Photo-physiology of healthy and bleached corals from the Mascarene Plateau

Ranjeet Bhagooli[1,2,3,4*], Mouneshwar Soondur[1,2], Sundy Ramah[1,5], Arvind Gopeechund[1,2], Sruti Jeetun[1,2], Deepeeka Kaullysing[1,2]

[1] Department of Biosciences and Ocean Studies, Faculty of Science & Pole of Research Excellence in Sustainable Marine Biodiversity, University of Mauritius, Réduit 80837, Republic of Mauritius

[2] The Biodiversity and Environment Institute, Réduit, Republic of Mauritius

[3] Institute of Oceanography and Environment (INOS), University Malaysia Terengganu, 21030 Kuala Terengganu, Terengganu, Malaysia

[4] The Society of Biology (Mauritius), Réduit, Republic of Mauritius

[5] Albion Fisheries Research Centre, Ministry of Blue Economy, Marine Resources, Fisheries & Shipping, Albion, Petite Rivière 91001, Republic of Mauritius

* Corresponding author: r.bhagooli@uom.ac.mu

Abstract

This study presents the first report of variable photo-physiology of healthy-looking and bleached corals from the upper mesophotic waters of the Mascarene Plateau. In May 2018, during the FAO EAF-Nansen research expedition cruise, coral bleaching was visually observed. Five coral species from Saya de Malha Bank, namely *Heliopora coerulea, Favites* sp. and *Porites* sp. from 27 m and *Acropora* sp. and *Lithophyllon repanda* from 30 m, and three coral species from the Nazareth Bank, namely *Acropora* sp. and *Galaxea fascicularis* from 36 m and *Stylophora*-like species from 58 m were studied using the Video-Assisted Multi-Sampler (VAMS) and collected using a Van Veen grab. Chlorophyll *a* fluorescence parameters such as effective quantum yield at photosystem II (Φ_{PSII}), relative maximum electron transport rate ($rETR_m$), photosynthetic efficiency (α), photoinhibition (β), saturating light level (E_k) and maximum non-photochemical quenching (NPQ_m) were measured using a Diving-Pulse-Amplitude-Modulated (D-PAM) fluorometer to study variable photo-physiology in bleached and non-bleached corals. All photo-physiological parameters varied significantly among coral species tested and between coral conditions, except for β. The interaction between species and coral conditions was only significant in the case of β, but generally not significant. A two-way ANOVA indicated significant effects of depth and coral conditions in *Acropora* sp. on almost all photo-physiological parameters, except for β, and the effect of depth on $rETR_{max}$ and α, and the effect of depth along with its interaction with coral conditions on E_k. Φ_{PSII} did not differ in bleached and healthy-looking coral parts of *Porites* and *Lithophyllon* from 27 m, *Galaxea* and *Acropora* from 36 m while it decreased significantly in *Heliopora* and *Favites* at 27 m, *Acropora* from 30 m, and *Stylophora*-like at 58 m. NPQ_m did not change for *Porites*, *Acropora* (30 m) and *Galaxea* but it tended to increase for *Heliopora*, *Acropora* (36 m), *Lithophyllon*, *Galaxea*, and decrease for *Favities*, *Acropora* (30 m) and *Stylophora*-like. The thermally tolerant coral *Porites* exhibited normal photo-physiology even in bleached conditions while the bleached parts of *Favites*, *Acropora* (30 m) and *Stylophora*-like corals exhibited photo-physiological dysfunctioning. This study revealed that the seven studied corals from the upper mesophotic waters of the Mascarene Plateau are not spared from the bleaching phenomenon and exhibit variable photo-physiology in bleached and non-bleached conditions. Further studies are warranted to thoroughly understand the coral bleaching patterns and severity during summer periods at the Saya de Malha and Nazareth Banks.

Keywords: coral bleaching, Nazareth, PAM, photo-physiology, Saya de Malha, VAMS

http://dx.doi.org/10.4314/wiojms.si2021.2.8

Introduction

Coral bleaching has become more frequent and severe worldwide (Hoegh-Gulberg *et al.* 1999; Hughes *et al.* 2018) with variable impacts on reefs (Darling *et al.*, 2019). Coral bleaching events have not spared the Western Indian Ocean region (Obura *et al.* 2017) including the Islands of the Mascarene Plateau (Bhagooli and Taleb-Hossenkhan, 2012; Mattan-Moorgawa *et al.*, 2012, 2018; Bhagooli and Kaullysing, 2019; McClanahan and Muthiga, 2020). Under environmentally stressful conditions, mainly elevated sea temperature and high solar irradiance, corals bleach, whereby they lose either their symbiotic zooxanthellae (Hoegh-Guldberg and Smith, 1989; Brown, 1997; Le Tissier and Brown, 1996) or their photosynthetic pigments, or both (Kleppel *et al.* 1989), and appear white. If corals do not regain their symbiont-associated pigmentation in due course, they succumb. Sea surface temperature-based models indicate that some reefs would suffer from "local extinctions" (Sheppard, 2003; Bhagooli and Sheppard, 2012).

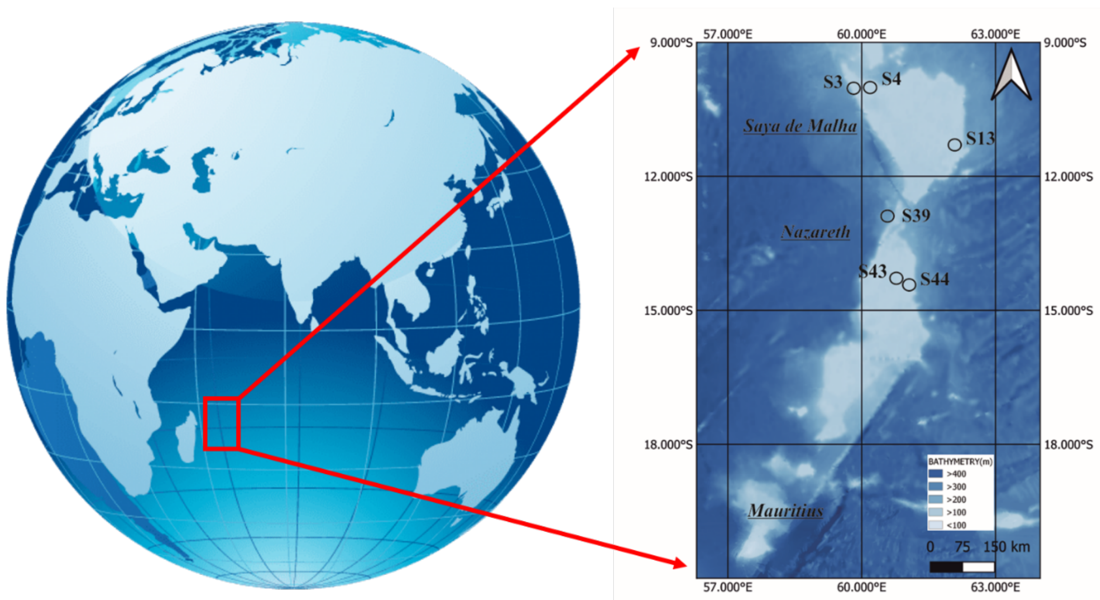

Figure 1. A. Mascarene Plateau on the global map. B. Map of Mascarene Plateau indicating the sampling locations for corals at Saya de Malha (S4 and S39) and Nazareth Banks (S44 and S47).

