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Differential responses of effective quantum yield to acute thermal stress in scleractinian corals including pre- and post-transplanted *Acropora muricata*

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Abstract. *Jeetun S, Ricot M, Taleb-Hossenkhan N, Kaullysing D, Flot J-F, Bhagooli R. 2023. Differential responses of effective quantum yield to acute thermal stress in scleractinian corals including pre- and post-transplanted* Acropora muricata. *Indo Pac J Ocean Life 7: 54-63.* Global climate change has had a serious impact on the health status of coral reefs and has led to the use of active reef restoration measures to remediate the decline in coral cover and assist in the recovery of depleted coral populations. This study aimed to assess the thermal photo-physiological responses of *Acropora muricata* pre- and post-transplantation from reef, lagoon, and nearshore stations to the experimental nearshore station and of four other non-transplanted coral species, namely, *Acropora cytherea*, *Galaxea fascicularis*, *Pocillopora damicornis* and *Lithophyllon repanda* from the reef. A visual assessment of dinoflagellate symbiont loss was conducted during summer bleaching events in 2011, 2016, and 2019 for *A. muricata* at the three stations, nearshore, lagoon, and reef, and for the other four corals at the reefs of Belle Mare (BM), Mauritius. The 2016 bleaching event appeared to be more severe for *P. damicornis* and *L. repanda*. A first experiment was carried out using pre-transplanted *A. muricata* from the reef, lagoon, and nearshore, respectively, in 2012, and a second one was conducted with post-transplanted *A. muricata* from the nearshore station in 2020, and *A. cytherea*, *G. fascicularis*, *P. damicornis* and *L. repanda* from the reef in both 2012 and 2020. The coral specimens were incubated at 28°C, 30°C, and 32°C for 3hrs. The results showed an enhanced photo-physiological thermo-tolerance through the measurement of the effective quantum yield of *A. muricata* following transplantation from the reef and lagoon to the nearshore station. Significantly different photo-physiological responses of the other four corals occurring on the reef were also reported between 2012 and 2020. These findings suggest that the nearshore transplanted *A. muricata* may have acclimatized, leading to enhanced thermo-tolerance when exposed to 30°C and *A. cytherea* among the test corals may have improved its thermo-tolerance at 30°C and 32°C possibly following several bleaching events. Further studies using longer experimental exposures and involving the symbiont species, antioxidant responses, symbiont cell density, and chlorophyll content along with coral genetics may shed light on possible mechanisms for such enhanced thermo-tolerance.

Keywords: Bleaching susceptibility, climate change, coral, Mauritius, PAM, resilience, thermal stress, transplantation

INTRODUCTION

Coral reefs are the most biodiverse ecosystems on Earth, supporting an estimated 25% of all marine life (Spalding et al. 2001). They offer a panoply of benefits to the marine environment and the world. They are not only highly significant for nature, but represent a very high value for humankind as they support millions of people whose lives depend on these natural resources for a source of food and income (Moberg and Folke 1999). Coral reefs form natural barriers protecting the coastlines from the damaging effects of wave action and tropical storms, preventing erosion. Coral reefs are responsible for the creation of marine biodiversity hotspots which are of great importance ecologically, economically and aesthetically that is energy-dependent on the coral-zooxanthellae symbiosis (Baumgarten et al. 2015). However, coral reefs are under high pressure from a combination of direct human impacts and global climate change (Wilkinson 2000). These stressors can affect the delicate balance between the reef corals and their symbiotic microalgae (zooxanthellae). This process, known as coral bleaching, is characterized by the loss of photosynthetic pigment and/or loss of zooxanthellae (Kleppel et al. 1989). The physiology of bleached corals is compromised and bleaching occurring over extended periods in time frequently results in high mortality rates in corals (Spalding and Brown 2015; Eakin et al. 2016).

Global climate change has had a serious impact on the health status of coral reefs through bleaching events which are recurrent and increasing in intensity (Hughes et al. 2018). Mild to moderate bleaching was reported in numerous lagoon and off-lagoon areas around Mauritius Island in 2016, although post-bleaching assessments revealed that most bleached corals recovered. The most impacted locations were Belle Mare, Flic en Flac, and Ile aux Bénitiers, with more than 65% of their live corals partially bleached and the most affected coral genera were *Acropora* with more than 85% and 70% bleaching observed in *A. muricata* and *A. cytherea*, respectively (Obura et al. 2017). Coral communities were monitored over a 15-year period during thermal stress episodes and a 40% decrease in hard coral cover was observed, with the disappearance of three coral taxa facing the risk of extinction (McClanahan and Muthiga 2021). Similarly, overall live coral cover showed a noticeable decreasing trend between 2007 and 2009, while algal cover increased significantly at most sites (Bhagooli et al. 2021a; Bhagooli and Kaullysing 2019). A study done during the 2010 bleaching event revealed differential recovery of different corals under variable bleaching conditions at Belle Mare, stating that there was no significant change in the PSII functioning of the pale colonies of *Pocillopora damicornis* and *Galaxea fascicularis* post-bleaching while bleached *A. muricata* had a higher Fv/Fm and a faster recovery than *A. cytherea* (Mattan-Moorgawa et al. 2018). Differential coral bleaching and photo-physiological responses among corals are not restricted to around Mauritius only but have also been reported at the Saya de Malha, Mascarene Plateau, Indian Ocean (Bhagooli et al. 2021b).

