandon	Saya de Malha
Latitude	20°17'S	16°20'S	11°22'S
Longitude	57°33'E	59°38'E	62°16'E
Population ^a	1.32 M	<100	Nil
Economic activities ^a	Tourist, fishing and agriculture	Fishing(<MSY)	Fishing (<MSY)
Landmass	1865 km ²	1.3 km ²	Submerged banks
Coastline	322 km	Hydrodynamic sandy banks	No coast – submerged bank
Lagoon area	243 km ²	190 km ² - Sandy banks	Shallow banks
Reef type	Fringing, barrier and patches	Fringing, barrier and patches	Patches
Climatic condition	Mild tropical	Windy Tropical	Tropical
Temperature	20.4 °C–24.7 °C	23.6 °C–27.4 °C	25.4 °C–29.8 °C
Dominant currents	SE Trade Winds	SE Trade Winds	South Equatorial Currents
Ecological Importance	Rich flora and fauna	Rich flora and fauna Yet to be inventoried	Rich flora and fauna

2.2. Satellite SST anomaly data and data on ocean colour for the Mascarene Plateau

Twenty-eight years of minimum SST and SST anomaly satellite metadata were extracted from NOAA National Centres for Environmental Information by specifying the timescales to 'All Months', from '1995 to 2023' region to approximate coordinates for Saya de Malha (10°02.41'S; 60°06.51'E), St Brandon (16°42.11'S; 59° 36.26'E) and Mauritius (20°20.75'S; 57° 48.11'E). The SST anomaly refers to the mean SST anomaly data from 1995 to 2023 set as baseline from which the SST anomalies were compiled and analysed for the studied geographical regions (Huang et al., 2021). Likewise, satellite data on monthly chlorophyll-a concentration was extracted from May 2022 to May 2023 from NASA Ocean Color (April 2024) to determine the surface nutrient level at SDM, SB and MAU which included the experimental period.

2.3. Experimental design

2.3.1. Corals under study

Both *P. indiana* and *H. coerulea* (Table 2) occur in SDM (Ramah et al., 2021a), SB and MAU (Munbodhe et al., 2023), however, little is known on their ability to resist anomalous SST increment in the Indian Ocean. *P. indiana* is a regionally endemic reef-building scleractinian coral species geographically limited to the Indian Ocean (Obura, 2012), whereas thermal resistant but threatened *H. coerulea* is a reef-building non-scleractinian octocoral (also known more commonly as the Blue Coral) exhibiting wide morphological plasticity (Villanueva, 2016).

2.3.2. Collection of coral samples

An experimental laboratory was set up on-board R/V SA Agulhas II in November 2022, whereby the thermal stress experiment was carried out on two corals from SDM (10°02.41'S; 60°06.51'E) and SB (16°42.11'S; 59° 36.26'E). A similar experiment was run on land on conspecifics from MAU (20°20.75'S; 57° 48.11'E) in January 2023. During the research expedition, coral samples were collected by SCUBA diving from SDM and SB, at depths ranging between 15 and 22 m. The occurrences of both

Table 2

Morphology, occurrences and identification features of *P. indiana* and *H. coerulea*, the two targeted coral species for the thermal stress experiment.

	<i>P. indiana</i> (Veron, 2000, WoRMS Editorial Board, 2024)	<i>H. coerulea</i> (Pallas, 1766)
Coral type	Scleractinia	Non-Scleractinian octocoral (WoRMS Editorial Board, 2024)
Morphology	Cylindrical compact branches with outward or upwards elongated verrucae (Veron, 2000)	Colonies occur as large patches in shallow reefs mainly in laminar and digitate forms (Yasuda et al., 2014)
Occurrence	Regionally endemic – Western Indian Ocean (Obura, 2012)	Occurs mainly in the Indian Ocean regions ⁹⁰ extending in the Western Pacific regions (WoRMS Editorial Board, 2024).
Identification features	Indian Ocean, coastal region in the upper shallow reefs (Veron, 2000)	Elongated digitate branches compactly close to each other with easily visible verrucae (WoRMS Editorial Board, 2024)
		Easily identifiable because of its exceptional blueish grey coloration

regionally endemic *P. indiana* and understudied *H. coerulea* throughout the MP, presented appropriate coral candidates for investigating cross-latitudinal and inter-specific thermal threshold variability within the MP.

2.3.3. Thermal stress experiment and photo-physiological data collection

Plastic aquaria (500 L, N = 9) equipped with air pump, thermostat, light control device and thermometer were used for thermal stress experiment on coral nubbins. The collected corals were fragmented into several nubbins and kept for 2 h in a storage tank in ambient seawater temperature to allow the corals to acclimatize. Replicate aquaria (N = 3) were used for each seawater treatment at varying temperatures of 26 °C, 29 °C, and 32 °C. Nubbins (N = 3) of each coral species approximately 5 ± 2 cm in length) were placed in each aquarium.

Prior to the start of the experiment (T_0), and prior to placing the coral nubbins in their respective treatment tanks, measurement of chlorophyll *a* fluorescence from each nubbin was recorded using Imaging-PAM Fluorometry (Hill and Ralph, 2006). Ten random Areas of Interest (AOIs) of 5 mm diameter were placed over each coral nubbin sample using the Imaging-Win Software (Walz) for the initial and temperature-stressed samples at each time-point. The pixel values within each AOI and for all the 10 AOIs were averaged to calculate Φ_{PSII} for each coral nubbin.

A weak measuring light ($\sim 1 \mu\text{mol quanta m}^{-2}\text{s}^{-1}$) and a saturating pulse ($2700 \mu\text{mol quanta m}^{-2}\text{s}^{-1}$) were applied to measure the minimum/background (F_0) and maximum (F_m) fluorescence, respectively. Φ_{PSII} was then calculated as per the following formula (Maxwell and Johnson, 2000):

$$\text{Effective Quantum Yield } (\Phi_{PSII}) = (F_m - F_0) / F_m$$

The effective quantum yield data collection exercise was repeated on all the coral nubbins under the different temperature treatments at T-6 hours ($T_{6\text{hrs}}$), T-12 h ($T_{12\text{hrs}}$) and T-22 h ($T_{22\text{hrs}}$). Based on previous studies and given the time-constraints onboard, the experiment was limited to 22h with acute thermal stress reaching 32 °C aligning with +1.5 °C critical average SST anomaly (IPCC Report, 2023), Table 3.