Several studies have suggested that damage to the zooxanthellar photosynthetic apparatus and/or its repair (Jones *et al.*, 1998; Warner *et al.* 1999; Takahashi *et al.*, 2004; Bhagooli, 2013) is implicated in the bleaching process. This has led to the increased use of chlorophyll *a* fluorescence techniques to study the normal and stress photo-physiology of the endosymbiont dinoflagellates, commonly called zooxanthellae, in corals (Bhagooli *et al.*, 2021). Several studies have indicated that different zooxanthellae species (LaJeunesse *et al.*, 2018) have variable photo-physiological thermal tolerance (Rowan, 2004; Sampayo *et al.*, 2008). However, other studies have shown that thermal bleaching may occur without thermally-induced dysfunctioning of the photosystem II as photosynthetically competent zooxanthellae are released under stress (Ralph *et al.*, 2001; Bhagooli and Hidaka, 2004). Observations of photosynthetic functioning of zooxanthellae indicated a decline in photochemical efficiency in some stressed corals (Rodrigues *et al.*, 2008) and variable changes for some corals in the field (Mattan-Moorgawa *et al.*, 2012, 2018). These stress photo-physiological studies have focused mostly on shallow-water corals while the thermal stress photo-physiology of deep water corals is not well documented.

Ample evidence documenting differential bleaching patterns among coral taxa (Marshall and Baird, 2000; Loya *et al.*, 2001; Bhagooli and Yakovleva, 2004; Mattan-Moorgawa *et al.*, 2012) and depths (Glynn, 1996; Lesser, 2009; Bongaerts *et al.*, 2010; Muir *et al.*, 2017) exist. However, with increasing frequency and severity of coral bleaching events recently, it appears that coral genera that were previously tolerant and/or resilient to bleaching in both shallow and deep waters may become vulnerable to increasing thermal anomaly severity

(McClanahan and Muthiga, 2020), and deep water mesophotic coral ecosystems from the Caribbean and Great Barrier Reef, for example, may not act as potential climate refugia (Smith *et al*., 2016; Frade *et al*., 2018). Though Frade *et al*. (2018) documented variable bleaching susceptibilities among deep water coral species, their stress photo-physiology is almost unchartered.

This study, therefore, aimed at a snap-shot investigation of the variable photo-physiological performance, using a Diving-Pulse Amplitude Modulated (D-PAM) fluorometer, in seven coral species collected from the upper mesophotic waters of the Saya de Malha and Nazareth Banks on the Mascarene Plateau, Western Indian Ocean, a region that has been very poorly studied. The objectives were to 1) qualitatively observe bleaching in corals, and 2) assess the photo-physiological performance of i) healthy-looking corals, and ii) their conspecific bleached corals from depths >25 m at the Saya de Malha and Nazareth Banks.

Methodology

Sample collection from studied locations

The studied locations were within the Saya de Malha Bank, an area jointly managed by the Republic of Mauritius and Seychelles, and the Nazareth Bank, which is within the Exclusive Economic Zone of the Republic of Mauritius. The samples of the symbiotic cnidaria were collected using the van Veen grabs on the VAMS at station S4 at Saya de Malha Bank on 8th May 2018 at a depth of 27 m, and at S39 at Nazareth Bank on 22nd May 2018 at a depth of 30 m. At the Nazareth Bank, stations included S44 at a depth of 36 m and S47 at a depth of 58 m and collection was carried out on 27th May 2018 (Fig. 1). Live coral samples were preliminarily identified on the research vessel and used for photo-physiological studies onboard. Chlorophyll fluorescence measurements were conducted between 09:00 and 14:00 hrs at the studied locations. Samples were frozen at -20 °C for further detailed identification at a later stage.

Coral morphological identification

Corals (cnidarian) were collected and preliminarily identified onboard. After close-up pictures were taken, samples were frozen at -20°C for later laboratory identification. Advanced identification of corals was done using skeletal morphological methods such as light and scanning electron microscopy (SEM). Corals were identified from external morphologies using Corals of the World (Veron, 2000) and relevant papers documenting scanning electron micrographs.

For SEM analyses, the coral samples were treated with 10 % sodium hypochlorite, washed with water, and air-dried prior to SEM. The coral fragments were cut into smaller pieces to fit on the SEM stub. The coral samples were mounted on the stub using carbon tape and sputter coated with a thin layer of gold/platinum. SEM observations were performed with a Vega Tescan microscope (Stefani *et al*., 2011).

Photo-physiology of corals – Chlorophyll *a* fluorescence measurement

The Diving-PAM fluorometer (Submersible Photosynthesis Yield Analyzer, Walz, Germany) was used to assess the photo-physiology of collected corals by measuring, in triplicates, the fluorescence of chlorophyll *a* on-board the ship immediately after collection. In a non-dark-adapted sample, the initial fluorescence (F) and the maximal fluorescence (F_m') were measured by applying pulses of weak red light (< 1 μmol quanta m^{-2} s^{-1}) and a saturating pulse (4000 μmol quanta m^{-2} s^{-1}, 0.8 s duration), respectively. The ratio of the change in fluorescence ($\Delta F = F_m' - F$) caused by the saturating pulse to the maximal fluorescence (F_m'), in a light adapted sample can be considered as a proxy for the effective maximum quantum yield of the photosystem II (PSII) (Genty *et al*., 1989). The chlorophyll fluorescence parameters included the effective quantum yield ($\Delta F/F_m'$, Φ_{PSII}), the relative electron transport rate (rETR) and non-photochemical quenching (NPQ) when exposed to a series of rapidly (10 s) changing light climates (Rapid Light Curves, RLCs) (Ralph *et al*. 1999; Bhagooli and Yakovleva, 2004). The irradiance levels were 0, 110, 150, 300, 400, 500, 800, 1000 and 1325 μmol quanta m^{-2} s^{-1}. Using the RLCs the rETR and NPQ were estimated at each irradiance.