Coral reefs around the world have been degraded to such an extent where natural recovery mechanisms and local conservation methods alone may not be sufficient for the preservation and restoration of the biodiversity (Goreau and Hilbertz 2005). Coral reef scientists and managers are resorting to active reef restoration as an important conservation tool to remediate the decline in coral cover and assist the recovery of depleted coral populations (Precht 2006; Edwards and Gomez 2007). The success of *A. muricata* transplantation on a concrete block at Belle Mare, Mauritius is fragment-size dependent, with fragments of size > 2.0 cm having a higher survival rate (Bhagooli et al. 2021c). However, the thermal responses of pre- and post-transplanted corals are yet to be investigated around Mauritius.

While many tropical corals exist near their upper thermal limit and are susceptible to slight variations in Sea Surface Temperature (SST) as small as 1-2°C over the typical summer maximum causing the coral-algal symbiosis to break down (Baker et al. 2008; Suggett and Smith 2011), some corals are able to resist and adapt to environmental stressors (Coles and Brown 2003; Douglas 2003; Venn et al. 2008). This adaption/acclimatization is due to several environmental factors such as bleaching history (Guest et al. 2012) and previous exposure to variable temperature regimes (Oliver and Palumbi 2011; Palumbi et al. 2014). For instance, *A. muricata* exposed to sea surface temperatures beyond 31°C (bleaching temperature) in nearshore sites were more resistant to bleaching than corals from lagoonal and reefal sites at Belle Mare, possibly suggesting acclimatization with potential restoration implications in an era of ongoing global climate change (Bhagooli and Taleb-Hossenkhan 2012). Though such variations in bleaching resilience can be used in creating bleaching-tolerant coral nurseries for restoration purposes, field observations of thermal resilience warrant further experimental verification. Therefore, this study aimed to assess the photo-physiological response of *A. muricata* post-transplantation from reef, lagoon and nearshore stations to the experimental nearshore station compared to four other reefal coral species under thermal stress conditions.

MATERIALS AND METHODS

Study area

The *A. muricata* fragments (n=5) of size 2 cm^2 each per station were collected from the nearshore, lagoon and reef stations and *A. cytherea*, *P. damicornis*, *Lithophyllon repanda* and *G. fascicularis* were collected at the reef station in March 2012 for the first experiment (Figure 1). In 2014, *A. muricata* from the nearshore, lagoon and reef stations were transplanted to the experimental nearshore station. Samples of transplanted *A. muricata* (n=5) from the nearshore station and *A. cytherea*, *P. damicornis*, *L. repanda* and *G. fascicularis* from the reef were collected for the second experiment in March 2020 (Table 1). The water depths varied between 0.5 to 1.5 m among these stations depending on tides. These locations were chosen because a difference in SST was observed at the nearshore, lagoon and reef stations at Belle Mare (Bhagooli and Taleb-Hossenkhan 2012). HOBO temperature data loggers were deployed to record temperature data during the first nine days in March in 2011, 2012, 2016, 2019 and 2020.

Bleaching survey

Bleaching observations (non-bleached, paling, partially bleached and bleached) of the test species were carried out during summer bleaching events in 2011, 2016 and 2019 at the three stations, namely nearshore, lagoon and reef for *A. muricata* and at the reef for *A. cytherea*, *P. damicornis*, *L. repanda* and *G. fascicularis* at Belle Mare (BM). Coral colonies were surveyed along three sets of 100 m^2 belt transect and a visual assessment of bleaching out of 30 colonies for *A. muricata* at all the three stations and 20 colonies for *A. cytherea*, *P. damicornis*, *L. repanda* and *G. fascicularis* at reef stations only in March 2011, 2016 and 2019 was conducted. The coral species were identified according to Corals of the World (Veron 2000) and the World Register of Marine Species (http://www.marinespecies.org/).

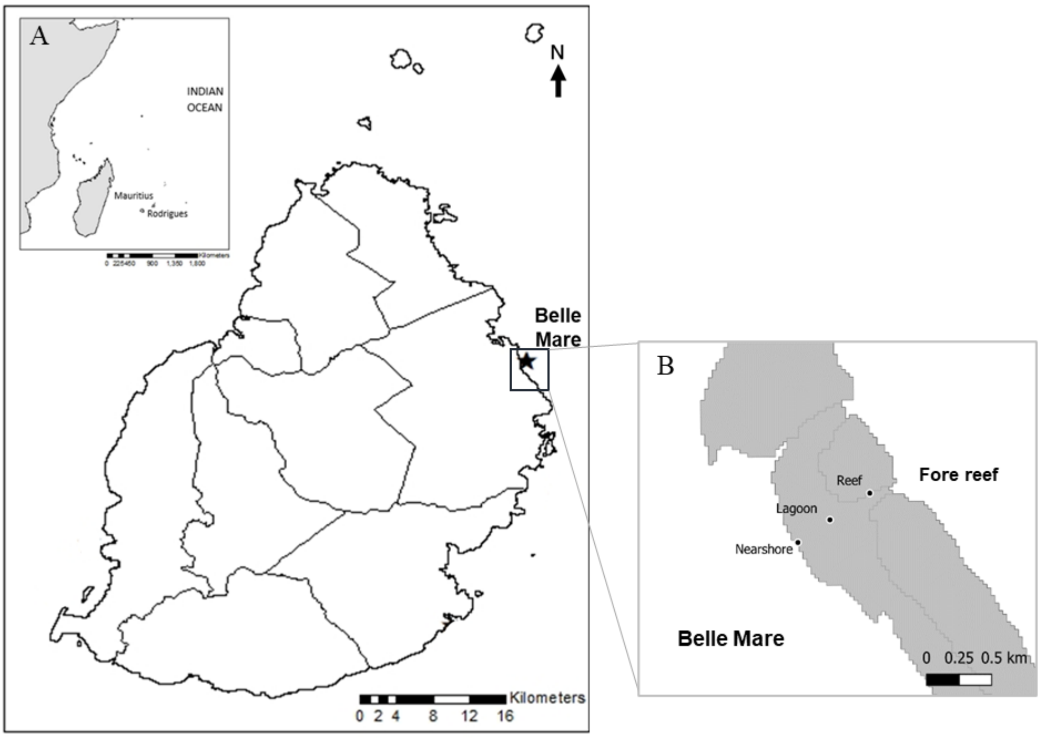


Figure 1. Location of Mauritius in the Indian Ocean (A) and the sampling sites (nearshore, lagoon and reef) (B) of transplanted *Acropora muricata* corals at Belle Mare. The grey area in (B) represents the marine waters at Belle Mare showing three stations, namely nearshore, lagoon and reef