Moreover, the active air pumps in the aquaria maintained dissolved oxygen at optimum levels (80–100%) and ensured constant water mixing and continuous water movement to avoid water stagnation, mimicking the natural environment. Furthermore, due to increasing turbidity and decreasing visibility, 80–90% seawater from each experimental aquarium was manually exchanged regularly every 6h. Water temperature was also checked every 6h to confirm that aquarium

Table 3

Thermal stress experiments exposing coral nubbins to temperatures varying from 25 to 39 °C for a duration of 4–96h depending on the geographical areas to study the photosynthetic performance accordingly, using Pulse-Amplitude-Modulated (PAM) fluorometer.

Thermal Exposures	Duration of exposure	Pulse-Amplitude-Modulated fluorometer	Chlorophyll fluorescence parameters	References
1. 28, 32, 34 and 36 °C	0, 12, 24, 48, 96h	Diving-PAM	Maximum quantum yield	Warner et al. (1996)
2. 28, 30, 32, 33 and 34 °C	1, 3 or 4h	Teaching and Diving-PAM	Effective and maximum quantum yields; Photochemical and Non-photochemical quenching	Jones et al. (1998)
3. 25 and 31.5 °C	8, 24, 48h	Diving-PAM	Maximum quantum yield	Warner et al. (1999)
4. 28 and 34 °C	3h	Mini-PAM	Maximum quantum yield	Bhagooli and Hidaka (2003)
5. 26, 32 and 34 °C	3h	Mini-PAM	Maximum quantum yield	Bhagooli and Hidaka (2004)
6. 26 and 33 °C	6 and 12h	Mini-PAM	Maximum quantum yield	Yakovleva and Hidaka (2004)
7. 27 and 33 °C	1, 2, 3, 4, 5, 6, 7, 8h	Imaging-PAM	Effective quantum yield	Hill et al. (2004)
8. 30, 33, 36 and 39 °C	18h short-term acute heat stress assay	Diving-PAM	Photosynthetic efficiency	Voolstra et al. (2020)

thermostats maintained experimental challenge temperatures within a range of 25.89 ± 0.38 °C for the treatment at 26 °C; $29.23 \pm 0.69 \pm 0.29$ °C for the treatment at 29 °C and 32.18 ± 0.26 °C for the treatment 32 °C.

2.3.4. Qualitative assessment on degree of bleaching and tissue sloughing

Observational responses of each coral nubbin to persistent exposure to thermal stresses was recorded in terms of percentage of coral fragment surface area bleached, based on the observations made at every session of photo-physiological data collection at time T_0 (initial), $T_{6\text{hrs}}$, $T_{12\text{hrs}}$ and $T_{22\text{hrs}}$. Bleaching in each coral individual was recorded as a percentage bleaching over the whole coral fragment and was categorized as: No Bleaching = <10%; Paling = <30%; Partly bleached = <50%; Bleaching to Severe bleaching = <90%; Complete bleaching = > 90% (Evensen et al., 2023). Tissue sloughing was recorded in individual coral nubbin based on tissue lesions observed (-, +, ++, +++) at low to high level of tissue sloughing.

2.4. Data analyses

R-Statistical software (Version 4.2.2, R Core Team, 2022) was used to compile and conduct statistical analyses on the SST anomalies and on the effective quantum yield data. Shapiro-Wilk's normality test ($W = 0.99$, $p\text{-value} = 0.87$) confirmed that the SST anomaly data was normally distributed, which allowed the use of one-way ANOVA to determine the thermal variabilities within the latitudinal gradient while Kruskal-Wallis pair-wise comparison, p -values adjusted with the Bonferroni method (Dunn, 1964), was performed to evaluate differences in monthly mean minimum SST from 1995 to 2023 between sites within the MP. Similarly, the sea surface mean monthly chlorophyll-*a* data was extracted from May 2022 to May for SDM, SB and MAU and the

variances of the monthly means for 13 months were compared between the study sites using F-Test two-samples for variances. For reliable comparisons among treatment and between the two studied coral species, relative effective quantum yield ($\Phi_{\text{PSII-REL.}}$) for each coral in respective treatment was derived by dividing the Φ_{PSII} by the initial Φ_{PSII} obtained prior to start of the thermal stress experiment (Bhagooli and Hidaka, 2003, 2004). The effective quantum yield data deviated significantly from normal distribution (Shapiro-Wilk normality test, $W = 0.67$, $p\text{-value} = 0.0001$). Subsequently, the data were arcsine transformed and then Generalised Linear Model, non-parametric comparison (Poisson-GLM) was performed (no. observations = 432, $r^2 = 0.966$) to compare the corals photo-physiological responses (Φ_{PSII}) among treatments against time of exposure, among treatments and time of exposure and among geographical zones.

3. Results

3.1. Latitudinal differences in SST and SST anomalies

Metadata analysis of the monthly mean sea surface temperature (SST) from 1995 to 2023 within the MP (Table 4; Fig. 2) varied significantly among SDM, SB and MAU (Kruskal-Wallis Chi-squared = 139.84, $d.f = 2$, $p < 0.0001$). The yearly mean latitudinal SST differences were 27.27 ± 1.32 °C for SDM, 26.5 ± 1.6 °C for SB and 25.65 ± 1.75 °C for MAU in 1995 to 28.02 ± 1.17 °C, 27.32 ± 1.42 °C and 26.49 ± 1.52 °C in 2023, respectively. The latitudinal SST limit showed that SDM had the highest monthly SST in the MP ($p < 0.0001$).

No significant difference in an overall SST anomaly trend was observed within the MP from 1995 to 2023 ($F_{2, 1041} = 0.73$, $p = <0.48$) (Table 4). However, during extreme heating events, SST anomaly nearly attained 1.5 °C in SB whereas the extreme SST anomaly for MAU and SDM has reached 1.2 °C (Fig. 3).

3.2. Variance in sea surface chlorophyll-*a* between the study sites

The mean monthly sea surface chlorophyll-*a* concentration from May 2022 to May 2023 (Fig. 4) at SDM and SB were 0.25 ± 0.09 mg/m³ and 0.30 ± 0.13 mg/m³, respectively, indicating relatively low fluctuation in chlorophyll-*a* distribution as compared to MAU which significantly varied when compared to that of SB ($p < 0.001$), SDM (F-Test Two-samples, $p < 0.01$) (Table 5). The chlorophyll-*a* concentration in the reefs of MAU varied between 0.04 and 0.75 mg/m³ with mean 0.44 ± 0.23 mg/m³ showing relatively the highest fluctuations.