At each irradiance, the respective relative electron transport rate (rETR) was calculated as the product of 0.5 x Φ_{PSII} x PAR, where PAR is the photosynthetically active radiance. Non-photochemical quenching (NPQ), determined by the ratio of F_m-F_m' to F_m', is the process by which oxygenic photoautotrophs harmlessly dissipate excess light absorbed as heat and fluorescence. When light energy absorption exceeds the capacity for utilization, there is a need to dissipate the energy to protect the light harvesting structures from photo-oxidative damage. The maximum rETR and NPQ were determined using sigma plots (Platt and Jassby, 1976). The initial slope of the light curve prior to the onset of saturation (α) and the slope of the light curve beyond the onset of photo-inhibition (β), representing the light-use efficiency and photo-inhibitory

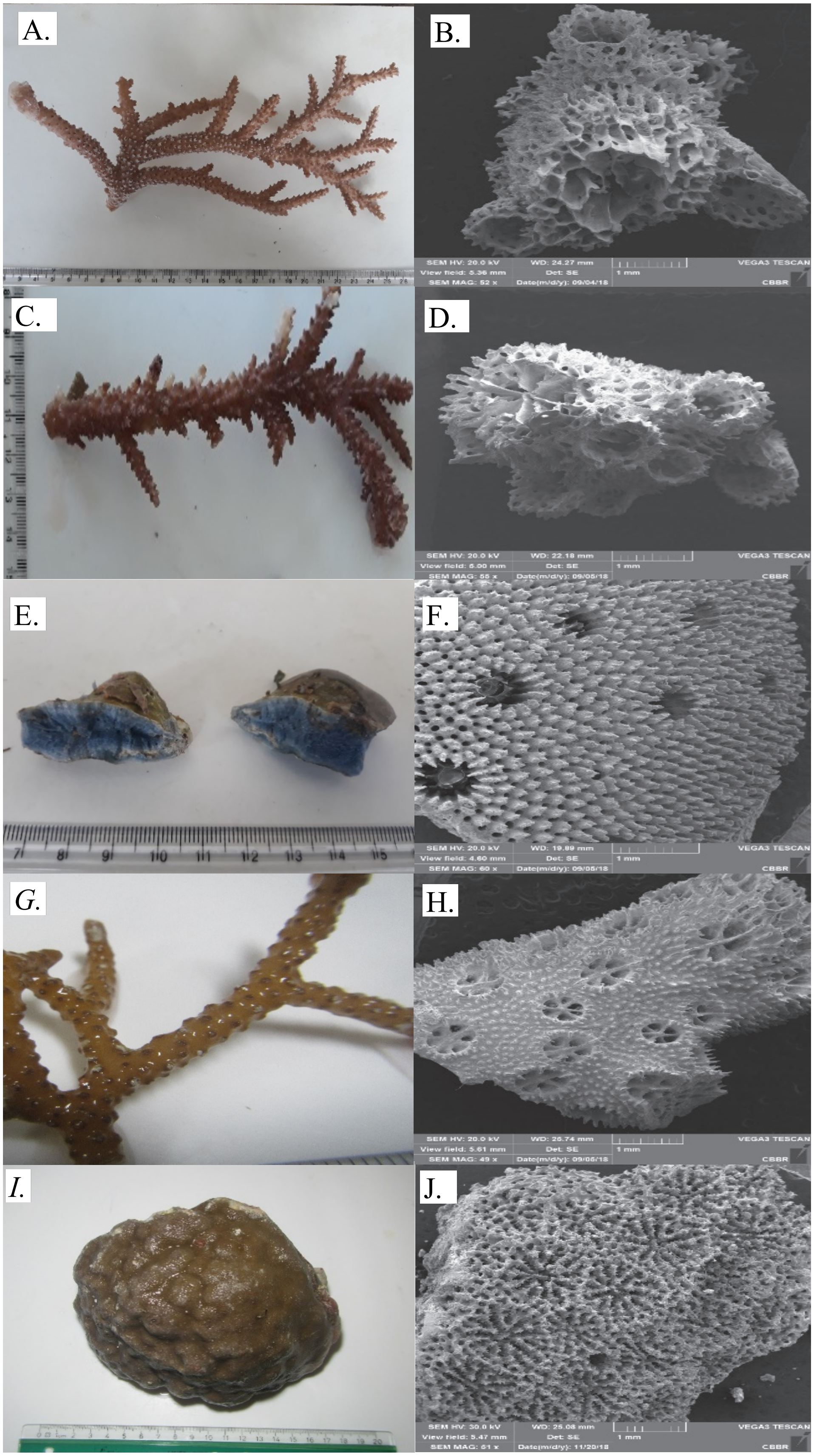

Figure 2. Fragments and scanning electron micrographs of the studied corals from Saya de Malha (SMB) and Nazareth (NB) Banks. A and B – *Acropora* sp. from SMB; C and D – *Acropora* sp. from NB; E and F – *Heliopora coerulea* from SMB; G and H – *Stylophora*-like sp. from NB; and I and J – *Porites* sp. from SMB.

factors, respectively, were determined through curve fitting of the RLC. The E_k was calculated as $rETR_{max}/\alpha$ and represents the minimum saturating irradiance. Chlorophyll fluorescence measurements were done in three replicates (n=3). Based on visual observations prior to chlorophyll fluorescence measurements, corals were grouped into three categories: healthy-looking; bleached (whitish); and pale (intermediate between the former two). Not all coral species studied could be categorised into all three conditions and thus some had data collection for only two categories.

Statistical analyses

Φ_{PSII}, $rETR_m$, NPQ_{max}, α, β, and E_k were statistically analysed using the software PASW Statistics 18. The data was expressed as mean±SD from three replicates (n=3). The raw data was Arcsine square root transformed prior to ANOVA tests. The two-way ANOVA was employed to test the effect of species and coral conditions in seven coral species. Since *Acropora* sp. were found at two depths (30 m and 36 m) the two-way ANOVA was run twice: 1) with *Acropora* sp. from 30 m; and 2) with *Acropora* sp. from 36 m. A separate two-way ANOVA was conducted to test for the effects of depths and coral condition in *Acropora* sp. The Tukey post hoc significance difference test was used for multiple comparison of means at $P<0.05$.