Table 1. Transplant experimental design of *Acropora muricata* and sample collection pre- and post-transplantation for heat stress experiment. It should be noted that *Acropora cytherea*, *Pocillopora damicornis*, *Lithophyllon repanda* and *Galaxea fascicularis* were not transplanted but collected directly from the colonies

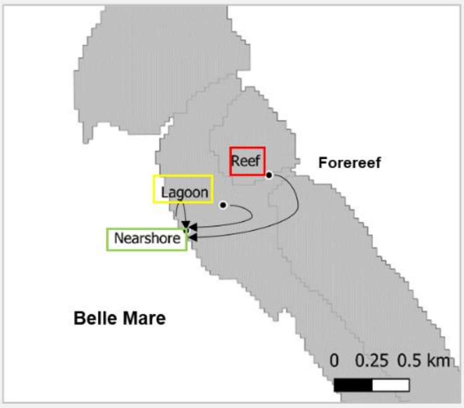
Stations	Pre-transplantation (2012)	Transplantation (2014)	Post-transplantation (2020)
Nearshore	*A. muricata* (n=5) 	*A. muricata* 	*A. muricata* (n=5)  Nearshore  Lagoon  Reef Experimental nearshore
Lagoon	*A. muricata* (n=5) 		-
Reef	*A. muricata* (n=5)  *A. cytherea* (n=5) *G. fascicularis* (n=5) *L. repanda* (n=5) *P. damicornis* (n=5)		*A. cytherea* (n=5) *G. fascicularis* (n=5) *L. repanda* (n=5) *P. damicornis* (n=5)

Photo-physiological response

Five 2 cm^2 fragments each from parent colonies of *A. muricata* were collected from the reef, lagoon and nearshore, respectively, using pliers prior to transplantation in 2012. Coral transplantation was performed using *A. muricata* from parent colonies from the reef, lagoon and nearshore (20 m from the shore) to the experimental nearshore site at BM in 2014 (Bhagooli et al. 2021c). Transplanted *A. muricata* (n=5) were collected from the nearshore station in 2020. The *A. cytherea*, *G. fascicularis*, *P. damicornis* and *L. repanda* fragments were collected from the reef station. The coral specimens were incubated at different temperature conditions of 28, 30 and 32°C for 3hrs (Bhagooli and Hidaka 2003). The SST ranges from 28.1°C in March to greater than 30°C, the highest recorded temperature in the lagoon of BM at which bleaching onsets (Bhagooli and Taleb-Hossenkhan 2012; Bhagooli et al. 2021c). The effect of temperature on photo-physiological responses of the *in hospite* zooxanthellae was assessed using chlorophyll *a* fluorescence determined by Pulse-Amplitude-Modulated Fluorometry (Genty et al. 1989; Bhagooli et al. 2021d). The effective quantum yield of photosystem II (ΦPSII) measurements were taken initially and after 3-hr stress exposure.

Data analysis

The Shapiro-Wilk test was performed to test for normality of data. The effective quantum yield (ΦPSII) of each species relative to their initials were calculated and were arcsine (square-root) transformed before Analysis of Variance (ANOVA) to ensure normality. The Tukey *post hoc* test was performed after statistical significance to compare means between groups (IBM SPSS 21).

RESULTS AND DISCUSSION

Temperature variations at Belle Mare stations

The temperature trends at the beginning of March 2011 indicated that the nearshore and lagoon stations experienced temperatures of 32°C and 31°C, while the reef station reached at least 30°C (Figure 2A). Seawater temperatures in 2012 reached 30°C at the nearshore and lagoon stations while the reef station was about 29°C (Figure 2B). In 2016, seawater temperatures were mostly at 31°C, with nearshore and lagoon stations quite often reaching 32°C (Figure 2C). In 2019, the nearshore station tended to approach 32°C for the first three days and remained below 31°C for the rest of the days, while at the reef station it was 30°C or less (Figure 2D). In 2020, five out of nine days seawater temperatures reached 31°C or above (Figure 2E).

Bleaching survey

During the 2010-2011 bleaching event, bleaching was observed in two corals species only, *A. muricata* and *A. cytherea* (Table 2). In 2016, bleaching was observed in all selected coral species at BM. The *A. muricata* and *A. cytherea* were the most susceptible to bleaching whereas *L. repanda* was the least affected (Figure 3). A two-way ANOVA was used to test the effect of year (2011, 2016 and 2019) and species on the percentage bleaching (Table 3). There was a significant difference in the percentage coral colonies bleached between the bleaching years ($p<0.001$). Tukey *post hoc* test revealed that the percentage bleached colonies was higher (0.98 ± 0.04%) in 2016 compared to 2011 and 2019 (0.22 ± 0.04%).