3.3. Latitudinal variation in PS-II efficiency

Both *P. indiana* and *H. coerulea* exhibited significantly different photosynthetic responses over acute exposure to thermal stress at 32 °C ($p < 0.001$) with an overall better latitudinal photo-physiological performances displayed by *H. coerulea* ($p < 0.001$), (Table 6). Moreover, the study further demonstrated variability in latitudinal Φ_{PSII} responses with corals from both SDM and SB revealing better performances as compared to conspecifics from MAU ($p < 0.01$) (Table 6). Finally, the results showed that after 6-h of exposure at 32 °C, the thermal resistance of *P. indiana* from MAU significantly decreased to 38% photosynthetic activities (12-h). The thermal resistance declined further upon

Table 4

Cross-latitudinal thermal variability in monthly mean SST among the different study sites from 1995 to 2023 using Dunn (1964) Kruskal-Wallis multiple comparison, p -values adjusted with the Bonferroni method, $p < 0.0001$.

Comparison among study sites	z	p-unadj.	p-adj.
Saya de Malha - St Brandon	5.59	<0.0001	<0.0001
Saya de Malha - Mauritius	-6.23	<0.0001	<0.0001
St Brandon - Mauritius	-11.82	<0.0001	<0.0001

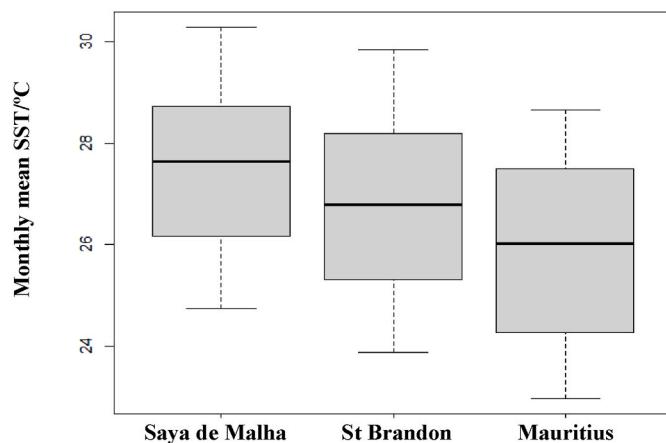


Fig. 2. Mean monthly SST in °C from January 1995 to December 2023 for Saya de Malha, St Brandon and Mauritius.

continued exposure to 32 °C for 22-h which led to coral mortality, contrary to conspecific from SDM and SB which showed significantly higher thermal threshold over persistent exposure to 32 °C.

Overall, *P. indiana* from SDM was first to show sign of bleaching (paling) with significant drop in effective quantum yield at 22-h of exposure to 29 °C ($\Phi_{PSII(SDM)} = 0.38 \pm 0.04$, $n = 9$, $p < 0.0001$), with 42% decrease in photo-physiological activities, Figs. 5 and 6A, respectively and Table 6. However, it maintained lower photosynthetic responses at T_{6hrs} at 32 °C ($\Phi_{PSII(SDM)} = 0.44 \pm 0.08$, $\Phi_{PSII-REL} = 68\%$) as compared to *P. indiana* fragments from SB and MAU, which were over 90% photo-physiological efficient. The photosynthetic activity of *P. indiana* from SDM further decreased with increasing exposure duration to 32 °C ($T_{12hrs@32}^0 \Phi_{PSII(SDM)} = 0.33 \pm 0.08$), Fig. 5. Conspecifics from SB exhibited 75% photosynthetic activities while a drop of 62% was detected in the fragments from MAU at 12h exposure to 32 °C, Fig. 6A. Similar trend in photo-physiological activities was observed over persistent exposure to 32 °C at 22h with 33% relative photosynthetic efficiency in *P. indiana* fragments from SB followed by SDM ($\Phi_{PSII-REL} = 23\%$) whereas no photosynthetic activity was noted in *P. indiana* fragments from MAU.

Irrespective of geographical locations, at 26 °C (controls) all corals exhibited over 95% photosynthetic activities throughout the

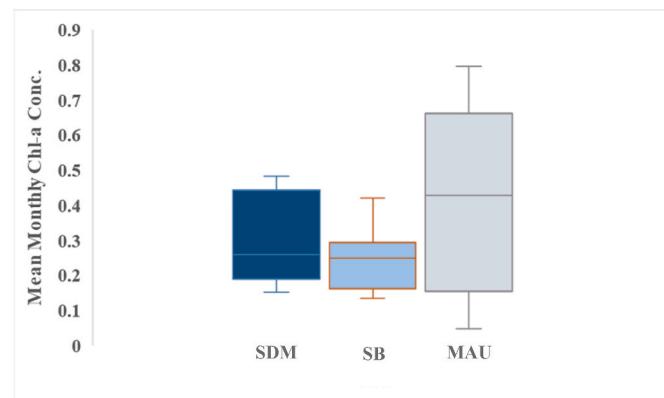


Fig. 4. Mean monthly sea surface chlorophyll-a concentrations in mg/m^3 from the study sites (SDM, SB and MAU, respectively) from May 2022 to May 2023.

Table 5

Mean SST anomaly (°C) from SDM, SB and Mauritius from 1994 to 2023 (One-way ANOVA).

	d.f.	SS	MS	F-value	Pr(>F)
Sites	2	0.234	0.117	0.730	0.4817
Residues	1041	167.074	0.160	NA	NA

Table 6

Comparisons of the monthly mean sea surface chlorophyll-a concentrations between MAU and SDB and SB using F-Test two-samples for variances, $p < 0.01$. The text in bold and italics correspond to the mean and variance of each site as per the row.