Results and discussion

Coral identification

At Saya de Malha Bank, the corals at S4 included *Heliopora coerulea*, *Favites* sp., and *Porites* sp. from a depth of 27 m, while at S39, *Acropora* sp. and *Lithophyllon repanda* were recorded from a depth of 30 m. At Nazareth Bank, the corals recorded at S44 from a depth of 36 m were *Acropora* sp. and *Galaxea fascicularis*, and at S47 *Stylophora-like* sp. From the colony and fragment morphologies, and scanning electron micrographs, the same *Acropora* sp. was observed at both Saya de Malha S39 (Fig. 2A, B) and Nazareth S44 (Fig. 2C, D). *H. coerulea* at S4 was confirmed through their colony and fragment morphologies, and scanning electron micrograph (Fig. 2E, F). At S47, the colony/fragment morphologies and the SEM analysis revealed a *Stylophora*-like sp. (Fig. 2G, H). At S4, the massive coral was confirmed to be a *Porites* sp. based on the colony morphology and scanning

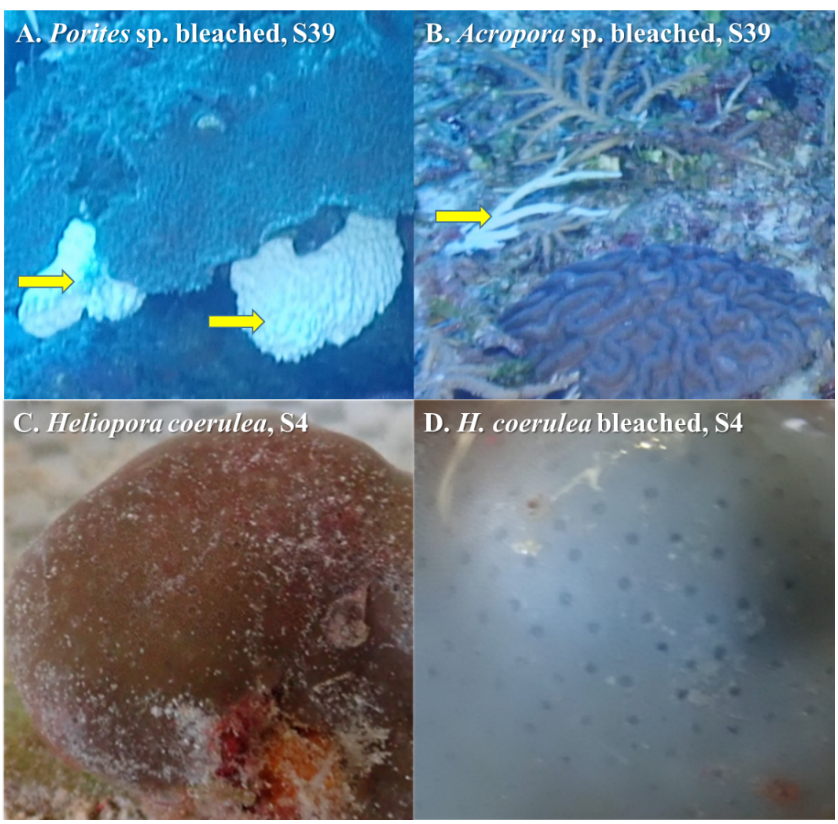

Figure 3. Healthy-looking and bleached conditions of corals. A. *Porites* sp. (EAF-Nansen, 2018), and B. *Acropora* sp. healthy and bleached colonies observed via the VAMS in the field at study location S39 at Saya de Malha (EAF-Nansen, 2018). The yellow arrows indicate the bleached corals in the field; C. Healthy and D. Bleached *Heliopora coerulea* post-collection observation following sampling from S4 at Saya de Malha.

micrograph (Fig. 2I, J). The morphology of the *Acropora*, *Stylophora*-like and *Porites* species looks quite different from their genera reported around Mauritius (Moothien-Pillay *et al.* 2002; Bhagooli *et al.* 2017) and Rodrigues (Fenner *et al.*, 2004), though these reports did not use SEM. The SEM analyses done in this study indicated clear fine micro-level details in these coral specimens, but they could not be identified clearly at the species level. Further molecular level identification work is required to be able to reveal the species level identity of these specimens.

Field- and post-collection observed bleaching conditions

The VAMS used in the study allowed for qualitative observations. Several coral colonies belonging to the genera *Porites* (Fig. 3A) and *Acropora* (Fig. 3B) could be observed *in situ* through the videos of the VAMS. Post-collection, the grabs attached and operated through the VAMS provided samples of *Heliopora* (Fig 3C, D), *Porites*, *Acropora*, *Galaxea fascicularis*, *Lithophyllon repanda, and Stylophora*-like species in healthy and bleached-conditions. Variable levels of bleaching

Table 1. Two-way ANOVA for the effect of species (*Heliopora coerulea, Favites* sp., *Porites* sp., *Acropora* sp., *Lithophyllon repanda*, *Galaxea fascicularis* and *Stylophora*-like species) and coral condition (healthy-looking and bleached) on photo-physiological features of test corals. Since *Acropora* sp. was found at 30 m and 36 m, the ANOVA test was run with *Acropora*-30m and *Acropora*-36m, separately. Asterisks (***) represent significant differences at $P<0.001$.

	Parameters	Source of Variation	SS	df	MS	F	P-value
With *Acropora* at 30 m	Φ_{PSII}	Species	0.702	6	0.117	17.675	0.000***
		Condition	0.234	1	0.234	35.394	0.000***
		Species x Condition	0.290	6	0.048	7.303	0.000***
	$rETR_m$	Species	0.070	6	0.012	35.601	0.000***
		Condition	0.062	1	0.062	190.857	0.000***
		Species x Condition	0.021	6	0.004	10.893	0.000***
	NPQ_{max}	Species	0.060	6	0.010	18.997	0.000***
		Condition	0.056	1	0.056	106.523	0.000***
		Species x Condition	0.033	6	0.005	10.254	0.000***
	α	Species	0.322	6	0.054	13.077	0.000***
		Condition	0.198	1	0.198	48.179	0.000***
		Species x Condition	0.252	6	0.042	10.221	0.000***
	β	Species	0.140	6	0.023	9.033	0.000***
		Condition	0.000	1	0.000	0.082	0.777
		Species x Condition	0.033	6	0.006	2.136	0.080
	E_k	Species	0.292	6	0.049	24.453	0.000***
		Condition	0.042	1	0.042	21.199	0.000***
		Species x Condition	0.112	6	0.019	9.368	0.000***
With *Acropora* at 36 m	Φ_{PSII}	Species	0.774	6	0.129	19.928	0.000***
		Condition	0.181	1	0.181	27.896	0.000***
		Species x Condition	0.320	6	0.053	8.230	0.000***
	$rETR_m$	Species	0.071	6	0.012	35.778	0.000***
		Condition	0.057	1	0.057	172.034	0.000***
		Species x Condition	0.020	6	0.003	10.188	0.000***
	NPQ_{max}	Species	0.103	6	0.017	32.238	0.000***
		Condition	0.044	1	0.044	82.959	0.000***
		Species x Condition	0.024	6	0.004	7.669	0.000***
	α	Species	0.370	6	0.062	13.728	0.000***
		Condition	0.186	1	0.186	41.487	0.000***
		Species x Condition	0.253	6	0.042	9.378	0.000***
	β	Species	0.173	6	0.029	10.257	0.000***
		Condition	0.001	1	0.001	0.185	0.670
		Species x Condition	0.034	6	0.006	2.029	0.095
	E_k	Species	0.294	6	0.049	24.929	0.000***
		Condition	0.035	1	0.035	18.012	0.000***
		Species x Condition	0.106	6	0.018	8.973	0.000***

