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coral reef paper

Morphological and genetic characterization of *Stylophora madagascarensis*, *Pocillopora acuta*, and *Pocillopora verrucosa* in Mauritius and their thermal photophysiological stress responses

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ABSTRACT.—Increasing frequency and intensity of marine heatwaves worldwide warrant characterizing and understanding variation in thermal response among reef corals through in situ and ex situ experimentation to ultimately help with coral conservation and management strategies. This study first characterized species of Pocilloporidae, including two morphs of *Stylophora* and *Pocillopora* spp., from the Mauritian waters using morphology and genetics. The photophysiological responses and bleaching sensitivity were then examined when exposed to experimental and natural thermal stress. *Pocillopora acuta* and *Pocillopora verrucosa* were identified from Grand Gaube (GG) and harbored a species of *Cladocopium* (clade C) as their symbiont. The two morphs of *Stylophora madagascarensis* from Amber Island (AI) and GG were genetically similar and harbored a unique species of *Durusdinium* (clade D). These pocilloporid taxa exhibited differential bleaching responses during warm water events that occurred in March 2016 and again in 2019. The latter year was characterized by narrower daily

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variations in sea surface temperature allowing for minimal acclimatization, and possibly explains why bleaching was more severe. Coral nubbins subjected to 28, 30 and 32 °C, and 170 and 10 μ mol quanta m^{-2} s^{-1} light levels for a period of 55 hrs revealed variable thermal photophysiological responses. These findings indicate that the regionally endemic morphotypes of *S. madagascarensis* are thermally robust and *P. acuta* tended to be more heat tolerant than *P. verrucosa*. These results indicate how increasing episodes of thermal stress are likely to affect coral populations in the region and have implications for coral conservation.

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Reef corals are under increasing threat worldwide from the effects of regional marine heatwaves. When exposed to abnormal warm temperatures, microalgal endosymbionts are expelled from the coral hosts and/or their photosynthetic pigments are significantly reduced (Hoegh-Guldberg and Smith 1989, Kleppel et al. 1989, Suzuki et al. 2015), turning the coral colonies pale or white, and leading to mass mortality when severe. In many tropical regions, sea surface temperatures are likely to increase by 1–2 °C in the coming decades leading to increased coral bleaching, exacerbated by other factors, for example, pollution (Hoegh-Guldberg 1999, McClanahan et al. 2007, Pandolfi et al. 2011, Barkley et al. 2018, Lough et al. 2018).

There are large differences in sensitivity to thermal stress among coral species around the world (Marshall and Baird 2000, Loya et al. 2001, Bhagooli and Hidaka 2002, Bhagooli and Yakovleva 2004, Sampayo et al. 2008, Baird et al. 2009, Bhagooli 2009), including the Western Indian Ocean (WIO) region (McClanahan et al. 2004, Bhagooli and Taleb-Hossenkhan 2012, Mattan-Moorgawa et al. 2018, 2020, Bhagooli and Kaullysing 2019, Bhagooli et al. 2021a,b, McClanahan and Muthiga 2021, Jeetun et al. 2023, Munbodhe et al. 2023). This variation in physiological responses to thermal stress is mainly attributed to both the identity of the hosts and their respective microalgal endosymbiont. Indeed, the combined attributes to the host and symbiont species, even among individual genotypes within species (Parkinson and Baums 2014), affect a coral's tolerance to environmental instability and physical stressors (Chauka and Macdonald 2019).

The microalgal endosymbionts of corals belong to a large and diverse group of dinoflagellates in the family Symbiodiniaceae (LaJeunesse et al. 2018). This family currently comprises 11 genera, among which *Cladocopium* and *Durusdinium* are common among Indo-Pacific Scleractinia (LaJeunnesse et al. 2010, 2014, Stat et al. 2015). Members of the genus *Durusdinium* are generally more thermally tolerant than members of *Cladocopium* (Berkelmans and Van Oppen 2006, LaJeunesse et al. 2014, Hoadley et al. 2019, Turnham et al. 2023), with some exceptions (Abrego et al. 2008, Hoadley et al. 2019). Microalgal endosymbionts adapted to different environments exhibit large differences in photosynthetic responses to thermal stress.

Photosynthetic dysfunction appears to be the leading reason for initiating symbiont cell loss and coral bleaching (Warner et al. 2006, Warner and Suggett 2016). Moreover, the identity of the host species is also important in how these mutualisms respond to physiological stressors (Bhagooli and Hidaka 2003, Baird et al. 2009, Hoadley et al. 2019). Thus, accurate coral identification, especially in the case of cryptic species complexes, is essential for biodiversity conservation and management (Bickford et al. 2007).

The traditional reliance on skeletal morphology in taxonomy and systematics has led to significant confusion surrounding their evolutionary relationships and species diversity (Fukami et al. 2004, Budd et al. 2010, 2012, Ramírez-Portilla et al. 2022). The convergent evolution as well as phenotypic plasticity and variability among skeletal characters within species complexes affect accurate species identification. With the use of genetic evidence, many morphologically cryptic species are being resolved (Pinzón and Lajeunesse 2011, Rippe et al. 2021). These coral species occupy a variety of environments and respond differentially to climate fluctuation as a result of different adaptations (Struck et al. 2018). The misidentification, or nonrecognition, of morphologically cryptic species can hinder understanding of how coral communities are responding to climate change and efforts to protect and conserve coral biodiversity (Fišer et al. 2018). Therefore, it is crucial to assess coral diversity using detailed morphological analyses and genetics. Once delimited, it is important to assess how they differ in physiology so as to predict the future of their populations and to determine how to best protect them (Bálint et al. 2011).

Pocilloporid corals are widespread throughout the Indo-Pacific and are often abundant in many reef habitats. Recent work has begun to improve our understanding of the diversity and ecology of *Stylophora*. Genetic approaches have helped resolve species boundaries among members of the genus *Pocillopora* and *Stylophora* (Flot et al. 2010, 2011, Keshavmurthy et al. 2013, Torda et al. 2013, Johnston et al. 2017), unlike previous morphological classifications that were problematic due to the high phenotypic plasticity observed between and within colonies. These advancements in species recognition have improved our understanding of their physiology, ecology, and evolution (Pinzón and Lajeunesse 2011, Johnston et al. 2017, Turnham et al. 2021).