Site(s)	Obs.	mean	Var.	df	F-value	F Critical one-tail	P(F ≤ f) one-tail
MAU	13	0.406	0.075	12			
MAU- SDM	13	0.301	0.016	12	0.2157	0.3722	0.0064
MAU- SB	13	0.251	0.008	12	0.1118	0.3722	0.0003
SDM- SB				12	0.5184	0.3722	0.1346

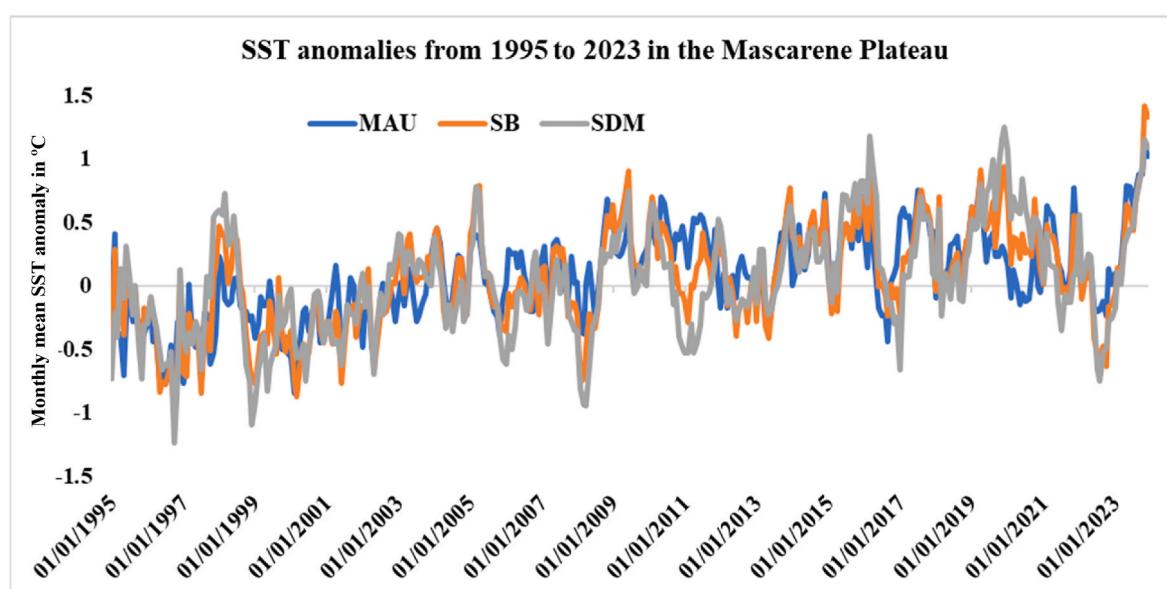


Fig. 3. SST anomalies from January 1995 to December 2023 for Mauritius (MAU), St Brandon (SB) and Saya de Malha (SDM).

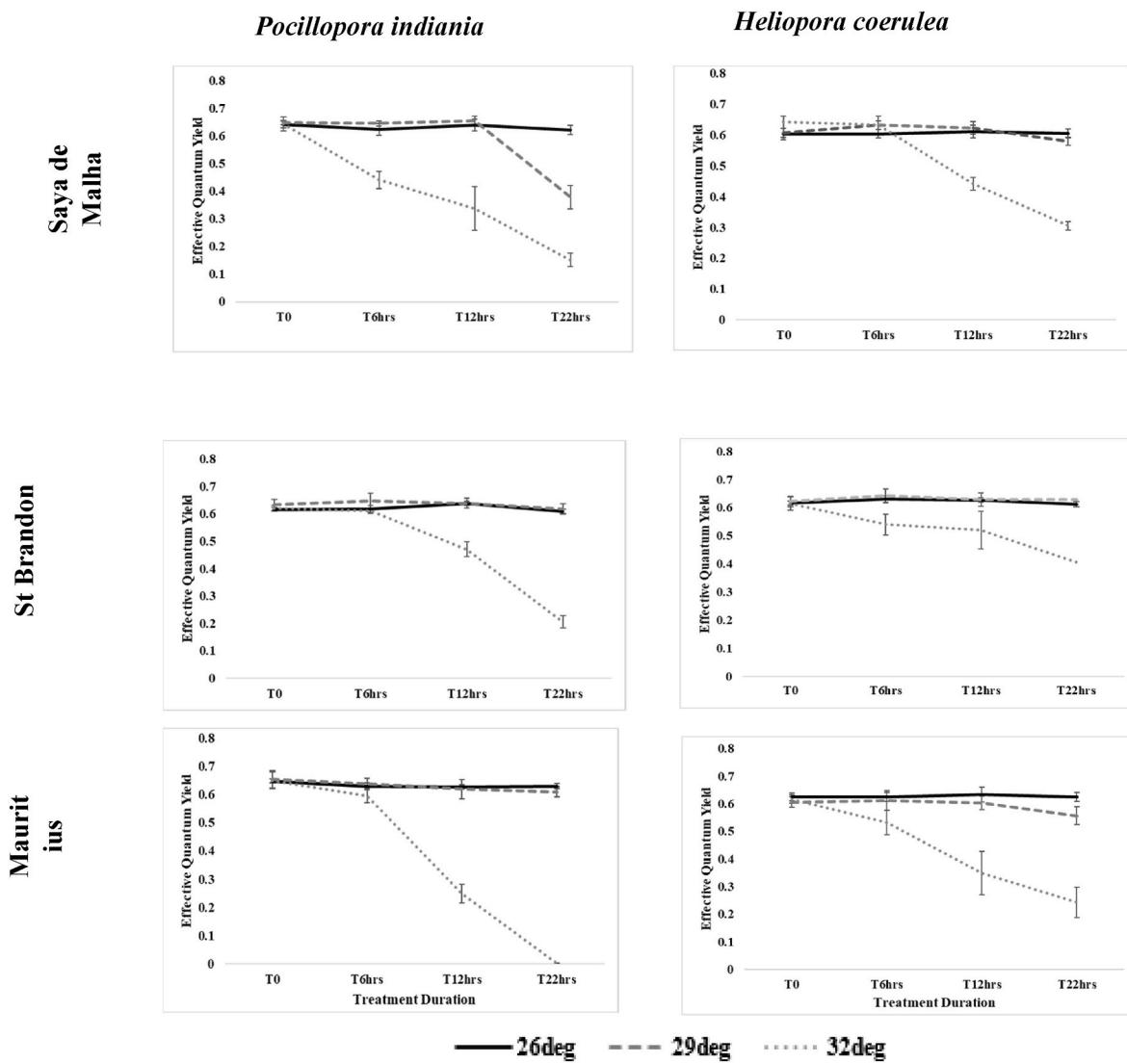


Fig. 5. Effective Quantum Yield (Φ_{PSII}) measured prior to the experiment (T_0) and post-exposure to treatment (6h - T_{6hrs} ; 12h - T_{12hrs} ; 22h - T_{22hrs}) of *P. indiania* (left) and *H. coerulea* (right) fragments from Saya de Malha (SDM), St Brandon (SD) and Mauritius (MAU) per site over 22h of exposure to respective treatment at 26, 29 and 32 °C. Data represent mean \pm SD (n = 3).

experiment, Fig. 6A & B. The relative photo-physiological activities decreased significantly at 22h of exposure to 32 °C (Poisson GLM, $p < 0.001$) with 24% relative photosynthetic yield ($\Phi_{PSII-REL}$) exhibited by *H. coerulea* from MAU, followed by SDM ($\Phi_{PSII-REL} = 48\%$) and SB ($\Phi_{PSII-REL} = 58\%$), Fig. 4. *P. indiania* from SDM and SB responded with $\Phi_{PSII-REL} = 24\%$ and $\Phi_{PSII-REL} = 33\%$ photosynthetic activities, respectively, whereas *P. indiania* from MAU experienced complete bleaching with relatively no photo-physiological response over acute exposure to 32 °C (Fig. 6A).