Relative effective quantum yield of transplanted *A. muricata*

The effective quantum yield indicated declines at 30°C and 32°C 3-hr treatments for the pre-transplanted corals in 2012, while it is only at 32°C that such declines were observed in post-transplanted *A. muricata* samples in the 2020 experiment (Figure 4). There was a significant difference ($p < 0.05$) in relative ΦPSII in the combined effect of zones and temperature (Table 4). In 2012, the relative ΦPSII of *A. muricata* in the nearshore remained almost unchanged at 28°C and 30°C, however, decreased by half at 32°C (Figure 5A). In contrast, corals from the lagoon and reef showed a similar decrease in relative ΦPSII (0.6 times) at 30°C compared to 28°C, and a 0.2- and 0.3-fold increase, respectively, at 32°C compared to 30°C (Figures 5B, C). In 2020, the response of nearshore-to-nearshore transplanted corals showed a similar trend when exposed to different temperature regimes, nonetheless, the relative ΦPSII at 32°C was slightly lower (9% decrease) compared to 2012. Transplanted *A. muricata* from the lagoon and reef differed in effective quantum yield relative to their respective initials when exposed to 30°C compared to their prior locations (both 80% higher). A decrease in relative ΦPSII was noted in both corals transplanted from the lagoon and reef at 32°C exposure compared to 30°C, but still exhibited a 20% higher relative ΦPSII after transplantation at 32°C.

Relative effective quantum yield (ΦPSII) of other studied coral species

Temperature treatments, year and a combination of any, had significant effects on ΦPSII (relative to their initial) of the *in hospite* zooxanthellae in different species (Table 5). In 2012, *A. cytherea* showed a 0.4-fold decrease in relative ΦPSII at 32°C compared to 28°C and remained almost unchanged in *L. repanda* (Figure 6). In 2020, an increase in relative ΦPSII was noted in all four coral species at 30°C compared to 28°C, however, they behaved differently at 32°C compared to 30°C, *A. cytherea* experienced a decrease (0.3 times) while in *G. fascicularis* and *P. damicornis* increased and remained constant in *L. repanda*. A significant difference was observed in the relative ΦPSII of the coral species between 2012 and 2020 ($p < 0.05$). *A. cytherea*, *G. fascicularis* and *P. damicornis* responded differently at 32°C in 2020 compared to 2012, a higher relative ΦPSII was noted, 0.3-fold, 0.5-fold, and 0.3-fold, respectively. As for *L. repanda*, a slightly lower relative ΦPSII was recorded.

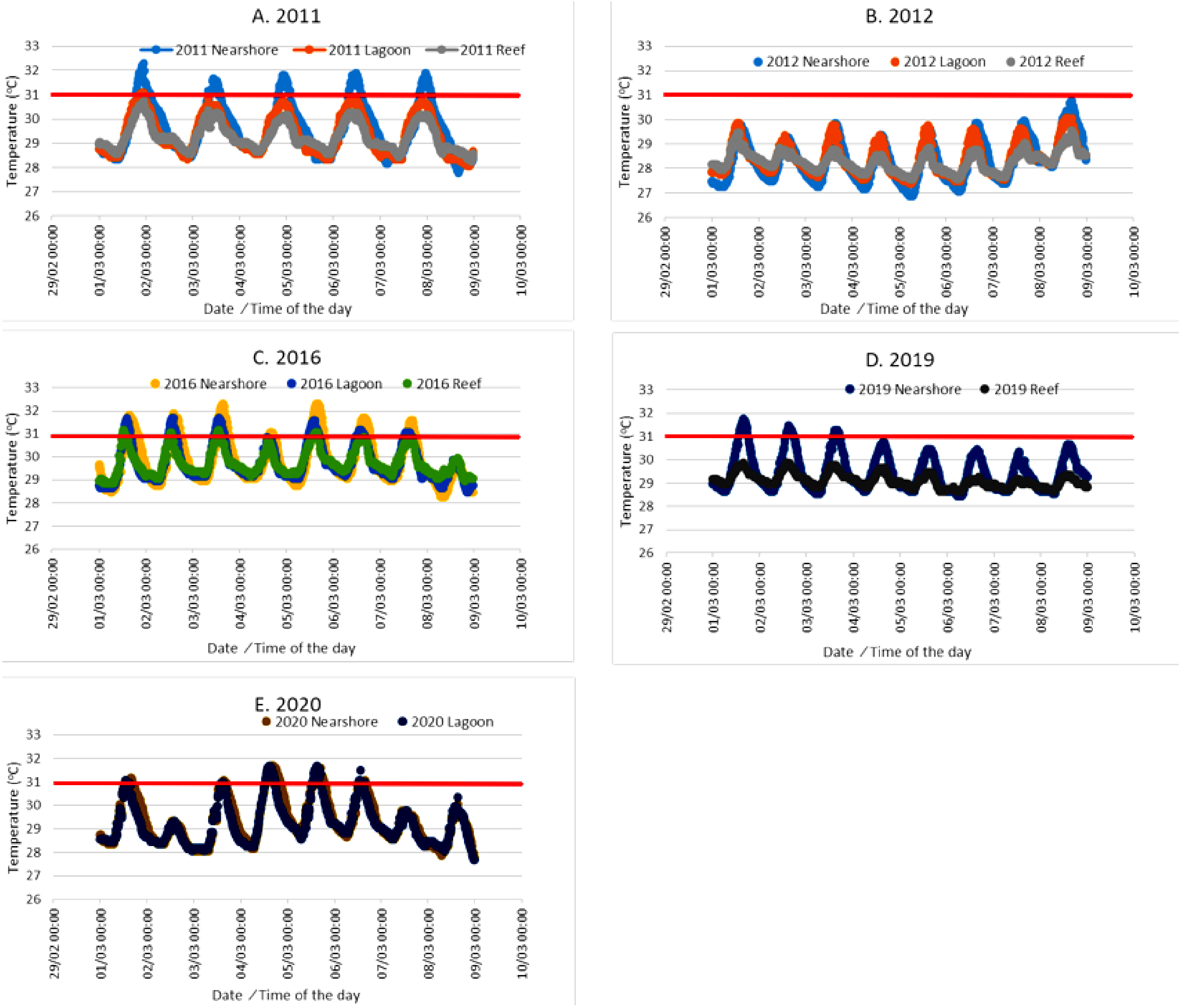


Figure 2. Temperature (°C) records at some or all the three stations (nearshore, lagoon, reef) at Belle Mare in the first week of March (01 to 09) in 2011 (A), 2012 (B), 2016 (C), 2019 (D) and 2020 (E). Red solid line represents reference line at 31°C