While pocilloporid corals remain understudied in the Western Indian Ocean, relative to other regions of the Indo-Pacific, efforts are underway to correct these gaps in knowledge. The genus *Stylophora* exhibits its highest morphological 'species' richness in the Indian Ocean, which appears to be the region of origin for this genus (Flot et al. 2011). Indeed, the diversity of this genus may be even greater and widespread than previously thought. Bhagooli et al. (2017) observed *Stylophora pistillata*-like morphs around Mauritius, but whether these constituted different species was not answered. *Stylophora madagascarensis* was initially thought to be restricted to Madagascar, however, its geographic distribution was expanded to the Gulf of Aden (Veron 2000, Stefani et al. 2011, Keshavmurthy et al. 2013). Similarly, there has been limited research on corals in the genus *Pocillopora* from the Indian Ocean (Pinzón et al. 2013, Johnston et al. 2017). New research in the region has also begun to improve our appreciation of their diversity and ecology. The South African Maputaland Reef Complex (MRC) contains unique populations of *Pocillopora* that were previously misidentified: *Pocillopora meandrina*/*Pocillopora eydouxi* were often incorrectly identified as *Pocillopora verrucosa*, which was sometimes properly recognized but equally frequently mistaken for *Pocillopora damicornis* sensu lato,

and *Pocillopora villosa* was in most cases misidentified as *Pocillopora grandis* (= *P. eydouxi*; Chiazzari et al. 2019).

While taxonomic and therefore ecological research remains limited for Indian Ocean corals, even less is known about their responses to ocean warming. McClanahan et al. (2004) reported that *Stylophora* and *Pocillopora* were consistently susceptible to bleaching along the coast of Kenya. The ability of these corals to cope with environmental stressors requires further study including characterization of their symbiont diversity (LaJeunesse et al. 2010). Therefore, the aim of this study was to genetically characterize pocilloporid corals and their microalgal endosymbionts from Mauritius and investigate variation in thermal stress tolerances among them. These findings should help with coral conservation and management efforts to deal with the warming oceans impacting Mauritius.

Materials and Methods

Study Site and Environmental Condition.—The study sites Amber Island (AI; 20°01′32.0″S, 57°41′53.8″E) and Grand Gaube (GG; 20°00′40″S, 57°41′16″E) were located in the north of Mauritius in the Western Indian Ocean (Fig. 1). These sites were selected as *Stylophora pistillata*-like morphotypes were previously spotted and identified by Bhagooli et al. (2017) at this location. *Stylophora* morph 1 (M1) was from AI and *Stylophora* morph 2 (M2) was from GG. *Pocillopora* spp., with rounded and sharp tips, samples were also collected from GG. The seawater depths at these sites varied between 0.5 to 2.0 m (Table 1). HOBO Pendant® Temperature/Light sensors were placed at both sites to continuously record the seawater temperature at 15 min intervals from December to March of the years 2015 to 2016 and 2018 to 2019.

Bleaching Survey.—Bleaching observations of *Stylophora* M1 and M2, *Pocillopora* (rounded tips) and *Pocillopora* (sharp tips) were carried out at a depth of 0.5 to 2 m during summer bleaching events from December to March of 2015 to 2016 and 2018 to 2019 at AI and GG. Coral colonies were visually assessed for bleaching using the Coral Health Chart of Coral Watch by observing their color as an indicator of their health along triplicate 100 m^2 belt transects out of the first 30 colonies encountered for each species.

Sample Collection.—The Ministry of Blue Economy, Marine Resources, Fisheries and Shipping, the Rodrigues Regional Assembly, the Outer Islands Development Cooperation; and the Department for Continental Shelf, Maritime Zone Administration & Exploration at the Prime Minister's Office granted the required authorization for coral collection. Underwater photographs of the colony form and close-ups of the target coral specimens were taken in situ. Three fragments of 2 cm each from three different parent colonies of *Stylophora* M1 from AI as well as three colonies of each of *Stylophora* M2, *Pocillopora* (with rounded and sharp tips) were collected from GG by snorkeling in March 2022. The samples were transferred into a bucket of seawater for transportation to the laboratory and experimental trials. For molecular analyses, additional fragments from more colonies from each studied species/morph were collected and then stored at –20 °C until DNA extraction.

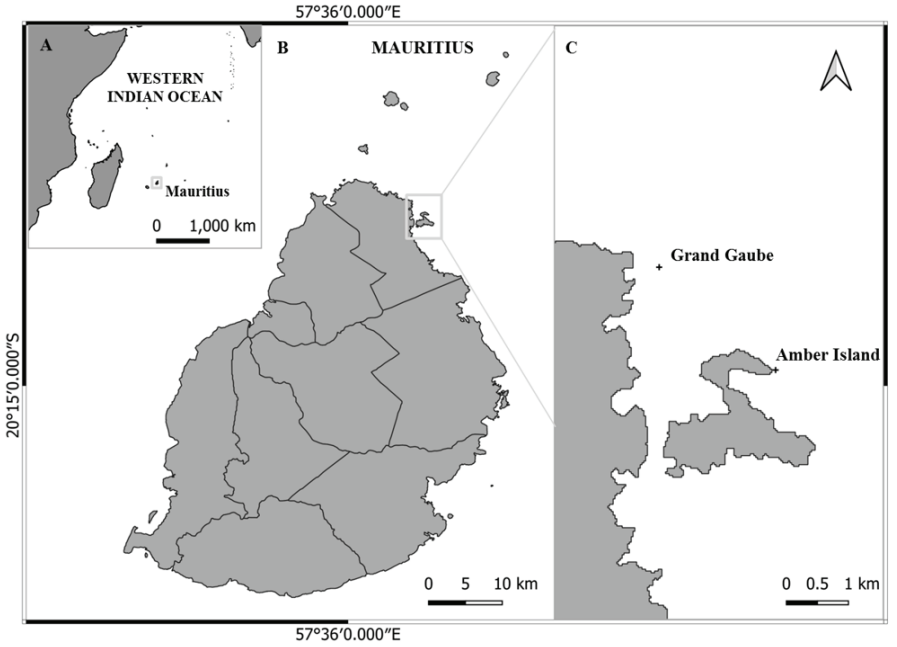

Figure 1. Location of Mauritius in the (A) Western Indian Ocean region, (B) study sites in the north of Mauritius, and (C) survey and sampling sites: Amber Island and Grand Gaube.

Morphological Analysis.—Scanning electron microscope (SEM) analyses were conducted using the modified protocol of Stefani et al. (2011) to reveal detailed fine-scale structures of the corallites. The soft tissues of the coral specimens were removed, and the skeletons were bleached in sodium hypochlorite, washed in fresh water and allowed to air dry. The samples for SEM were broken from the coral skeleton specimen, then carefully cut so as not to damage the delicate structures of the corallite. Then, they were mounted on stubs and sputter coated. SEM observations were performed using a TESCAN VEGA3 microscope. The corals were identified by their gross colony morphology, corallite arrangement and size and the presence or

Table 1. Location and depth of each *Stylophora* and *Pocillopora* sample included in the present study.