In contrast, *H. coerulea* nubbins from all the study sites maintained over 90% photosynthetic activities over persistent exposure to 29 °C (Fig. 6B). However, the photo-physiological performances of conspecific from MAU were reduced to 57% of photo-physiological responses with $\Phi_{PSII} = 0.35 \pm 0.04$ at 12h exposure to 32 °C, which further dropped to 39% ($\Phi_{PSII} = 0.24 \pm 0.04$) over persistent exposure ($T_{22hrs@32}$). Comparatively, conspecific from SDM and SB remained photosynthetically active over persistent exposure to 32 °C with better photosynthetic yield, $\Phi_{PSII} = 0.31 \pm 0.01$ (48%) and $\Phi_{PSII} = 0.36 \pm 0.04$ (58%), respectively.

3.4. Degree of bleaching and tissue sloughing on acute thermal stress

Major physico-biological and behavioural changes were observed in experimental tanks at $T_{22hrs@29}^0$, $T_{22hrs@32}^0$, $T_{22hrs@32}^0$ as compared to their respective treatments at 26 °C. Both corals experienced significant degree of bleaching accompanied by high prevalence of tissue sloughing resulting in increased turbidity with increasing heat intensity in treatments $T_{22hrs@29}^0$, $T_{22hrs@32}^0$, $T_{22hrs@32}^0$ Tables 7 and 8. Despite records of paling, irrespective of geographical locations, no obvious sign of tissue sloughing was observed in *H. coerulea* fragments during the entire thermal stress experiment, whereas pronounced tissue sloughing was observed in *P. indiania* fragments from MAU after 12h of exposure at 32 °C which gradually intensified at 22h (Table 8). The water visibility worsened gradually from $T_{6hrs@32}^0$ to $T_{22hrs@32}^0$ with the highest rate of tissue sloughing in *P. indiania* fragments from MAU at $T_{22hrs@32}^0$. Both *P. indiania* and *H. coerulea* from SDM and SB maintained over 30% photo-physiological activities over persistent exposure to 32 °C. *H. coerulea* from MAU survived with 24% photosynthetic activities whereas *P. indiania* fragments bleached completely (see Table 9).

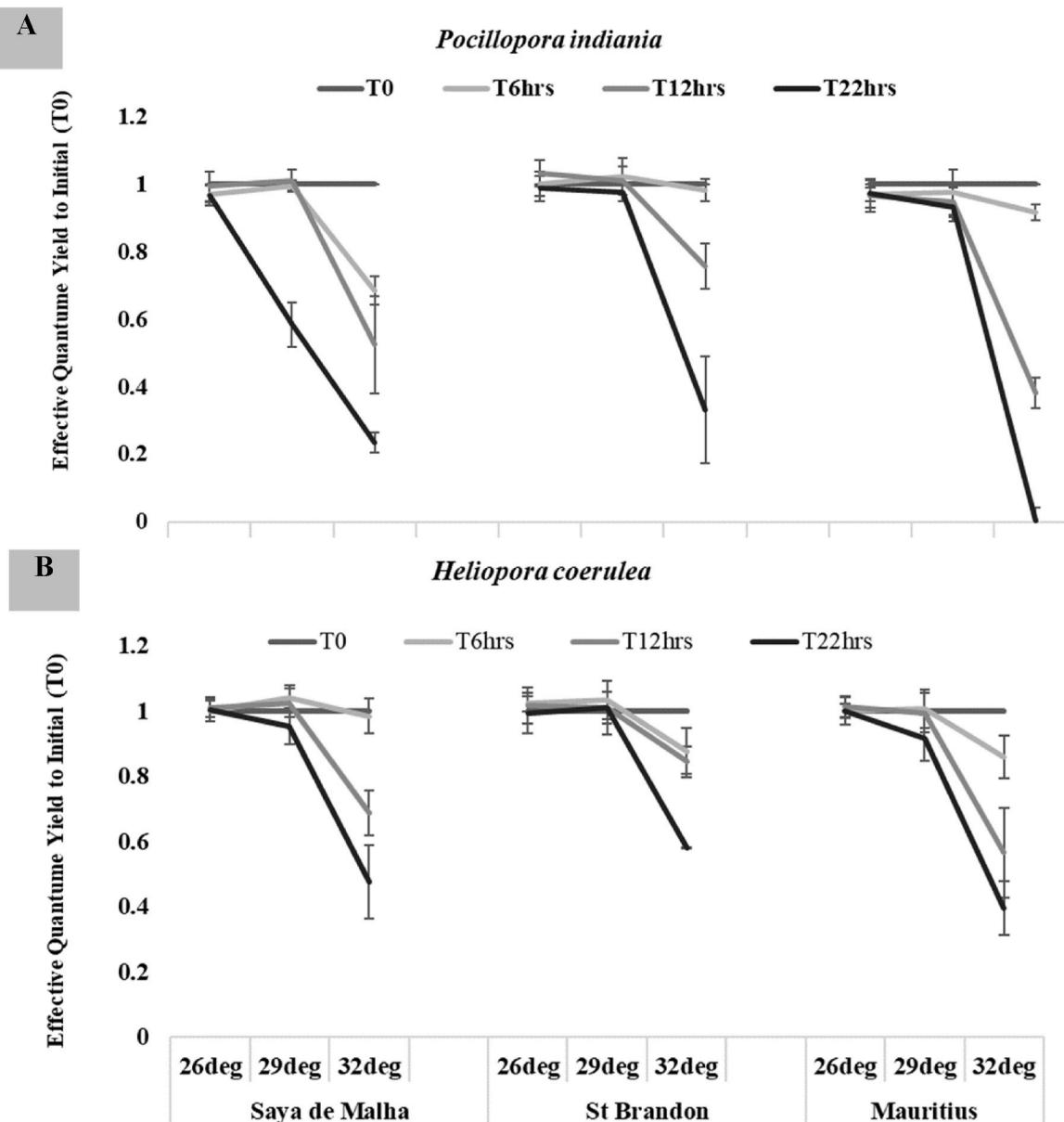


Fig. 6. Changes in the relative PS-II performance ($\Phi_{PSII-REL}$) ratio with respect to initial Φ_{PSII} of each respective coral fragment prior to exposure to their respective treatment at 26, 29 and 32 °C (n = 3) at time: 0-h(initial); 6h, 12h and 22h. Data represent mean \pm SD (n = 3). *P. indiana* (6A) and *H. coerulea* (6B).