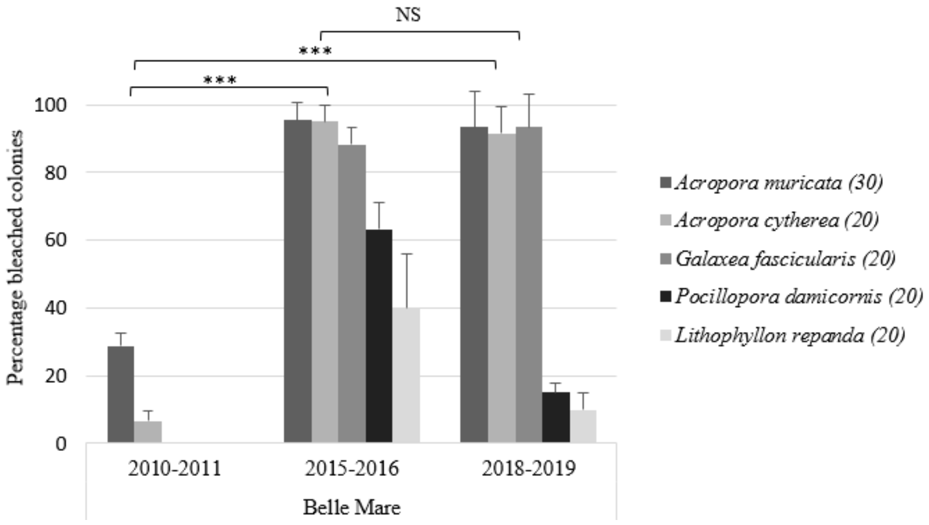


Figure 3. Percentage bleaching of five coral species (out of 30 colonies for *A. muricata* and out of 20 colonies for *A. cytherea*, *P. damicornis*, *L. repanda* and *G. fascicularis* within a 100m^2 area) at BM reefs during 2011, 2016 and 2019 bleaching events. Data represent mean ± SD (n=3)

Table 2. Bleaching observations of the coral species at BM during 2011, 2016 and 2019 bleaching events

Species	**Bleaching year**		
	2010-2011	**2015-2016**	**2018-2019**
A. muricata (nearshore)	Non-bleached	Non-bleached/paling	Non-bleached
A. muricata (lagoon)	Bleached	Bleached	Bleached
A. muricata (reef)	Bleached	Bleached	Bleached
A. cytherea (reef)	Non-bleached	Bleached	Bleached
P. damicornis (reef)	Paling	Bleached	Bleached
L. repanda (reef)	Non-bleached	Bleached	Bleached
G. fascicularis (reef)	Paling	Bleached	Bleached

Table 3. Two-way analysis of variance (2-way ANOVA) of effects of species and year on the percentage bleaching at BM reef

Source of variation	**ANOVA**			
	DF	**MS**	***F***	**p**
Species	4	1.053	103.760	$<0.001^{***}$
Year	2	3.963	390.359	$<0.001^{***}$
Species × Year	8	0.141	13.924	$<0.001^{***}$

Note: p < 0.05 *, p <0.01 **, p < 0.001 ***, NS- not significant

Table 4. Three-way analysis of variance (3-way ANOVA) of the effects of temperature (28, 30 and 32°C), zone of collection (nearshore, lagoon, reef) and year (2012 vs 2020) on the effective quantum yield (ΦPSII) of *in hospite* symbiont relative to initial, for transplanted *A. muricata* corals after 3hrs stress exposure

Source of variation	**ANOVA**			
	DF	**MS**	***F***	**p**
Zones	2	0.004	2.391	0.106^{NS}
Temperature	2	0.015	9.587	$<0.001^{***}$
Year	1	0.014	8.559	0.006^{**}
Zones × Temperature	4	0.004	2.735	0.044^{*}
Zones × Year	2	0.006	3.515	0.040^{*}
Temperature × Year	2	0.016	10.022	$<0.001^{***}$
Zones × Temperature × Year	4	0.001	0.685	0.607^{NS}

Note: p < 0.05 *, p <0.01 **, p < 0.001 ***, NS- not significant

Table 5. Three-way analysis of variance (3-way ANOVA) of the effects of coral species (*G. fascicularis*, *P. damicornis*, *A. cytherea* and *L. repanda*), temperature (28, 30 and 32°C) and year (2012 vs 2020) on the effective quantum yield (ΦPSII) relative to initial following 3hrs exposure

Source of variation	**ANOVA**			
	DF	**MS**	***F***	**p**
Species	3	0.037	4.708	$<0.001^{***}$
Temperature	2	0.041	5.236	0.012^{**}
Year	1	0.206	26.109	0.001^{***}
Species × Temperature	6	0.050	6.385	0.001^{***}
Species × Year	3	0.065	8.172	0.001^{***}
Temperature × Year	2	0.048	6.129	0.001^{***}
Species × Temperature × Year	6	0.012	1.538	0.188^{NS}