Morphospecies	Sample name	Collection date	Coordinates	Depth (m)
Stylophora madagascarensis (M1)	22Mru01	March 2022	20°01′32.0″S, 57°41′53.8″E	1.5
	22Mru02	March 2022	20°01′32.0″S, 57°41′53.8″E	1.5
	22Mru03	March 2022	20°01′32.0″S, 57°41′53.8″E	1.5
Stylophora madagascarensis (M2)	22Mru04	March 2022	20°00′40″S, 57°41′16″E	2
	22Mru05	March 2022	20°00′40″S, 57°41′16″E	2
	22Mru06	March 2022	20°00′40″S, 57°41′16″E	2
Pocillopora verrucosa	22Mru07	March 2022	20°00′40″S, 57°41′16″E	2
	22Mru08	March 2022	20°00′40″S, 57°41′16″E	2
	22Mru09	March 2022	20°00′40″S, 57°41′16″E	2
Pocillopora acuta	22Mru10	March 2022	20°00′40″S, 57°41′16″E	2
	22Mru11	March 2022	20°00′40″S, 57°41′16″E	2
	22Mru12	March 2022	20°00′40″S, 57°41′16″E	2

absence of septa with reference to the morphological descriptions and taxonomic classification given by Flot et al. (2011), Keshavmurthy et al. (2013), and Veron (2000).

Coral Host Identification.—To characterize *Stylophora* and *Pocillopora* species, the amplification of the coral host DNA was performed by PCR and sequencing of two DNA markers published previously. The first marker, a portion of the mitochondrial Open Reading Frame (ORF) of unknown function, was amplified using primers FATP6.1: 5′-TTT GGG GAT TCG TTT AGC AG-3′ and RORF: 5′-GCC AAT ATG TTA AAC ACC ATG TCA-3′ (Flot et al. 2008) for identifying *Pocillopora* samples. The second marker was the Internal Transcribed Spacer 2 region (ITS2), located in the nuclear ribosomal DNA gene cluster using ITS2 primers ITSc2-5 5′-AGC CAG CTG CGA TAA GTA GTG-3′ and R28S1 5′-GCT GCA ATC CCA AAC AAC CC-3′ (Flot et al. 2008), and was used for identifying *Stylophora* samples.

Stylophora ITS sequences were compared to the reference sequences in Flot et al. (2011), whereas *Pocillopora* ORF sequences were compared to the reference sequences in Poquita-Du et al. (2017). Sequences were aligned using MAFFT's E-INS-i mode, and maximum-likelihood analyses were performed using IQTREE2 (Minh et al. 2020) with 10,000 ultrafast bootstrap replicates (Hoang et al. 2018); the resulting trees were displayed using FigTree v1.4.4.

Characterization of Coral Microalgal Endosymbionts.—The coral tissue and endosymbiotic dinoflagellates were isolated using a Waterpik® water flosser filled with "Endosymbiont Isolation Buffer" as previously described by Rowan and Powers (1991). DNA was extracted using the Wizard® Genomic DNA Purification Kit. The small subunit ribosomal RNA (ssRNA) gene from the DNA samples were amplified using zooxanthellae-specific PCR primers. The forward ss5Z (an equimolar mixture of the oligonucleotides 5′-GCA GTT ATA ATT TAT TTG ATG GTC ACT GCT AC -3′ and 5′-GCA GTT ATA GTT TAT TTG ATG GTT GCT GCT AC- 3′) and reverse ss3Z (5′-AGC ACT GCG TCA CTC CGA ATA ATT CAC CGG-3′) zooxanthellae-specific primers were used (Rowan and Powers 1991). The sequences obtained were then subjected to a similarity search using NCBI's BLASTN to compare the query sequence to open-source DNA sequences already deposited in the GenBank database for species identification.

Experimental Setup.—Coral fragments (n = 3) each from the respective species/morphotypes, namely *Stylophora* M1, *Stylophora* M2, *Pocillopora* with rounded and sharp tips, were collected in March 2022 from AI and GG and were placed in 80 × 60 × 42.5 cm closed aerated tanks filled with natural seawater, 10% of which was replaced every day. Three colonies of about 10–30 cm in size from each species were selected and fragmented. All coral fragments were acclimated in a holding tank for 2 d at an ambient condition of about 28 °C using thermostats and 50 µmol quanta $m^{-2}\,s^{-1}$. Three nubbins (1–2 cm long) from each colony were placed in each of the three temperature treatments, 28 °C (control), 30 °C, and 32 °C in triplicates. The corals were exposed to two light conditions (12 hr light : 12 hr dark): moderate-light (ML: approx. 170 µ mol quanta $m^{-2}\,s^{-1}$) and low-light (LL: approx. 10 µ mol quanta $m^{-2}s^{-1}$). Temperature was ramped up in the morning till noon to 28, 30 and 32 °C and brought back to 28 °C during the afternoon in order to mimic field-like daily thermal variations during exposure to temperatures of 28, 30 and 32 °C for a period of 55 hrs.

Temperature and light intensity were recorded using HOBO Pendant® Temperature/Light sensors at 15-min intervals.

Each day, measurements were taken using the Imaging Pulse-Amplitude-Modulated (I-PAM) Fluorometer (M Series, Waltz, Germany; measuring light frequency 1–10 µmol quanta m^{-2} s^{-1}, actinic light intensity 2–20 µmol quanta m^{-2} s^{-1}, actinic width 0, gain 10, damping 2, saturation pulse intensity 7, saturation width pulse 4), following the ramping up of the temperatures, to assess the effective quantum yield (ϕPSII). The maximum electron transport rate ($rETR_{max}$) and nonharmful heat dissipation at PSII, nonphotochemical quenching parameter (NPQ) were determined from the rapid light curves (RLCs) generated by the I-PAM. These parameters have been documented to be the most common employed chlorophyll fluorescence parameters in symbiotic marine invertebrates' stress response studies (Bhagooli et al. 2021c). The double exponential function (Platt et al. 1980) was used for curve fitting to the RLCs of relative ETR versus irradiance rapid light curves using SigmaPlot® (v12.0).

The relative electron transport rate ($rETR_{max}$) was determined as follows:

$$rETR_{max} = \phi PSII \times PAR \times 0.5$$

where ϕPSII is the effective quantum yield of PSII, PAR is the photosynthetic active radiation (µ mol photon $m^{-2}s^{-1}$) and the energy distribution between PSI and PSII is taken into consideration by the factor 0.5.

Statistical Analyses.—The Shapiro–Wilk test was performed to check the data for normality. The percentage bleached coral colonies and ϕPSII, $rETR_{max}$ and nonphotochemical quenching (NPQ_{max}; relative to their respective initial) of in hospite zooxanthellae were arcsine (square-root) transformed to ensure normality of data prior to conducting statistical analyses. An independent *t*-test was performed to compare the percentage bleaching between different sites AI and GG and different bleaching years 2016 and 2019, respectively.

A multifactor ANOVA was performed to test the interaction effects of temperature, light treatment and days of exposure on the ϕPSII, $rETR_{max}$ and NPQ_{max} (relative to their respective initial) in hospite zooxanthellae of the test coral species. A *P*-value less than 0.05 was considered statistically significant. The Tukey post hoc test was performed after statistical significance to compare means between species (IBM SPSS 21).