were observed in these coral species but no quantitative assessments were undertaken. It is noteworthy that in other shallow-water locations of the Mascarene Plateau, both intra- and inter-species variable bleaching observations have been made; for example by Hilbertz and Goreau (2002) at the Ritchie Bank of the northern Saya de Malha, Bhagooli and Taleb-Hossenkhan (2012), Mattan-Moorgawa *et al*. (2012, 2018) and McClanahan and Muthiga (2020) around Mauritius Island, and Hardman *et al*. (2004, 2008) around Rodrigues Island. These studies in general indicated that *Porites* and *Galaxea* are more tolerant to bleaching than some *Acropora* species. The present study, for the first time, reports qualitative bleaching observations from the Mascarene Plateau at depths of 27 and 36 m. Further quantitative studies on bleaching vulnerability observations in the Saya de Malha and Nazareth Banks are necessary to understand the bleaching status of corals on the Mascarene Plateau.

Photo-physiological performance of healthy-looking and bleached corals

All photo-physiological parameters varied significantly among coral species tested and between coral conditions, except for β, irrespective of the analysis including *Acropora* sp. from 30 m or 36 m (Table 1). The interaction between species and coral condition was not significant; only in the case of β. The two-way ANOVA indicated significant effects of depth and coral condition in *Acropora* sp. on almost all photo-physiological parameters, except for β, and the effect of depth on $rETR_{max}$ and α, and the effects of depth along with its interaction with coral condition on E_k (Table 2).

The effective quantum yield at PSII did not differ in bleached and healthy samples for *Porites* and *Lithophyllon* from 27 m, *Galaxea* and *Acropora* from 36 m, while it decreased significantly in *Heliopora* ($P<0.05$) and *Favites* ($P<0.01$) at 27 m, *Acropora* ($P<0.001$) from 30 m, and *Stylophora*-like ($P<0.001$) at 58 m (Fig. 4A). $rETR_m$ decreased ($P<0.05$) or tended to decrease in all bleached species except for *Porites* where it tended to increase (Fig. 4B). NPQ_m did not change ($P>0.05$) for *Porites*, *Acropora* (30 m) and *Galaxea*, while it tended to increase for *Heliopora*, *Acropora* (36 m) ($P<0.05$), *Lithophyllon*, *Galaxea*, and decrease for *Favities*, *Acropora* (30 m), *Stylophora*-like ($P<0.05$), respectively (Fig. 4C). Usually, under thermal stress conditions, there is a tendency for effective yield at PSII and $rETR_m$ to decrease and NPQ_m to increase as a sign of coping with thermal stress, and a decrease in all these parameters indicates damage to the photosynthetic apparatus of the zooxanthellae in the corals. The thermally tolerant coral, *Porites*, exhibited no change in PSII effective yield and NPQ_m and a tendency to have an increased $rETR_m$ in bleached conditions, which is in accordance with Bhagooli and Yakovleva (2004). Conversely, *Favites, Acropora* (30 m) and *Stylophora*-like corals showed a clear decrease in effective yield at PSII, $rETR_m$ and NPQ_m suggesting some level of damage to

Table 2. Two-way ANOVA for the effect of depth (30 m and 36 m) and coral condition (healthy-looking and bleached) on photo-physiological features of *Acropora* sp. Asterisks ***, ** and * represent significant differences at *$P<0.001$*, *$P<0.01$* and *$P<0.05$*, respectively.

Parameters	Source of Variation	SS	df	MS	F	P-value
Φ_{PSII}	Depth	0.021	1	0.021	25.012	0.001**
	Condition	0.012	1	0.012	14.649	0.005**
	Depth x Condition	0.012	1	0.012	14.886	0.005**
$rETR_m$	Depth	0.001	1	0.001	10.017	0.013*
	Condition	0.025	1	0.025	250.848	0.000***
	Depth x Condition	0.000	1	0.000	4.560	0.065
NPQ_{max}	Depth	0.012	1	0.024	59.341	0.000***
	Condition	0.046	1	0.039	97.033	0.000***
	Depth x Condition	0.001	1	0.003	6.460	0.035*
α	Depth	0.007	1	0.012	5.682	0.044*
	Condition	0.002	1	0.046	21.931	0.002**
	Depth x Condition	0.000	1	0.001	0.285	0.608
b	Depth	0.007	1	0.007	1.269	0.293
	Condition	0.002	1	0.002	0.333	0.580
	Depth x Condition	0.000	1	0.000	0.042	0.843
E_k	Depth	0.000	1	0.000	0.012	0.916
	Condition	0.040	1	0.040	27.522	0.001**
	Depth x Condition	0.001	1	0.001	0.725	0.419