4. Discussion

Under business-as-usual scenario, the anomalous increase of the ocean temperature surpassing 1.5 °C (IPCC, 2023) critically threatens the ocean biogeochemical processes (Bass et al., 2021) and associated marine species (Wernberg et al., 2024). Despite similar latitudinal SST heating within the MP, here, the findings showed remarkable differences in latitudinal thermal thresholds of two commonly occurring but morphologically different reef-building corals. Both *P. indiana* and *H. coerulea* from SDM and SB showed significantly higher Φ_{PSII} responses to acute exposure to 32 °C, temperature beyond the 1.5 °C lethal anomalous SST limit, while conspecifics from MAU displayed higher thermal vulnerability. Although, *P. indiana* from SDM was the first to show signs of bleaching after acute exposure to 29 °C, the coral thrived and persisted throughout the 22h thermal stress duration indicating certain level of thermal acclimation, whereas conspecific from MAU bleached and died following acute exposure to 32 °C. On the contrary, both *P. indiana* and *H. coerulea* from SB outperformed with the highest

Φ_{PSII} followed by SDM, displaying wider thermal threshold implying better thermal acclimation as compared to conspecifics from the reefs of MAU. The findings therefore indicated that both *H. coerulea*, and *P. indiana*, from SB displayed relatively higher degree of thermal acclimation (McCarthy et al., 2024) to acute exposure to 32 °C, temperature beyond the 1.5 °C lethal anomalous SST limit.

The significant decrease in Φ_{PSII} at elevated temperature in both *P. indiana* and *H. coerulea* from MAU indicated comparatively higher degree of damage at PSII with increasing thermal susceptibility. The decline in effective quantum yield at PSII has been associated to thermal stress response in hospite and isolated symbionts from corals (Jones et al., 1998; Warner et al., 1999; Bhagooli and Hidaka, 2003; Hill and Ralph, 2006) as well as bleaching/mortality of corals (Warner et al., 1996; Jones et al., 2000). The effective quantum yield at PSII is therefore considered as a rapid measure of the stress-response in corals for photosynthetic performances (Hill et al., 2004). Subsequently, because of the time constraints and to better optimize the objectivity of this study under the challenging oceanic weather conditions, the coral specimens

Table 7

Comparisons of photo-physiological responses of *H. coerulea* and *P. indiana* fragments (n = 9 per coral sp. per treatment) from SDM, SB and MAU exposed to three different temperature treatments for a period of persistent exposure of 22h compared to initial conditions. Generalised Linear Model, non-parametric comparison (Poisson-GLM) was used to assess the variabilities in photo-physiological responses of conspecifics among different geographical locations at different temperature; no. observations = 432, $r^2 = 0.966$, 95%-confidence interval, $p < 0.05$ -significant *Helio*- *H. coerulea*; *Pocillo* - *P. indiana*).

Photo-physiological Comparisons	Treatment x Time	Zones/Corals	Estimates	c.f (95%)	p-value
Treatment x Time	29 °C x T _{6hrs}		0.11	0.00–0.21	0.041
	32 °C x T _{12hrs}		-0.36	-0.47–0.26	<0.001
	32 °C x T _{22hrs}		-0.64	-0.75–0.54	<0.001
Corals x Treatment x Time	32 °C x T _{6hrs}	<i>Helio</i> vs <i>Pocillo</i>	-0.40	-0.55–0.26	<0.001
	32 °C x T _{12hrs}	<i>Helio</i> vs <i>Pocillo</i>	-0.25	-0.40–0.11	0.001
	32 °C x T _{22hrs}	<i>Helio</i> vs <i>Pocillo</i>	-0.38	-0.52–0.23	<0.001
Treatment x Time x Zones	32 °C x T _{6hrs}	SDM vs SB	-0.22	-0.36–0.07	0.004
		SDM vs MAU	-0.21	-0.35–0.06	0.005
	32 °C x T _{12hrs}	SDM vs SB	0.15	0.01–0.29	0.043
		SDM vs MAU	-0.20	-0.34–0.06	0.007
Corals x Time x Zones x Treatment	32 °C x T _{22hrs}	SDM vs SB	0.23	0.08–0.37	0.002
		SDM vs MAU	-0.14	-0.28–0.01	0.065
	29 °C x T _{22hrs}	SDM vs SB	0.46	0.26–0.67	<0.001
		SDM vs MAU	0.54	0.34–0.75	<0.001
	32 °C x T _{6hrs}	SDM vs SB	0.56	0.36–0.77	<0.001
		SDM vs MAU	0.51	0.30–0.71	<0.001
	32 °C x T _{12hrs}	SDM vs SB	0.12	-0.08–0.33	0.241
		SDM vs MAU	0.03	-0.18–0.23	0.796
	32 °C x T _{22hrs}	SDM vs SB	-0.07	-0.27–0.14	0.528
		SDM vs MAU	0.59	-0.79–0.38	<0.001

were acclimated for 2h prior to exposing to respective temperature for 22h (Munbodhe et al., 2023; Jeetun et al., 2023) at acute thermal stress at 32 °C with only one chlorophyll fluorescence parameter, Φ_{PSII} , investigated on all test samples at each treatment and time-point. While cruising from one station to another in the multi-disciplinary oceanographic expedition, all the activities were critically subject to the sea conditions and acquisition of the targeted species from the open ocean shallow bank and reef areas which also included the setting up of and executing the thermal stress experiment. As such, time factor played a crucial role in the effective setting up and running of the experiment which was first of its kind on-board a research vessel.