Results

In Situ Temperature Data.—The temperature ranged from 26.39 to 32.29 °C at AI and 26.88 to 31.88 °C at GG from December 2015 to March 2016 (Fig. 2A). The temperature varied from 26.78 to 32.50 °C at AI and 26.68 to 31.57 °C at GG from December 2018 to March 2019 (Fig. 2B).

Field Bleaching Survey.—There was a significant difference in the percentage of bleached corals between the 2016 and 2019 bleaching events with higher bleaching observed in 2019. Differential bleaching patterns were observed among the different test coral species at AI and GG (one-way ANOVA: $P < 0.01$). *Pocillopora* with rounded

tips was the most susceptible during both bleaching phenomena with percentage bleached colonies of 14.4% (SD 1.92%) in 2016 and 50.0% (SD 6.67%) in 2019 (Fig. 3). A higher percentage bleaching was observed in *Pocillopora* with rounded tips colonies compared to *Pocillopora* with sharp tips by 0.018 (SD 0.078%; Tukey post hoc test: $P < 0.05$). The percentage bleaching observed in *Stylophora* M2 was higher compared to *Stylophora* M1 during both bleaching years, by 0.077% (SD 0.078%).

Morphological Analysis.—*Stylophora* M1 had a compact colony of about 10–15 cm in size with short branches (Fig. 4A and B) having crowded spherical corallites which form hoods at the branch tips (Fig. 4C). Six primary septa were present fusing with a styliform columella at the center (Fig. 4D). *Stylophora* M2 had a caespitose colony form of size ranging from 15 up to 30 cm with broadly spaced branches which do not taper at the ends (Fig. 4E and F). The rounded corallites were arranged in rows with slight development of hoods (Fig. 4G) and septa connecting in the middle with the absence of a columella (Fig. 4H). *Pocillopora* colonies were morphologically clustered in two groups. The first had bushy and compact colony of

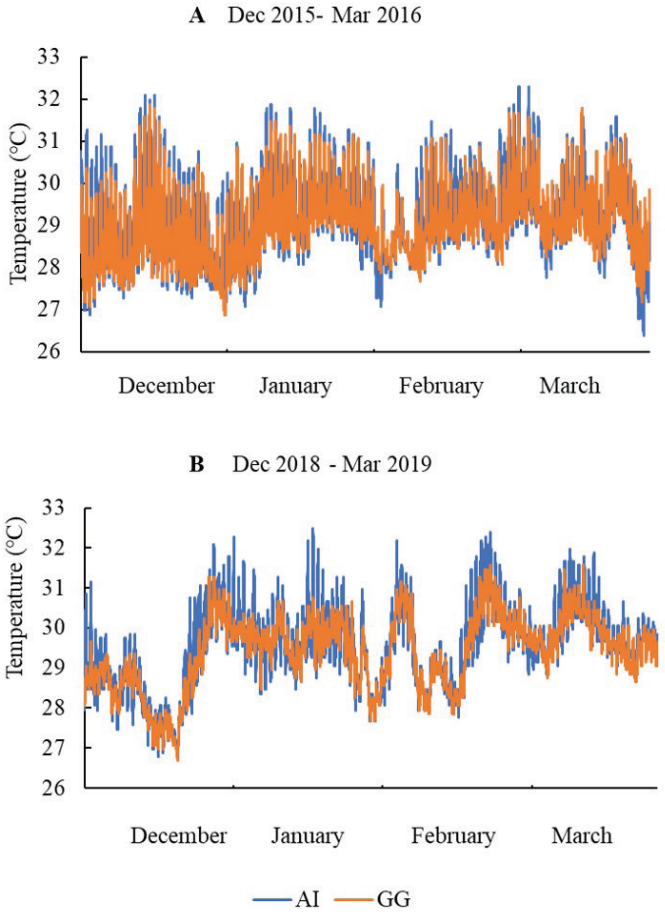

Figure 2. Temperature (°C) logs at AI and GG from December to March of (A) 2015 to 2016 and (B) 2018 to 2019.

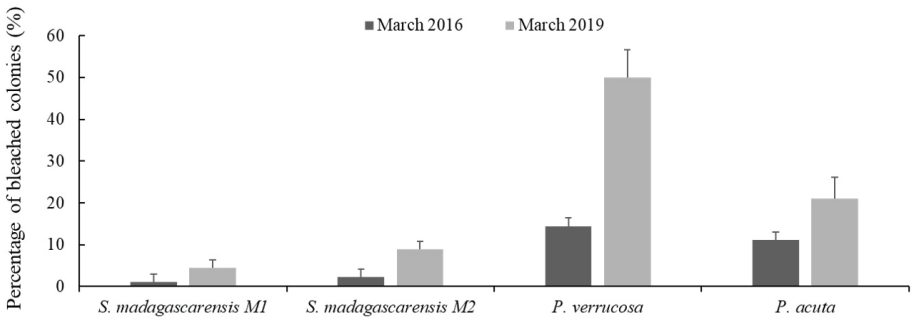

Figure 3. Percentage bleached colonies of *Stylophora* morphotype 1 (M1) and morphotype 2 (M2), *Pocillopora verrucosa,* and *Pocillopora acuta* (out of 30 colonies for within a 100 m^2 area) at Amber Island and Grande Gaube during 2016 and 2019 bleaching events. Data represent mean (SD; $n = 3$).

size 10–15 cm and had clustered branches with rounded tips (Fig. 4I, M). There was no clear distinction between the branches and the verrucae as they were merging into each other (Fig. 4J, N). The corallites were round to oval in shape with an absent to spinulate columella as described by Schmidt-Roach et al. (2014; Fig. 4K, O). The septa were poorly developed and septal teeth surrounded the inner walls of the corallite (Fig. 4L, P). These colonies were thus referred to *P. verrucosa*. In contrast, the second group included colony size of 10–15 cm but having fine branches sharply pointed at the tips (Fig. 4Q and R) with oval corallites and flat immersed columella ornamented with short spinules as described by Schmidt-Roach et al. (2014; Fig. 4 S and T) and thus referred to as *P. acuta*.

Coral Host Identification.—The six *Stylophora* individuals sampled were all successfully sequenced for the ITS2 marker while the six *Pocillopora* individuals were all successfully sequenced for the ORF marker. There were two ITS2 sequence types among the six individuals (3 M1 and 3 M2) sequenced: the three M1 (22Mru01, 22Mru02 and 22Mru03) shared one sequence, two of the M2 (22Mru04 and 22Mru05) shared the other sequence, whereas the third M2 (22Mru06) was heterozygous with both sequences (emphasizing that M1 and M2 are conspecific). Both M1 and M2 *Stylophora* samples grouped together with *Stylophora* sp. A from Flot et al. (2011), i.e., S. *madagascarensis* (Fig. 5A). The ORF sequences of all *Pocillopora* individuals were compared with reference sequences from Poquita-Du et al. (2017) to confirm the morphological identifications (Fig. 5B). The ORF sequences of all *Pocillopora* individuals with sharp tips (22Mru10, 22Mru11, and 22Mru12) were identical among themselves and matched *P. acuta*, whereas the ORF sequences of the *Pocillopora* individuals with rounded tips (22Mru07, 22Mru08, and 22Mru09) were identical among themselves as well and matched *P. verrucosa* .