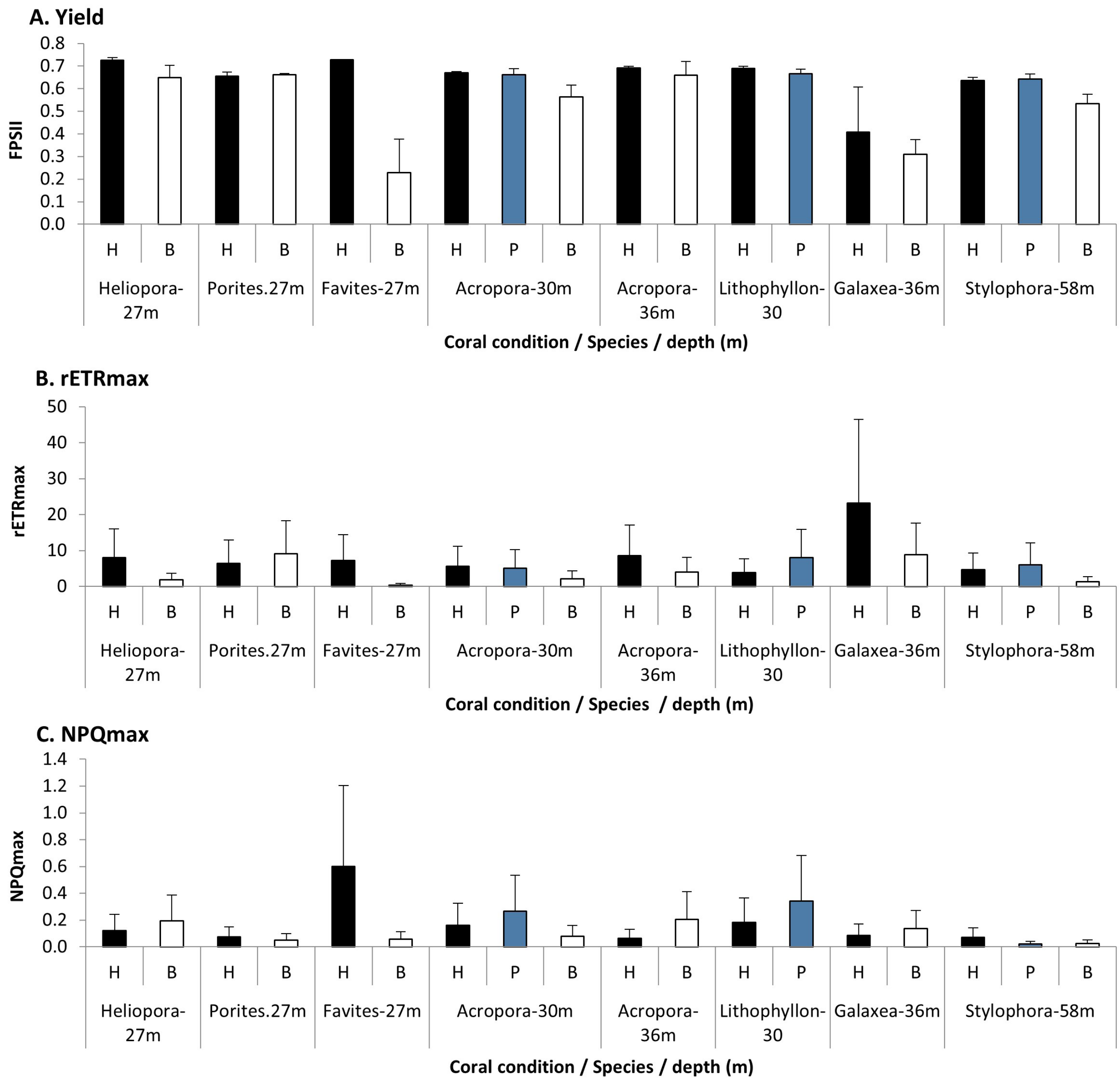

Figure 4. Photo-physiological parameters of healthy-looking and bleached parts of corals. A. Effective quantum yield at PSII (Φ_{PSII}); B. Maximum relative electron transport rate ($rETR_m$); and C. Maximum non-photochemical quenching (NPQ_{max}). H-Healthy-looking, P-Pale, and B-bleached. Bars represent Mean±SD (n=3).

the photosynthetic capacity of their symbiotic zooxanthellae. The other studied corals showed variable responses in these tested chlorophyll fluorescence parameters. These findings indicate that *Porites* symbionts may be photosynthetically thermally tolerant but still bleach to a certain degree, while *Favites*, *Acropora* (30 m) and *Stylophora*-like symbionts are photosynthetically thermally susceptible and bleach. It is noteworthy that Ralph *et al.* (2001) and Bhagooli and Hidaka (2004) showed that photosynthetically competent symbionts were released when corals like *Galaxea fascicularis* and *Pocillopora damicornis* were exposed to elevated temperature. Other studies have proposed that the photosynthetic machinery of the symbionts broke down or their repair mechanisms are affected and thus corals bleached (Jones *et al*., 1998; Warner *et al*., 1999; Takahashi *et al*., 2004; Bhagooli, 2013). Mattan-Moorgawa *et al*. (2012) studied eight shallow-water coral species and indicated a decline in PSII activity of four bleached corals that are usually susceptible to thermal bleaching, and out of the four thermally tolerant corals only pale *Pocillopora* and *Galaxea* showed a declining tendency in their PSII activities.

The E_k tended to decrease in bleached samples in most studied corals, except for *Galaxea* and *Stylophora*-like