However, as depicted by the SST anomaly meta-data analysis for the Mascarene Plateau, it is instrumental that thermal increment be ramped up further to +3 and +6 °C for a longer duration in future similar experiments. Furthermore, additional parameters such as maximum quantum yield at PSII (F_v/F_m), electron transport rate (ETR), non-

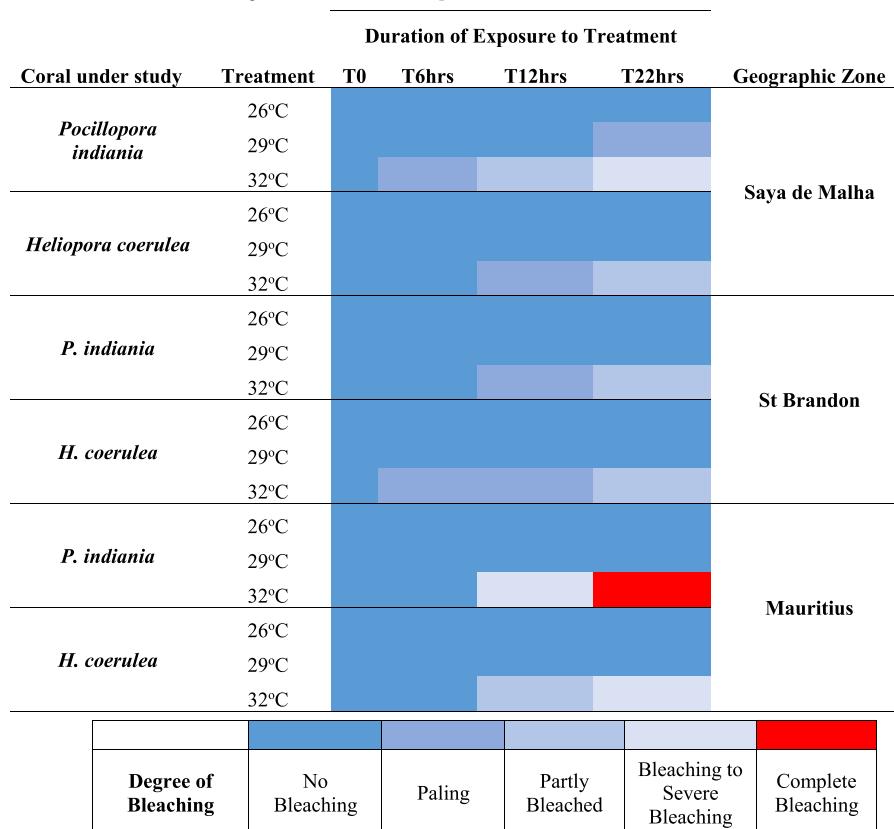
photochemical quenching (NPQ) (Bhagooli et al., 2021b) and variability of Φ_{PSII} within coral fragments (Ralph et al., 2015) should also be explored to have a thorough assessment of the photo-biological responses with respect to thermal acclimation and the degree of anthropogenic impacts in the lower latitude of the Mascarene Plateau. Nevertheless, this study demonstrated that conspecifics from higher latitude of the Mascarene Plateau (SDM: 28.02 ± 1.17 °C; SB: 27.32 ± 1.42 °C) have higher thermal thresholds with better photo-physiological performances which corroborate with the findings of Banc-Prandi et al. (2022) and Denis et al. (2024) who also reported similar latitudinal thermal threshold trends in corals from the Red Sea and the GBR, respectively. Likewise, despite showing initial thermal vulnerability when exposed to 29 °C, *P. indiana* from SDM exhibited better strategies of overall thermal tolerance to acute exposure to elevated temperature. The thermal threshold of the conspecific from MAU was limited to 6h of exposure to 32 °C, while the one from SB showed the highest thermal tolerance. Both conspecifics from St Brandon outperformed and demonstrated extended thermal tolerance to acute exposure to 32 °C exhibiting relatively higher level of thermal acclimation as compared to corals from SDM and MAU, respectively.

Several factors influence the response of corals to thermal stresses and subsequent local acclimation. Switch in feeding strategy from symbiotic dependency to heterotrophy (Baird and Atkinson, 1997; Morris et al., 2019), decreasing light intensity with increasing depth (Hoogenboom et al., 2012; Louis et al., 2016), endosymbiont-Symbiodiniaceae community structure (Lin et al., 2024), physiological plasticity (Keshavmurthy et al., 2021) and the bacterial community structure (Ricci et al., 2022) are amongst the microlevel adaptive strategies exhibited by corals. As such, the reefs of SDM and SB being geographically remote, experience limited human hindrance, mainly fishing activities, while in addition to fishing, the reefs of MAU are exposed to continuous deforestation related to coastal urbanization, infrastructural development (Januchowski-Hartley et al., 2020) and agricultural run-offs (Soondur et al., 2022), owing to ongoing economic development and increasing tourist arrivals (Standish et al., 2023). Subsequently, the thermal threshold of the *P. indiana* from MAU was limited to 6h of exposure to 32 °C whereas *H. coerulea* from MAU thrived through persistent exposure to 32 °C, but with lower photo-physiological efficiency displaying higher thermal vulnerability to acute elevated temperature. The thermally stressed *P. indiana* from MAU had the highest prevalence of tissue sloughing which might potentially be due to increased coral vulnerability to changes in microbiological biota of the coral under acute thermal stress (Chen et al., 2024). Such observations therefore suggest that the corals from the lower latitude, MAU, exposed to relatively cooler SST (26.49 ± 1.52 °C) are potentially more vulnerable to acute exposure to elevated temperatures of 32 °C while, active land-based alterations (Doorga et al., 2023) are more likely to exacerbate the corals vulnerability to thermal stresses.

Despite limited to Φ_{PSII} of the photo-physiological performances of the two corals, the present results corroborate with the findings of Grottoli et al. (2006) whereby in the presence of optimal concentration of nutrients (Nalley et al., 2023), thermally stressed corals might enhance thermal resistance by switching to heterotrophy thereby enhancing thermal acclimation. In this case, *P. indiana* from SDM, which showed certain degree of thermal vulnerability at 6h of exposure to 32 °C, remained photosynthetically active throughout the study while conspecific from MAU bleached and died. Such geographical differences in thermal threshold might further be explained by the variability in nutrient levels causing further stress (Standish et al., 2023) in the reefs of Mauritius as compared to stable nutrients concentration in the reefs of SB and SDM as represented by relatively low flux in sea surface chlorophyll-a concentration (0.25 ± 0.09 mg/m³) and (0.30 ± 0.13 mg/m³), respectively. In contrast, the chlorophyll-a concentration in the reefs of MAU significantly fluctuated from 0.04 to 0.75 mg/m³, (0.44 ± 0.23 mg/m³) which most probably originated mainly from anthropogenic sources via surface run-offs (McClanahan and Muthiga, 2021; Doorga

Table 8

Rapid bleaching observational chart indicating the degree of bleaching per coral species per site and treatment as recorded during the thermal stress experiment.