Symbiont Characterization.—The sequences obtained were subjected to a similarity search using NCBI's BLASTN with default parameters (accessed in October 2023) to compare the query sequence to DNA sequences already deposited in the GenBank database for species identification. Specifically, nucleotide collection

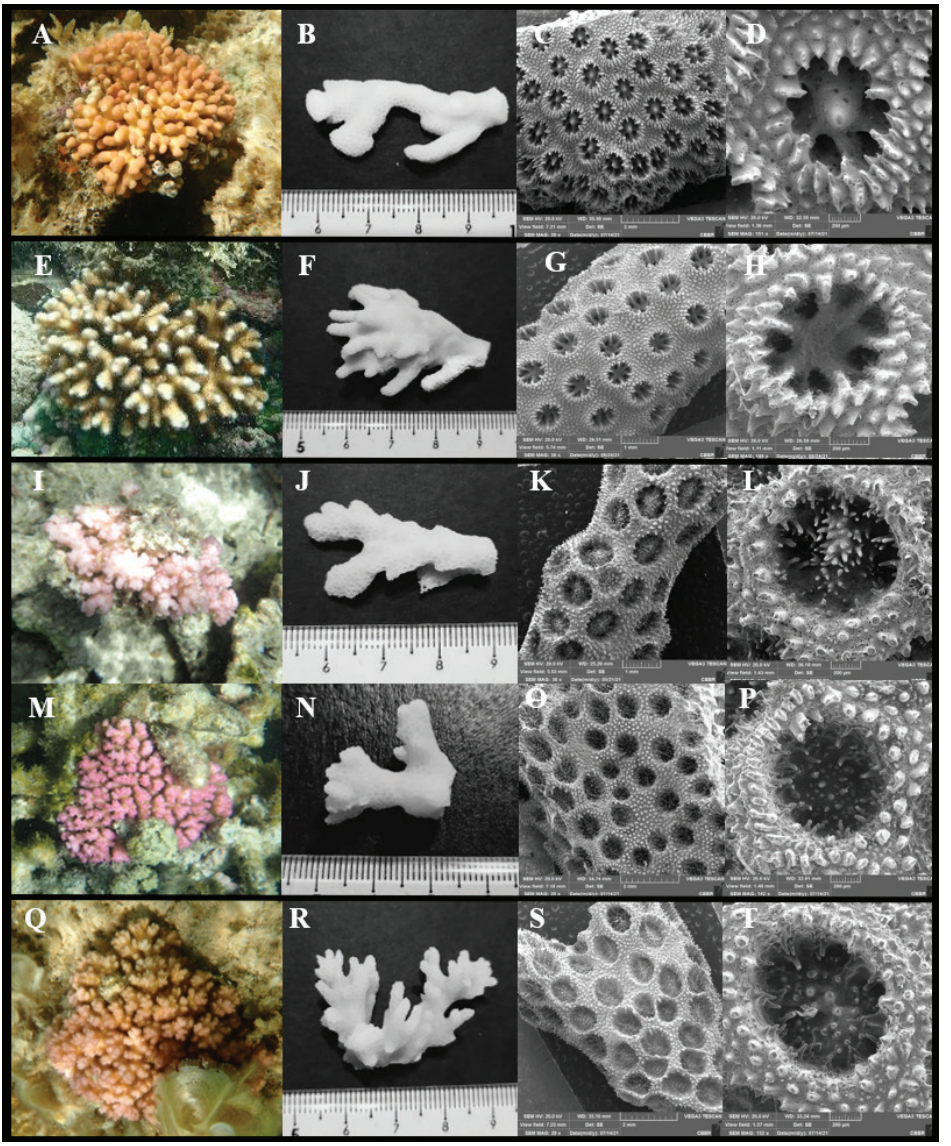

Figure 4. In situ colony form of *Stylophora* M1 (A), *Stylophora* M2 (E), *Pocillopora verrucosa* (I, M), *Pocillopora acuta* (Q), and their respective branch fragment (B, F, J, N, R); scanning electron micrograph (SEM) showing coenosteal spinules and corallite arrangement (C, G, K, O, S); and scanning electron micrograph (SEM) of a corallite close-up (D, H, L, P, T).

"(nr/nt)", the BLAST algorithm chosen was "Somewhat similar sequences (blastn)", with a maximum target sequences of 500, a Match score of 2, a Mismatch score of -3, a Gap initiation score of 5 and a gap extension score of 2. The symbiont type in *S. madagascarensis* was revealed to be *Durusdinium* sp. in M1 and M2, whereas *P. verrucosa* and *P. acuta* were found to be associated with *Cladocopium* sp. (Table 2).

Thermal Photophysiological Responses.—The temperature range was between 24.2 and 32.9 °C (Fig. 6A). Light intensity varied from 75.3 Lux (1.34 µmol