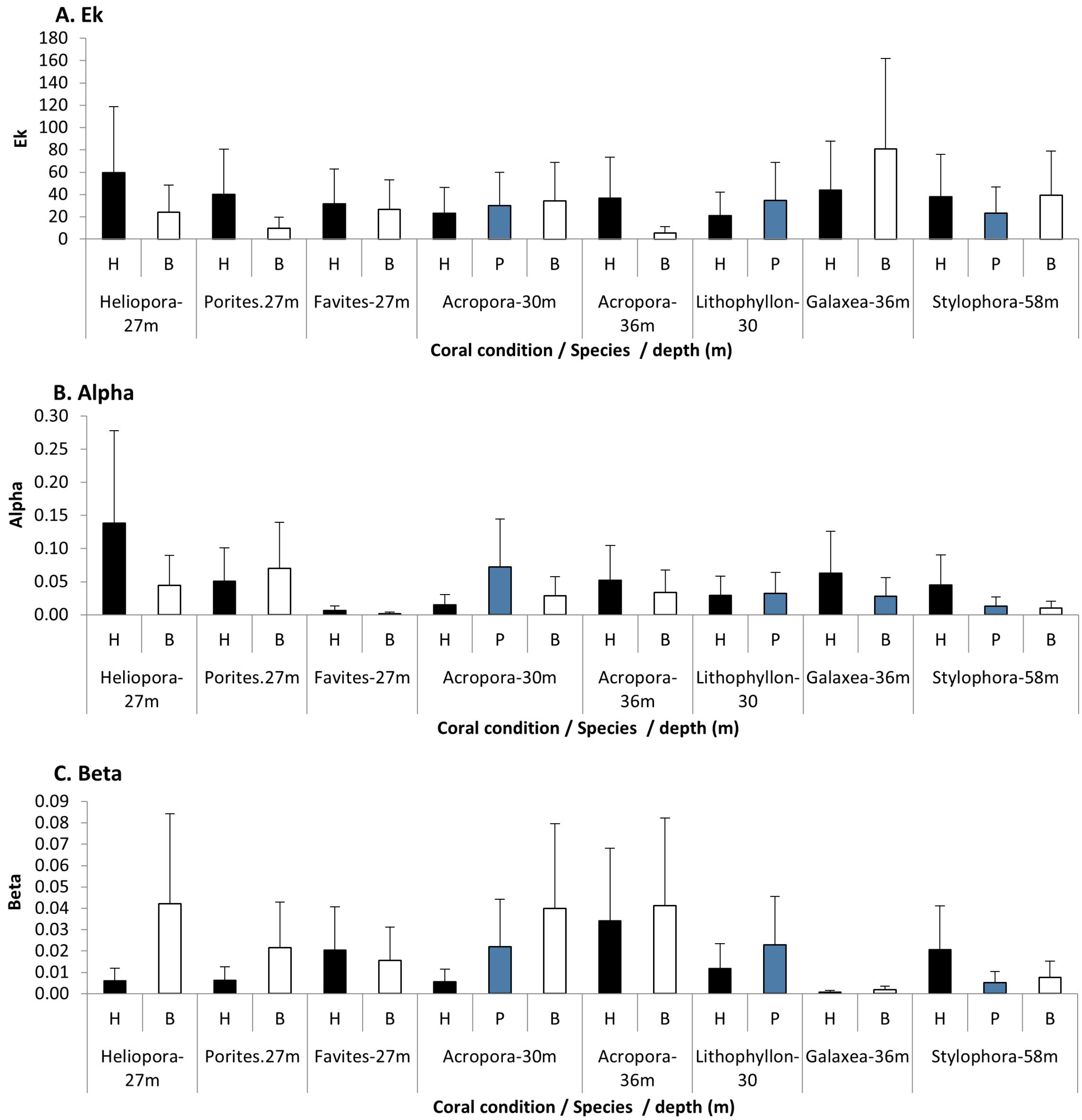

Figure 5. Photo-physiological parameters of healthy-looking and bleached parts of corals. A. Alpha (α, initial slope of the light curve prior to onset of saturation); B. Beta (β, the slope of the light curve beyond the onset of photo-inhibition); and C. E_k (the minimum saturating irradiance). H-Healthy-looking, P-Pale, and B-bleached. Bars represent Mean±SD (n=3).

samples (Fig. 5A), implying a lowering of the light saturation level. Alpha declined in bleached samples of *Heliopora*, and *Stylophora*-like only (Fig. 5B), suggesting a decline in the slope of the photosynthetic rate. Beta increased in bleached samples of *Heliopora*, *Porites* and *Acropora*-30 m (Fig. 5C), indicating increased photo-inhibition of photosynthesis in the symbionts of these corals. These chlorophyll fluorescence parameters were variable and not many studies have used these parameters in studies on photosynthetic marine invertebrates, including corals, and sea plants (Bhagooli *et al.*, 2021).

This is the first study to document *Stylophora*-like species at Nazareth Bank, and variable bleaching observations and their photo-physiological features in healthy and bleached conditions from both the Saya de Malha and Nazareth Banks. The qualitative field observations indicated that bleaching was readily spotted through the VAMS video for corals like *Porites* and *Acropora*, while for other small-colony forming corals such as *Favites*, *Galaxea*, *Heliopora*, *Lythophyllon*, *Stylophora*-like, grab collections revealed their bleaching conditions. For the bleached conditions, the well-known thermally tolerant coral *Porites* exhibited normal photo-physiology, while *Favites*, *Acropora* (30 m) and *Stylophora*-like showed some level of photo-physiological dysfunctioning. The water temperatures were 27.5, 26.8, 27 and 26 °C at S4, S39, S44 and S47, respectively. These were snap-shot measurements available from the ROV and are inadequate for explaining the intra- and inter-species variability in bleaching susceptibility at these studied depths on the Mascarene Plateau. It is noteworthy that Frade *et al.* (2008) has reported that *Madracis* spp. from the southern Caribbean region exhibit depth-dependent photo-physiological features in some species. Additional vertical profiling data or depth-specific data of temperature and light intensity for longer periods during summer, as done by Frade *et al.* (2008, 2018), would be needed to appropriately determine the influence of these parameters on coral bleaching patterns and photo-physiological functioning of corals in this part of the world. Further detailed studies undertaken prior- and post-field bleaching events at the Banks along with a thermal stress experiment may provide insights into the photo-physiology of bleaching tolerance and susceptibility of these corals at Saya de Malha and Nazareth Banks. Additionally, determination of the symbiont genetic types will provide important information related to the bleaching vulnerabilities among these corals from the Mascarene Plateau.

Acknowledgments

The authors are grateful to the Food and Agriculture Organization (FAO) EAF-Nansen programme for supporting their participation in the Indian Ocean Research Expedition 2018 (NORAD-FAO PROJECT GCP/INT/730/NOR) in the Saya de Malha and Nazareth Banks on board the "R/V Dr Fridtjof Nansen", the Department for Continental Shelf, Maritime Zones Administration & Exploration of Mauritius for co-leading and coordinating the scientific expedition, the Joint Management Commission for their support and assistance, the Ministry of Blue Economy, Marine Resources, Fisheries and Shipping for granting the permits for sampling and the University of Mauritius for logistic support. RB and SJ are thankful to the Higher Education Commission for funding (T0721) studies on corals of the Republic of Mauritius. The authors also acknowledge the support of the participants, the cruise members and the VAMS technicians during the expedition. The authors are thankful to the anonymous reviewers for insightful comments that have improved the manuscript.

References

Bhagooli R, Hidaka M (2004) Release of zooxanthellae with intact photosynthetic activity by the coral *Galaxea fascicularis* in response to temperature stress. Marine Biology 145: 329-337

Bhagooli R, Yakovleva I (2004) Differential bleaching susceptibility and mortality patterns among four corals in response to thermal stress. Symbiosis 37: 121-136

Bhagooli R, Sheppard CCR (2012) Prediction of recurrences of mass coral bleaching / mortality and vulnerability of reef-building corals to climate change in Mauritian and Japanese waters. Sustainable Marine Environment, University of Mauritius Research Journal, Special Issue 18A: 105-121

Bhagooli R, Taleb-Hossenkhan N (2012) Thermal spatial heterogeneity and coral bleaching: implications for habitat refuges. Proceedings of the 12th International Coral Reef Symposium 2012. Cairns, Australia. 6 pp [http://www.icrs2012.com/proceedings/manuscripts/ICRS2012_9D_1.pdf]

Bhagooli R (2013) Inhibition of Calvin-Benson cycle suppresses the repair of photosystem II in *Symbiodinium*: Implications for coral bleaching. Hydrobiologia 714: 183-190

Bhagooli R, Ramah S, Kaullysing D, Mattan-Moorgawa S, Taleb-Hossenkhan N, Gopeechund A, Soondur M, Flot J-F (2017) Field observation of five *Stylophora pistillata*-like morphotypes near Mauritius Island. Western Indian Ocean Journal of Marine Science, Special Issue 1/ 2017: 51-53