Note: p < 0.05 *, p <0.01 **, p < 0.001 ***, NS- not significant

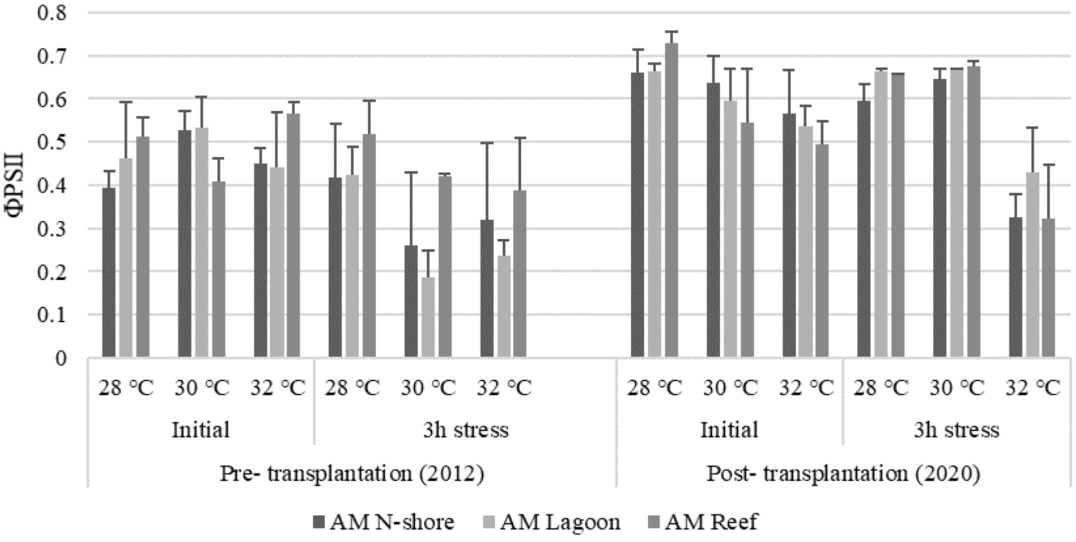


Figure 4. Effective quantum yield of pre-transplanted (2012) and post-transplanted (2020) *A. muricata* from nearshore, lagoon, reef to experimental nearshore in 2020. Data represent mean ± SD (n=3)

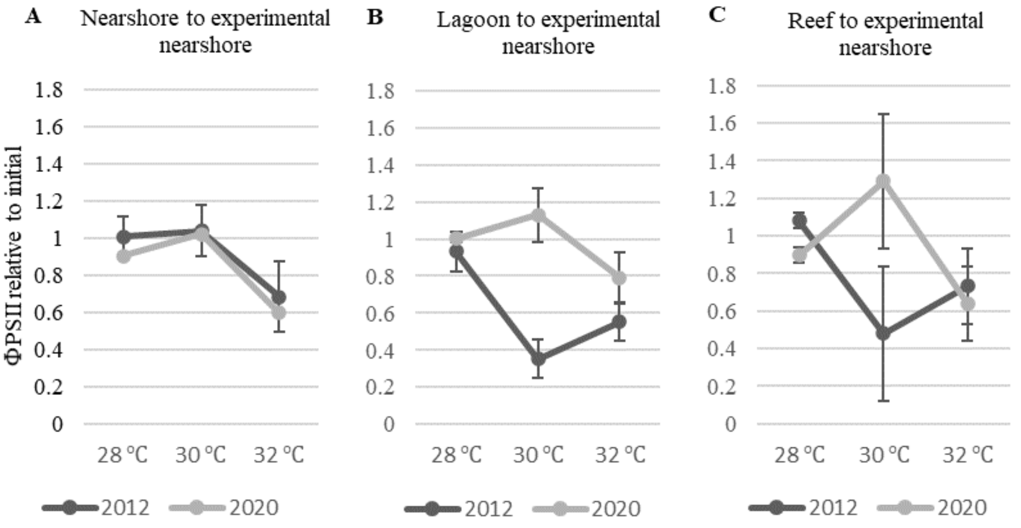


Figure 5. Relative (to initial) effective quantum yield following 3hrs exposure at 28, 30 and 32°C of pre-transplanted *A. muricata* in first experiment in 2012, and 2014 post-transplanted *A. muricata* from nearshore (A), lagoon (B), reef (C) to experimental nearshore zone in the second experiment in 2020. Data represent mean ± SD (n=3)

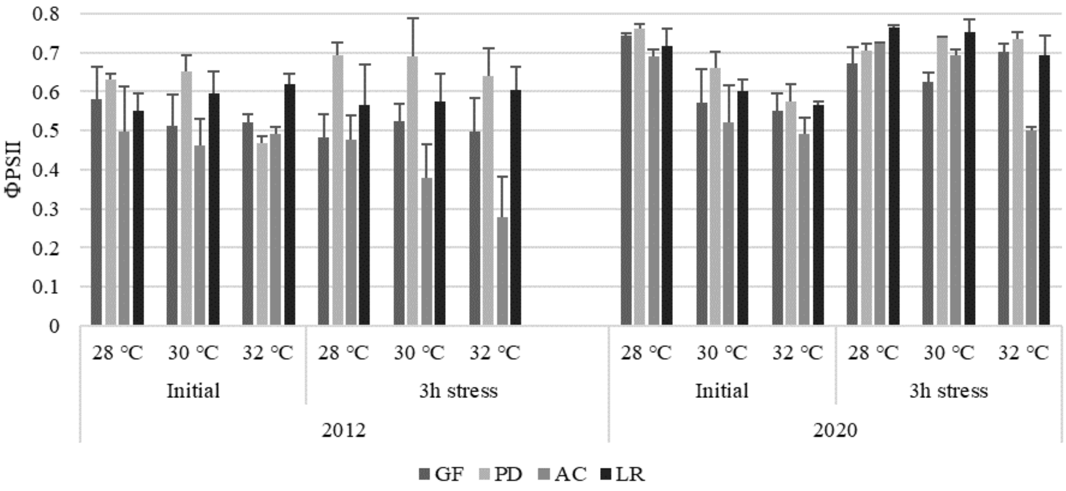


Figure 6. Effective quantum yield (ΦPSII) initially and after 3hrs exposure at 28, 30 and 32°C of *G. fascicularis*, *P. damicornis*, *A. cytherea* and *L. repanda* in years 2012 and 2020. Data represent mean ± SD (n=3)

Discussion

The results showed an increase in photo-physiological thermotolerance of *A. muricata* when the 2012 pre-transplanted stress responses were compared to the 2020 post-transplanted from reef and lagoon to the nearshore station experiments. A difference in the photo-physiological responses of other four different coral species occurring on the reef were also reported from the 2020 experiments.