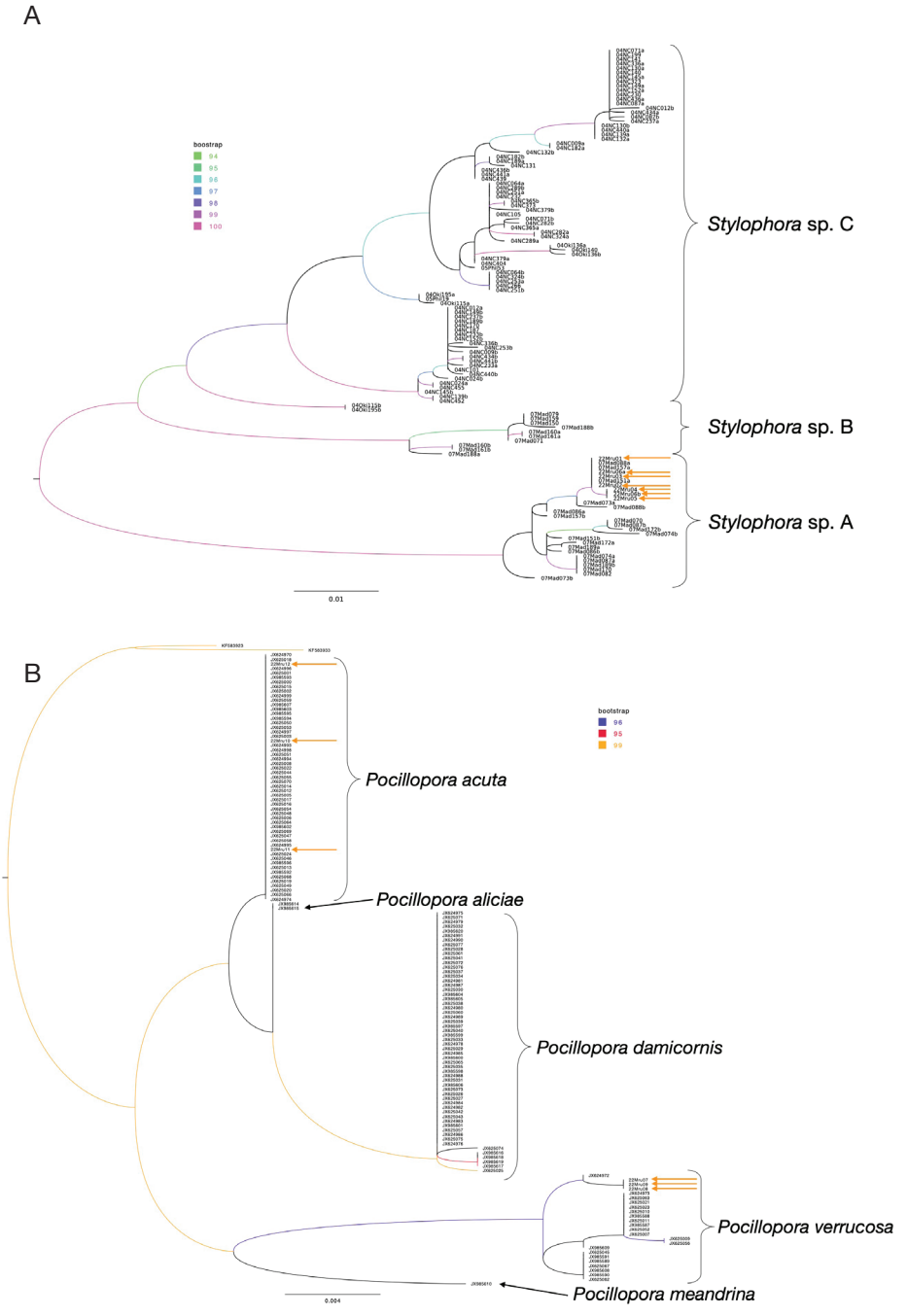

Figure 5. Phylogenetic tree of (A) *Stylophora* species based on the Internal Transcribed Spacer 2 region (ITS2) and (B) *Pocillopora* species based on the mitochondrial Open Reading Frame (ORF) region. Sequences of coral colonies from Mauritius are indicated by orange arrows. The colored branches in the tree indicate nodes with bootstrap support values higher than 94% (FigTree v1.4.4).

Table 2. Symbiont types associated with coral species sampled from Amber Island and Grand Gaube.

Site	Coral species	Symbiont type	Closest match with existing GenBank sequences (%identity)
Amber Island	*Stylophora madagascarensis* (M1)	*Durusdinium* sp.	97%
Grand Gaube	*Stylophora madagascarensis* (M2)	*Durusdinium* sp.	97%
	Pocillopora verrucosa	*Cladocopium* sp.	98.2%
	Pocillopora acuta	*Cladocopium* sp.	100%

s^{-1} m^{-2}) to 753.5 Lux (13.43 µmol s^{-1} m^{-2}) in low light (LL) conditions and 2238.9 Lux (39.9 µmol s^{-1} m^{-2}) to 9644.5 Lux (171.9 µmol s^{-1} m^{-2}) in moderate light (ML) conditions (Fig. 6B).

Temperature treatments had significant effects on ϕPSII, $rETR_{max}$ and NPQ_{max} (relative to their initial) of the in hospite zooxanthellae in different species ($P < 0.05$; Table 3). The Tukey post hoc pairwise comparison revealed a significant difference in the relative effective quantum yield between *P. verrucosa* and *P. acuta* (multifactor ANOVA: $P < 0.05$) while no difference was observed between *S. madagascarensis* M1 and M2 ($P > 0.05$). Contrarily, light conditions and a combination of both temperature and light treatments did not have a significant effect on the photophysiological parameters measured in the coral microalgal endosymbionts ($P > 0.05$).

In LL conditions, the relative ϕPSII in *S. madagascarensis* M1 and M2 increased slightly from Day 1 (D1) to Day 2 (D2) and remained almost unchanged until Day 3 (D3). However, in ML, a decrease in relative ϕPSII was observed from D1 to D3, with the largest decrease noted at 32 °C, in *S. madagascarensis* M1 by 2-fold and M2 by 1.8-fold (Fig. 7A, B). In ML conditions, relative ϕPSII of *P. acuta* remained almost constant at 28 and 30 °C after 3 d exposure (Fig. 7E). However, in the same light condition, *P. verrucosa* showed a sharp decrease in relative ϕPSII from D2 to D3 at 28 °C from 0.90 (SD 0.05) to 0.69 (SD 0.37) and at 32 °C from 0.91 (SD 0.09) to 0.62 (SD 0.37; Fig. 7D).

The relative $rETR_{max}$ in *S. madagascarensis* M2 showed an increase from D1 to D3 at 28 °C in both LL (2-fold) and ML (1.4-fold). However, at 30 and 32 °C, an increase was observed in relative $rETR_{max}$ from D1 to D2 followed by a decrease to D3 (Fig. 7F). In ML, *P. verrucosa* showed a 3-fold increase in $rETR_{max}$ from D1 to D2 and decreased from D2 to D3 (Fig. 7I). Contrarily, other corals species did not show significant changes in their $rETR_{max}$ in both LL and ML (Fig. 7G, H, J).

The relative NPQ_{max} of the *in hospite* zooxanthellae in *S. madagascarensis* M1 and M2 remained constant at 28 and 30 °C in both LL and ML and at 32 °C in LL, a 2.5- and 3.7-fold increase was noted in *S. madagascarensis* M1 and M2 from D1 to D3, respectively (Fig. 7K, L).

Discussion

The present study extends the geographical distribution of *S. madagascarensis* from the Gulf of Aden (Stefani et al. 2011) to the waters of Mauritius. These investigations also for the first time identified *Pocillopora acuta* around Mauritius. Additionally, these taxa exhibited significantly different photophysiological responses to natural and experimental thermal stress.