**Table 9**

Degree of tissue sloughing observed in coral fragments per site treatment per site recorded during the thermal stress experiment, -Absent; +sign of tissue sloughing/white dot; ++ partially scattered white dots; +++enlarged white patches; +++++overall whitening.

Region	Coral Species	Treatment	Tissue sloughing			
			T-0hrs	T-6hrs	T-12hrs	T-22hrs
Saya de Malha	<i>P. indiania</i>	26 °C	-	-	-	-
		29 °C	-	-	-	-
		32 °C	-	-	+	++
	<i>H. coerulea</i>	26 °C	-	-	-	-
		29 °C	-	-	-	-
		32 °C	-	-	-	-
St Brandon	<i>P. indiania</i>	26 °C	-	-	-	-
		29 °C	-	-	-	-
		32 °C	-	-	-	++
	<i>H. coerulea</i>	26 °C	-	-	-	-
		29 °C	-	-	-	-
		32 °C	-	-	-	-
Mauritius	<i>P. indiania</i>	26 °C	-	-	-	-
		29 °C	-	-	-	-
		32 °C	-	-	+++	++++
	<i>H. coerulea</i>	26 °C	-	-	-	-
		29 °C	-	-	-	-
		32 °C	-	-	-	-

et al., 2023; Jogee et al., 2024). Similar findings were reported by Becker et al. (2021) stating that at elevated temperature, corals exposed to optimal nutrient concentration, had 24% enhanced total tissue biomass and 50% higher endosymbiont densities leading to increased overall

coral physiological performance.

Furthermore, in contrast to many reef-building corals, in the events of marine heatwaves, the octocoral *H. coerulea* exhibits higher optimal thermal threshold (Zann and Bolton, 1985) with enhanced thermal resilience (Atrigenio et al., 2020). As such, *H. coerulea* from SDM and SB reefs maintained relatively higher thermal resistance as it is both morphologically (Villanueva, 2016) and physiologically robust, and capable of resisting thermal stresses of 31 °C for over three weeks (Guzman et al., 2019). However, *H. coerulea* from MAU displayed lower photosynthetic activities (39%) than conspecifics from SDM and SB, implying higher thermal stresses, but yet, thrived through the acute exposure to 32 °C, suggesting better thermal acclimation as compared to *P. indiania*. Moreover, this finding also indicated that *H. coerulea* from Mauritius exhibited certain level of thermal vulnerability which might potentially be associated to some extent to anthropogenic disturbances in a warming environment, SST anomalies beyond +1.5 °C.

Although the reefs of SDM experience upper thermal limits, conspecifics from SB had higher Φ_{PSII} compared to the other sites in response to acute thermal stress exhibiting higher thermal thresholds. This observation therefore concurs with the finding that coral thermal threshold varies within reefs (Denis et al., 2024), yet challenges the paradigm that corals exposed to high thermal averages display better photosynthetic performance (Banc-Prandi et al., 2022; Denis et al., 2024). Irrespective of geographical locations, the variability of the intra- and interspecific Φ_{PSII} , suggest the fact that corals under favourable environmental conditions are capable of exhibiting phenotypic plasticity and display better resistance against acute thermal stress, such as Symbiodiniaceae-type (Ulstrup et al., 2011), dissipating waves and high-energy waters (Page et al., 2021) resulting to low water residence time (Reid et al., 2020) under nutrient-rich conditions. In the same line,

the corals in the lagoons and the reef crests of SB are relatively well-developed (Evans et al., 2016; Van der Schyff, 2020) which is mostly influenced by the prevailing South East Trade Winds and the South Equatorial Currents (Bhagooli and Kaullysing, 2019), unlike the shallow oceanic coral patches in submerged bank of SDM (Bhagooli et al., 2021b; Ramah et al., 2021c) which is influenced by tidal and internal wave dynamics generated by the topographic reliefs (Coopen et al., 2021). Irrespective of latitudinal SST variation and despite intraspecific differences, overall, *H. coerulea* showed remarkable Φ_{PSII} response and subsequently thermal acclimation to acute thermal stress including conspecific from the reefs exposed to ongoing anthropogenic disturbances.

5. Conclusions

The latitudinal photosynthetic performances of the conspecifics and the bleaching pattern, accompanied by elevated prevalence of tissue sloughing at acute temperature exposure of 32 °C, have clearly demonstrated that corals from SB were thermally more resistant than SDM followed by MAU. Overall, this study was able to elucidate the latitudinal variation of the thermal thresholds of the regionally endemic *P. indiana* and commonly occurring thermally resistant *H. coerulea* in both reefs with relatively lesser human footprints indicating better thermal acclimation whereas the Φ_{PSII} of both conspecifics from MAU were the lowest of the MP. Although exposed to challenging oceanic conditions and time constraints, this experiment driven study provides a first insight on the latitudinal variability in thermal acclimation and susceptibility of conspecific corals from the MP, which is becoming more important than ever in the wake of a globally warming ocean and widespread bleaching and mortality of corals. Subsequently, this preliminary study confirmed that corals from reefs remote from human population centres were better able to cope with warming conditions than corals from impacted reefs and that it is imperative that these areas remain protected from direct impacts such that they might act as coral refugia under future climate change scenarios. In addition, further investigations on the site-specific biochemical changes, phenotypic and genetic plasticity of corals among and within sites with more in-depth photo-biological assessment are needed to thoroughly understand the adaptive strategies over a wider geographical area.

CRediT authorship contribution statement

Vikash Munbodhe: Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sundy Ramah:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Deepeeka Kaullysing:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Shakeel Yavan Joge:** Writing – review & editing, Software, Resources, Methodology, Investigation, Formal analysis. **Mariette Dine:** Writing – review & editing, Resources, Investigation. **Bryan Wilson:** Writing – review & editing, Resources, Investigation, Formal analysis. **Ranjeet Bhagooli:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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