In 2012, near coast samples exhibited different responses at 30°C than the lagoon and reef ones when exposed to the same temperature stress, corroborating with previous field observations by Bhagooli and Taleb-Hossenkhan (2012) at Belle Mare. It is noteworthy that Bhagooli and Taleb-Hossenkhan (2012) reported differential thermal regimes at the nearshore, lagoon and reef stations at Belle Mare. The nearshore stations experienced temperatures of above 31°C as from the second part of January 2011, while for lagoon and reef stations such temperatures were observed at the end of February 2011. At the end of February 2011, only the nearshore stations had maximal temperature of 32°C. This study reported the thermal bleaching tolerance of *A. muricata* in coastal waters compared to the lagoon and reef even though temperature records were beyond the bleaching threshold. A plausible explanation to this disparity in bleaching susceptibility may be due to acclimatization of the corals to fluctuating temperature regimes.

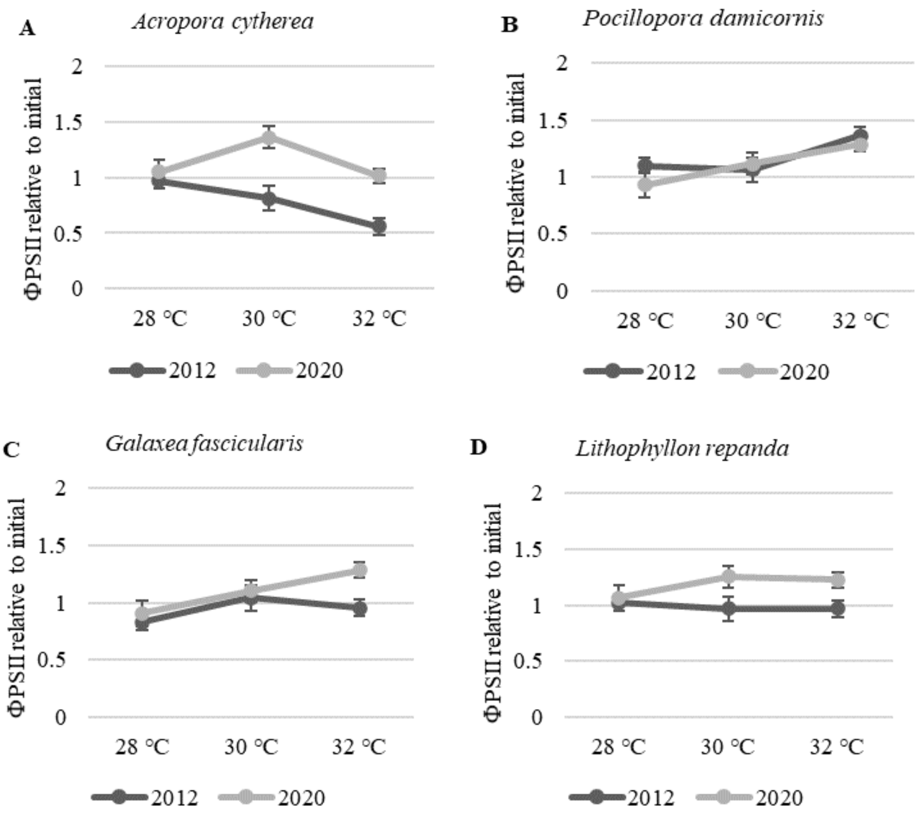


Figure 7. Effective quantum yield (ΦPSII) relative to initial of *A. cytherea* (A), *P. damicornis* (B); *G. fascicularis* (C); and *L. repanda* (E) in 2012 and 2020. Data represent mean ± SD (n=3).

It has been shown that corals subjected to a thermally dynamic environment become more resilient to thermal stress (Schoepf et al. 2015; Safaie et al. 2018). Further evidence of higher chlorophyll a content, estimated productivity, Hsp70 gene expression and protein synthesis in *A. muricata* coast colonies supports this difference in photo-physiological response (Louis et al. 2016a, b, 2020). A study documented highly variable irradiance levels at Belle Mare where lower irradiance was recorded in the coast compared to the reef flat and lagoon possibly due to variations turbidity levels (Bhagooli and Taleb-Hossenkhan 2012). These results are important as they show that thermal history, in addition to light history, can influence the response of reef-building corals to thermal stress and therefore have implications for the modeling of bleaching events.