Field Bleaching Observations.—The highest worldwide oceanic temperatures of 2015–2017 initiated severe, widespread, and prolonged mass coral bleaching and mortality (Eakin et al. 2019). Over 40% of the live coral cover around Mauritius

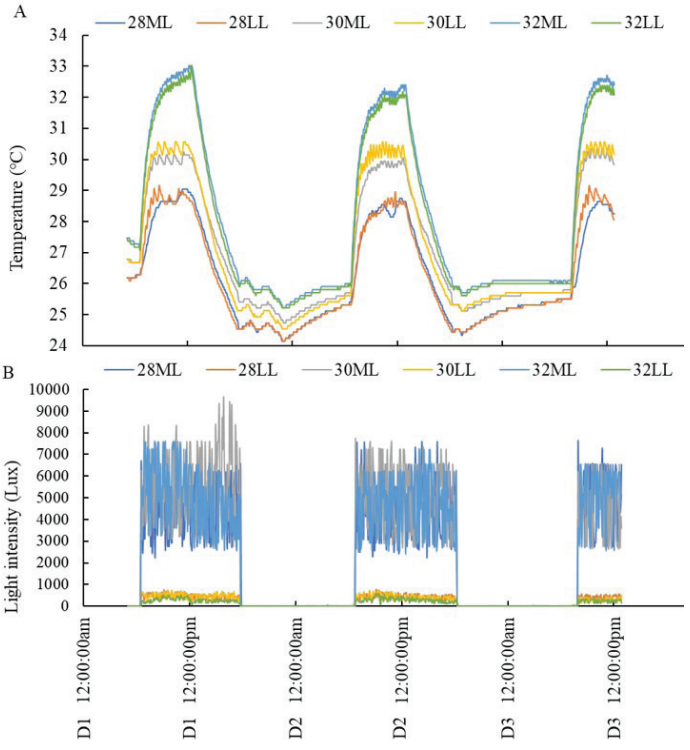

Figure 6. (A) Temperature (°C) and (B) light intensity (Lux) recorded from data loggers set in the experimental tanks exposed to different temperature and light conditions.

bleached (Gudka et al. 2020), but later recovered with a low coral mortality rate (Obura et al. 2017).

A higher percentage of *P. verrucosa* bleached compared to *P. acuta* (Fig. 3). Similarly, *P. acuta* showed little signs of bleaching on the Great Barrier Reef during the marine heatwave of 2016 (Epstein et al. 2019). Branch sizes may potentially influence differences in thermal tolerance among *Pocillopora*. In addition, individual colonies of the same species with different branch sizes and growth forms respond differently to thermal stress (Burgess et al. 2021). Bleaching can also have a greater impact on larger colonies compared to smaller colonies (Brandt 2009), which could be a plausible explanation for the difference observed in the higher percentage bleaching in *S. madagascarensis* M2 compared to *S. madagascarensis* M1 during both bleaching years. To thoroughly understand variations in bleaching in the two morphs of *S. madagascarensis* and *P. acuta*, further studies of the physiological and biochemical mechanisms underlying heat tolerance will be warranted.

Morphomolecular Characterization of Coral Host.—A combination of genetic evidence and skeleton morphology has proved to be a powerful technique for a thorough review and classification of coral species (Ramírez-Portilla et al. 2022). The fine-scale skeletal observations of *S. madagascarensis* were consistent with the study by Stefani et al. (2011), corresponding to the descriptions of small colony *S* morph. However, the branch thickness differed: M2 from GG had thinner branches while

Table 3. Multi-factor ANOVA on effects of temperature, light treatment, and days of exposure on the effective quantum yield (ϕPSII), relative electron transport (rETRmax), and nonphotochemical quenching (NPQmax; relative to their respective initial) in hospite zooxanthellae of the test coral species. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant.

Source of variation	DF	ϕPSII relative to their respective initial			rETRmax relative to their respective initial			NPQmax relative to their respective initial		
		MS	*F*	*P*	*MS*	*F*	*P*	*MS*	*F*	*P*
Species	3	0.023	25.904	0.000 ***	0.614	61.732	0.000 ***	0.536	8.010	0.000 ***
Temperature	2	0.005	5.613	0.004 **	0.189	19.028	0.000 ***	1.076	16.067	0.000 ***
Light	1	0.001	0.903	0.342 NS	0.008	0.816	0.367 NS	1.573	23.498	0.000 ***
Days	2	0.001	1.200	0.302 NS	0.152	15.291	0.000 ***	1.434	21.423	0.000 ***
Species × Temperature	6	0.002	2.005	0.063 NS	0.007	0.752	0.608 NS	0.338	5.052	0.000 ***
Species × Light	3	0.015	16.234	0.000 ***	0.020	2.059	0.105 NS	0.517	7.728	0.000 ***
Species × Days	6	0.004	4.920	0.000 ***	0.042	4.265	0.000 ***	0.149	2.231	0.039 *
Temperature × Light	2	0.000	0.550	0.577 NS	0.028	2.800	0.062 NS	0.014	0.213	0.808 NS
Temperature × Days	4	0.001	0.860	0.488 NS	0.018	1.774	0.133 NS	2.217	33.114	0.000 ***
Light × Days	2	0.043	47.705	0.000 ***	0.064	6.453	0.002 **	0.839	12.538	0.000 ***
Species × Temperature × Light	6	0.001	0.890	0.502 NS	0.012	1.255	0.276 NS	0.221	3.304	0.003 **
Species × Temperature × Days	12	0.002	2.049	0.019 *	0.025	2.523	0.003 **	0.110	1.646	0.075 NS
Species × Light × Days	6	0.006	6.896	0.000 ***	0.023	2.318	0.032 *	0.175	2.615	0.016 *
Temperature × Light × Days	4	0.004	4.421	0.002 **	0.014	1.432	0.222 NS	0.050	0.745	0.561 NS
Species × Temperature × Light × Days	12	0.003	3.545	0.000 ***	0.014	1.361	0.180 NS	0.077	1.145	0.320 NS

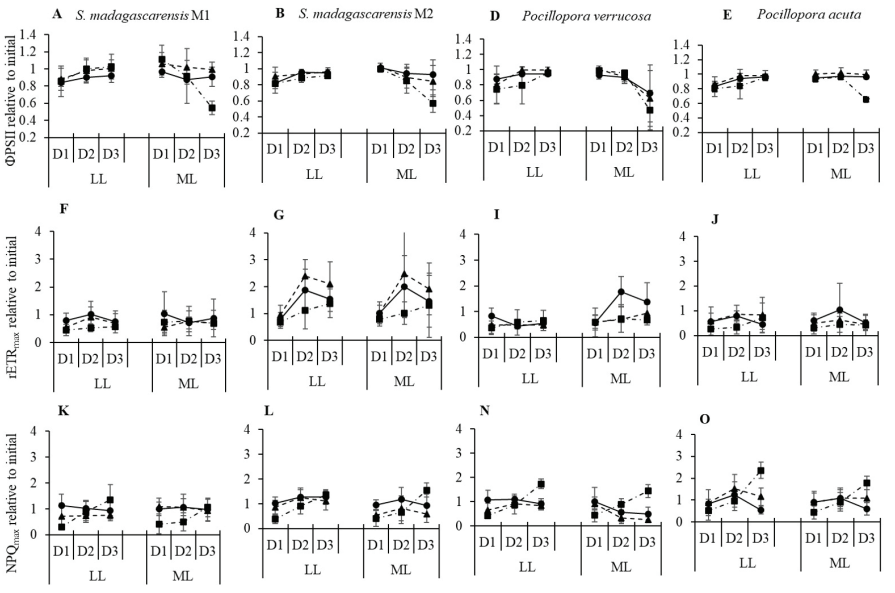

Figure 7. Effective quantum yield (ϕPSII), $rETR_{max}$ and NPQ_{max} (relative to initial) at PSII of in hospite zooxanthellae of the coral species (A, E, I) *Stylophora madagascarensis* M1, (B, F, J) *Stylophora madagascarensis* M2, (C, G, K) *Pocillopora verrucosa,* and (D, H, L) *Pocillopora acuta,* respectively, at midday during 3 d stress exposure at 28, 30, and 32 °C in moderate light (ML) and low light (LL) conditions.