Bhagooli R, Kaullysing D (2019) Seas of Mauritius – Chapter 12. In: Sheppard CCR (ed.) World seas: An environmental evaluation, 2nd edition, volume II: The Indian Ocean to the Pacific. Elsevier. Academic Press. pp 253-277 [Paperback ISBN: 9780081008539, 912p]

Bhagooli R, Mattan-Moorgawa S, Kaullysing D, Louis YD, Gopeechund A, Ramah S, Soondur M, Pilly SS, Beesoo R, Wijayawanti DP, Bachok ZB, Monrás VC, Casareto BE, Suzuki Y, Baker AC (2021) Chlorophyll fluorescence - a tool to assess photosynthetic performance and stress photo-physiology in symbiotic marine invertebrates and seaplants. Marine Pollution Bulletin. 165 [https://doi.org/10.1016/j.marpolbul.2021.112059]

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29: 309-327

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16, Suppl. S: 129-138

Darling, ES, McClanahan, TR, Maina, J *et al*. (77 more authors) (2019) Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. Nature Ecology and Evolution 3: 1341-1350

Fenner D, Clark TH, Turner JR, Chapman B (2004) A checklist of the corals of the island state of Rodrigues, Mauritius. Journal of Natural History 38: 3091–3102

Frade PR, Bongaerts P, Winkelhagen AJS, Tonk L, Bak RPM (2008) *In situ* photobiology of corals over large depth ranges: A multivariate analysis on the roles of environment, host, and algal symbiont. Limnology and Oceanography 53 (6): 2711-2723

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

Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochimica et Biophysica Acta 990: 87-92

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Global Change Biology 2: 495-509

Hardman ER, Meunier MS, Turner JR, Lynch T, Taylor M, Klaus R (2004) The extent of coral bleaching in Rodrigues, 2002. Journal of Natural History 38: 3077-3089

Hardman ER, Thoma J, Stampfli NS, Desiré MS,Perrine S (2008) Small-scale variations in the effects of coral bleaching in Rodrigues. Proceedings of the 11th International Coral Reefs Symposium. pp 742-746

Hilbertz W, Goreau T (2002) Saya de Malha expedition, March 2002. 101 pp

Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. Journal of Experimental Marine Biology and Ecology 129: 279-303

Hoegh-Guldberg O (1999) Climate change: coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50: 839-866

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359: 80-83

Jones RJ, Hoegh-Guldberg O, Larkum AWD, Schreider U (1998) Temperature-induced bleaching of corals begins with impairment of the CO_2 fixation mechanism in zooxanthellae. Plant, Cell and Environment 21: 1219-1230

Kleppel GS, Dodge RE, Reese CJ (1989) Changes in pigmentation associated with the bleaching of stony corals. Limnology and Oceanography 34: 1331-1335

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Current Biology 28: 2570-2580

Le Tissier MDA, Brown BE (1996) Dynamics of solar bleaching in the intertidal reef coral *Goniastrea aspera* at Ko Phuket, Thailand. Marine Ecology Progress Series 136: 235-244

Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. Journal of Experimental Marine Biology and Ecology 375: 1-8

Loya Y, Sakai K, Yamazato K, Nakano J, Sambi H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecology Letters 4: 122-131

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19: 155-163

Mattan-Moorgawa S, Bhagooli R, Rughooputh SDDV (2012) Thermal stress physiology and mortality responses in scleractinian corals of Mauritius. Proceedings of the 12th International Coral Reef Symposium 2012. Cairns, Australia. 6pp [http://www.icrs2012.com/proceedings/manuscripts/ICRS2012_9A_6.pdf]

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

McClanahan TR and Muthiga NA (2020) Oceanic patterns of thermal stress and coral community degradation on the island of Mauritius. Coral Reefs. [https://doi.org/10.1007/s00338-020-02015-4]

Moothien-Pillay R, Terashima H, Venkatasami, A, Uchida H (2002) Field guide to corals of Mauritius. Albion Fisheries Research Centre (AFRC), Japan International Cooperation Agency (JICA). 334 pp

Muir PR, Marshall PA, Abdulla A, Aguirre JD (2017) Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef? Proceedings of the Royal Society B: Biological Sciences 284: 20171551

Obura DO, Gudka M, Abdou Rabi F, Bacha Gian S, Bigot L, Bijoux J, Freed S, Maharavo J, Munbodhe

V, Mwaura J, Porter S, Sola E, Wickel J, Yahya S, Ahamada S (2017) Coral reef status report for the Western Indian Ocean. Global Coral Reef Monitoring Network (GCRMN)/International Coral Reef Initiative (ICRI). 144 pp [https://www.icriforum.org/sites/default/files/COI%20REEF%20LR%20F2.compressed.pdf]

Platt T, Jassby AD (1976) The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. Journal of Phycology 12: 421-430

Ralph PJ, Larkum AWD, Gademann R, Schreiber U (1999) Photosynthetic responses of coral reef endosymbionts. Marine Ecology Progress Series 180: 139-147

Ralph PJ, Gademann R, Larkum AWD (2001) Zooxanthellae expelled from bleached corals at 33 °C are photosynthetically competent. Marine Ecology Progress Series 220: 163-168

Rodrigues LJ, Grottoli AG, Lesser MP (2008) Long-term changes in the chlorophyll fluorescence of bleached and recovering corals from Hawaii. Journal of Experimental Biology 211: 2502-2509

Rowan R (2004) Coral bleaching: thermal adaptation in reef coral symbionts. Nature 430: 742

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proceedings of the National Academy of Science USA 105 (30): 10444-10449

Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 245: 294-297

Smith TB, Gyory J, Brandt ME, Miller WJ, Jossart J, Nemeth RS (2016) Caribbean mesophotic coral ecosystems are unlikely climate change refugia. Global Change Biology 22: 2756-2765

Stefani F, Benzoni F, Yang SY, Pichon M, Galli P, Chen CA (2011) Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). Coral Reefs 30 (4): 1033

Takahashi S, Nakamura T, Sakamizu M, Van Woesik R, Yamasaki H (2004) Repair machinery of symbiotic photosynthesis as the primary target of heat stress for reef building corals. Plant and Cell Physiology 45: 251-255

Veron JE (2000) Corals of the world, Volumes 1-3. Australian Institute of Marine Science, Townsville. 1410 pp

Warner ME, Fitt WK, Schmidt GW (1999) Damage to photosystem II in symbiotic dinoflagellates: A determinant of coral bleaching. Ecology Proceedings of the National Academy of Science USA 96: 8007-8012