The thermal history of the coral in a particular environment also has an influence on the response of coral symbiosis to thermal stress. Experimental studies report that pre-stressed corals had more effective photo-protective mechanisms which was associated with decreased loss of symbionts and a lower decline in photosynthetic efficiency (Middlebrook et al. 2008). Similarly, the effective quantum yield of *A. muricata* (relative to its initial) was comparatively higher after transplantation from the lagoon and reef compared to 2012. These corals have witnessed two major thermal anomalies in 2016 and 2019 since their transplantation in 2014, the 2016 bleaching anomaly being the most severe during which Belle Mare was one of the most affected sites (>65 % partial bleaching) with more than 85 % and 70 % bleaching observed in *A. muricata* and *A. cyhterea*, respectively, possibly implying the acclimatization of nearshore *A. muricata.*

The difference in photo-physiological response is at least partially dependent on the residing host symbiont (Bhagooli and Hidaka 2003; Bhagooli 2009, 2010). Zooxanthellae “clades” have been recently redefined into eleven genera (LaJeunesse et al. 2009). *Symbiodinium* (clade A) enhances the survival of the coral host to thermal stress conditions and confers them with thermal resistance (Reynolds et al. 2008). Another study in Mexico looked at *Orbicella faveolata* colonies before, during, and after a thermal anomaly and found that colonies with *Symbiodinium* A3 (*S. fitti*) as their dominant clade were less susceptible to bleaching than colonies with *Brevolium* B17 or *Cladocopium* C7 as a result of their higher maintenance in quantum yield of photosystem II (Kemp et al. 2014). In Belize, 72% of Millepores were dominant in *Symbiodinium* at sites experiencing warmer temperature (Schwiesow et al. 2021). These observations are in line with previous reports of *Symbiodinium* sp. at both coast and reef of Belle Mare (Louis et al. 2016a,b). However, further genetic and microbiome analyses are warranted to characterize the algal symbiont residing in the coral species from Belle Mare.

Variable bleaching susceptibility pattern were observed in different taxa (Loya et al. 2001; Bhagooli and Yakovleva 2004; Yakovleva et al. 2005; Pratchett et al. 2013). The order of bleaching susceptibility based on their photo-physiological response to thermal stress were as follows: *A. cytherea* > *G. fascicularis* > *P. damicornis* > *L. repanda*. Similar results were highlighted in a study during the bleaching anomaly in 2009 at Belle Mare reporting *A. cytherea* as most susceptible and *P. damicornis, G. fascicularis* and *L. repanda* as more tolerant to thermal stress and mortality (Mattan-Moorgawa et al. 2012). It has been suggested that *Acropora* corals with a higher skeletal surface area to volume ratio are least tolerant to high temperature anomalies compared to those with lower ratio (Fujioka 1999). Thick-tissued massive and encrusting corals have a more effective photo-protective capacity as they retract their tissue and self- shade better than thin-tissued corals (Brown 1997; Hoegh-Gulberg 1999). A study on the differential bleaching observations and post-bleaching PSII functioning recovery showed paled *P. damicornis* and *G. fascicularis*, displayed no significant changes in fluorescence quantum yield while bleached *A. muricata* recovered faster than *A. cytherea* post- bleaching (Mattan-Moorgawa et al. 2018). Bleaching susceptibility was significantly different among corals ascribed to each growth form, whereby a much higher proportion of branching, tabular and submassive corals bleached, compared to encrusting, massive and free-living corals.

It has been documented that coral hosts have the ability to shuffle (alter the relative abundance of the extant symbionts) or shift (populated by new symbionts from the environment) their endosymbionts to a more thermotolerant one, thereby becoming more resistant to thermal stress (Jones 2008; LaJeunesse et al. 2009; Cunning et al. 2015; Silverstein et al. 2015; Swain et al. 2018). A difference in response in *G. fascicularis* was noted at 32°C in 2012 in comparison to 2020, most probably due to a change in symbiont type to adapt to warming temperatures. A previous study showed a high diversity of symbiont types in *G. fascicularis* with a higher abundance of thermally tolerant *Durusdinium* symbiont prevalent at sites experiencing maximum yearly average in sea surface temperature at Hainan Island, providing evidence of symbiont shuffling to cope with changes in the environment (Zhou et al. 2017).

An increased thermotolerance of *A. muricata* after being transplanted from reef and lagoon to the nearshore station was observed. Also, a difference in the photo-physiological response of different taxa occurring on the reef was also reported from 2012 to 2020 which suggests the possible acclimatization of these coral species as a consequence of their exposure to repeated thermal anomalies and a variable temperature regime at different stations at Belle Mare. However, to further elucidate the response of these corals to thermal stress conditions additional chlorophyll *a* fluorescence parameters such as the maximum relative electron transport rate ($rETR_{max}$) and the maximum non-photochemical quenching (NPQ_{max}) could be used as done by Bhagooli and Hikada (2006). Other management factors also need to be locally under control or within appropriate limits for survival of corals, such as water quality and predators, for instance, the corallivore *Drupella cornus*, following overgrowth of macroalgae (Kaullysing et al. 2016). There are other coral eating snail species (Kaullysing et al. 2019) that may require further investigations with respect to their links with water quality, macroalgal overgrowth on corals and predation.

The findings of this study are indicative that the nearshore transplanted *A. muricata* may have acclimatized yielding enhanced thermo-tolerance when exposed to 30°C and the non-transplanted *A. cytherea* among the other test corals may have improved its thermo-tolerance at 30°C and 32°C possibly following several bleaching events. Further studies involving the symbiont species, symbiont cell density and chlorophyll content along with coral genetics may shed light on possible mechanisms for such enhanced thermo-tolerance. The mechanisms involving antioxidant/ oxidative stress consisting of enzymatic and non-enzymatic processes can also be studied to investigate how corals counteract the damaging effects of Reactive Oxygen Species (ROS) as studies have reported higher total phenolic contents and ferrous-reducing antioxidant potential in *A. muricata* from nearshore than on the reef during summer at Belle Mare (Louis et al. 2016a,b). In addition, further work to mimic diurnal variation in temperature and light over a longer period of time is also warranted to assess the long-term response to continuous exposure to high-temperature anomalies.

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