M1 from AI had sturdy branches, possibly a result of the different environmental conditions such as turbidity, prevailing at the sites. The genus *Stylophora* is known to show wide plasticity (Shaish et al. 2006, 2007) due to the effects of environmental factors such as depth (Flot et al. 2011).

The morphomolecular approach, nevertheless, provided new insights in elucidating the *Stylophora* morphospecies present in Mauritius as previously documented elsewhere by Stefani et al. (2011) and Keshavmurthy et al. (2013). Molecular phylogenetic analyses of the ITS2 region of the *Stylophora* individuals, which were morphologically classified as Morphs 1 and 2 from Mauritius, revealed them to be *S. madagascarensis* with sequences identical to *S. madagascarensis* (*Stylophora* sp. A) collected from Madagascar (Flot et al. 2011). These findings represent the first detailed identification of *S. madagascarensis* around Mauritius and extend its geographic distribution to Mauritian waters.

Corals from the genus *Pocillopora* often exhibit varying morphological features among species, however, it is also hard to discern from intraspecific morphological plasticity (Lesser et al. 1994, Flot et al. 2010, Pinzón et al. 2013, Schmidt-Roach et al. 2013, Marti-Puig et al. 2014, Gélin et al. 2017). The genetic analyses in this study identified our samples as *P. verrucosa* and *P. acuta*, in agreement with the description provided by Schmidt-Roach et al. (2014) and initially defined as *P. damicornis* type γ and *P. damicornis* type β, respectively. *Pocillopora acuta* and *P. verrucosa* could be distinguished by the shape of the tip of their branches: pointed for *P. damicornis* type β (*P. acuta*) vs rounded for *P. damicornis* type γ (*P. verrucosa*). They both had similar microstructures, making it difficult to distinguish between the two species using morphology only. Similarly, Poquita-Du et al. (2017) reported that

the *P. damicronis*-like corals from Singapore waters were genetically identified as *P. damicornis* type β, that is, *P. acuta*.

Genetic Characterization of Coral Symbiont.—Symbiodiniaceae dinoflagellates are essential photosymbionts in corals and play a significant role in their ability to tolerate high temperatures and resist bleaching. Both *S. madagascarensis* M1 and M2 harbored *Durusdinium,* which is known to be thermo-tolerant and therefore makes the coral holobiont more resistant to rising sea surface temperature (Rowan 2004, Berkelmans and Van Oppen 2006, Díaz-Almeyda et al. 2017, Silverstein et al. 2017). *Durusdinium* sp. was present in *S. madagascarensis* M1, which has been reported to be more thermo-tolerant than other studied species (*Symbiodinium microadriaticum*, *Brevolium minutum*, and *Cladocopium goreaui*) under the combined effects of light and thermal stress (Lesser 2019). *Cladocopium* sp. was dominant in *Pocillopora* from this study, which shows a similar pattern with coral assemblages previously reported in Mauritius (McClanahan et al. 2005) and in the WIO region (LaJeunesse et al. 2010, Chauka and Macdonald 2019).

Thermal Photophysiological Stress Responses.—This is the first study documenting the thermal stress responses of *S. madagascarensis* morphotypes from Mauritius, indicating that *S. madagascarensis* M2 is slightly more tolerant to heat stress than M1. There are no photophysiological studies related to *S. madagascarensis* to date for comparison of the results. However, there are several studies documenting *S. pistillata*, from the same genus, as thermally susceptible (Loya et al. 2001). Another study from Okinawa, Japan reported the thermal sensitivity of the photophysiological parameters, $rETR_{max}$ and F_v/F_m of *S. pistillata* to a sudden increased temperature gradient (30–40 °C; Bhagooli 2009). However, NPQ responses differed according to the ITS2 symbiont types, with an increase in NPQ observed in *Cladocopium* type C59 and a decrease in *Cladocopium* type C1, implying that distinct ITS2 symbiont types harbored by the same species display different photophysiological responses to thermal stress. Moreover, distinct ITS2 microalgal endosymbionts in isolated states have been shown to exhibit variable ϕPSII responses to the thermal stress (Bhagooli 2010). Moreover, the relative ϕPSII of *P. acuta* remained almost constant at 28 °C and 30 °C, while, in the same light condition, that of *P. verrucosa* showed a sharp decrease. Similarly, minor changes in the F_v/F_m were noted in heat-stressed *P. acuta* colonies from Singapore indicating that PSII in the microalgal endosymbionts was not severely impaired (Poquita-Du et al. 2020). *P. acuta* corals from Thailand have been reported to be thermally robust in terms of their photosynthetic efficiency (Yucharoen et al. 2021, Sinutok et al. 2022).

Implications for Coral Conservation and Management.—*Stylophora madagascarensis* has been considered as regionally endemic but also reported from the Gulf of Aden (Stefani et al. 2011). This study provides evidence for *S. madagascarensis* to be officially included in the checklist of corals of the Republic of Mauritius. Since it is thermally robust but so far found only at two locations around Mauritius, propagation of this species around Mauritius could be envisaged for its protection and conservation. In case of *P. verrucosa* and *P. acuta*, given that *P. acuta* is more thermally tolerant, adaptive management strategies could include propagation of *P. acuta* to sites that have been affected by recent thermal anomaly

events. This may help increase the effectiveness of coral rehabilitation efforts and management around Mauritius. Furthermore, studies on the thermal bleaching tolerance of *S. madagascarensis* from Madagascar warrants attention for its possible enhanced local conservation and management. In a regional coral conservation and management context, studies on *P. acuta* and its thermal tolerance may be extended to the WIO region.

Conclusions

This study documents the occurrence of *S. madagascarensis* morphotypes in the Mauritian waters for the first time which was previously thought to be endemic to Madagascar and also reported in the Gulf of Aden. The results revealed for the first time the presence of *P. acuta* around Mauritius and distinguished it from similar-looking *P. verrucosa*, reiterating the importance of genetic analyses for accurate species characterization in addition to traditional morphological trait methods. *Stylophora madagascarensis* morphotype 1 (M1) and morphotype 2 (M2) harbored a species of *Durusdinium* (clade D) and were tolerant to heat stress in the test experiments. While both *P. verrucosa* and *P. acuta* both harbored a species of *Cladocopium* (clade C) as symbiont, *P. acuta* tended to be more tolerant to elevated temperature. These findings will be useful to guide accurate identification of pocilloporid corals during ecological surveys. Additionally, the differences in thermal stress tolerance we detected may inform adaptive coral reefs conservation and management efforts around Mauritius.

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