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The red coralline alga *Hydrolithon onkodes*, an attractor of coral larvae, is photosynthetically more susceptible to thermal stress than *Lithophyllum incrustans*

MARIE JEAN SYLVIO PERRINE[1,♥], SARVESH MUNDIL[2], DEEPEEKA KAULLYSING[1,2], RANJEET BHAGOOLI[1,2,3,♥♥]

[1]Department of Biosciences and Ocean Studies, Faculty of Science & Pole of Research Excellence, Sustainable Marine Biodiversity, University of Mauritius. Réduit 80837, Republic of Mauritius. Tel./Fax.: +230-4037916, email: ♥perrinsylvio13@gmail.com, ♥♥r.bhagooli@uom.ac.mu
[2]The Biodiversity and Environment Institute. Réduit, Republic of Mauritius
[3]The Society of Biology (Mauritius). Réduit, Republic of Mauritius

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Abstract. *Perrine MJS, Mundil S, Kaullysing D, Bhagooli R. 2023. The red coralline alga* Hydrolithon onkodes, *an attractor of coral larvae, is photosynthetically more susceptible to thermal stress than* Lithophyllum incrustans. *Indo Pac J Ocean Life 7: 91-99.* Red Coralline Algae (RCAs) are important components of coral reefs and are involved in reef-building via calcification, cementation, the synthesis of anti-fouling compounds and of chemicals to aid recruitment, settlement and metamorphosis of reef species. This study aimed to investigate the distribution of RCAs at four sites around Mauritius Island and the effects of thermal stress on the effective photosynthetic yield of photosystem II (Φ_{PSII}) of two species of RCA namely, *Lithophyllum incrustans* (Philippi, 1837) and *Hydrolithon onkodes*, known to attract coral larvae. Out of the nine RCA species observed, two non-geniculate RCAs, *H. onkodes* and *L. incrustans*, were among the most dominant, especially at the lagoonal and reef zones of the four studied sites Flic en Flac, Belle Mare, Trou aux Biches and Flat Island. These two RCAs were collected, acclimated for 24 hours on a 12h:12h dark-light cycle and then exposed to 27°C, 30°C and 33°C for 3 (T_3), 6 (T_6) and 19 (T_{19}) hours. After 3, 6 and 19 hours, relative change in Φ_{PSII} compared to initial (T_0) was used for comparison among tested species. At 27°C the Φ_{PSII} did not fluctuate significantly during the experiment for both RCAs. At a temperature 30°C only *H. onkodes* significantly decreased from 0.541 ± 0.54 at T_0 to 0.445 ± 0.116 at T_{19}. At 33°C, *L. incrustans* showed a significant decline of 24.82 ± 7.4% while *H. onkodes* decreased by 90 ± 12.6%. Visual observations revealed that *H. onkodes* changed from the initial healthy-looking color of light grey to pale purple after thermal exposure. These findings indicate that the coral larvae-attracting *H. onkodes* is more susceptible than the *L. incrustans* to thermal stress, implying subsequent possible impacts on coral recruitment process especially in the wake of climate change-driven ocean warming.

Keywords: PAM fluorometry, photosynthetic parameters, red coralline algae, thermal tolerance

INTRODUCTION

Worldwide mean surface temperature has so far increased by almost 0.87°C in the last one and a half centuries (during the interval 1850-2015) as reported by International Panel on Climate Change (IPCC) and will probably rise more by 3°C by the end of this century (Masso-Delmotte et al. 2018). Rising ocean surface temperature is amongst the chief impacts disturbing marine ecosystems (Stenseth et al. 2002), which can affect the abundance and distribution of marine organisms, and likewise lead the way to extinction of populations situated at the extremity of their thermal tolerance (Sanford et al. 2019). Moreover, a marine heatwave can intensely impact ecosystem function and structure by provoking extensive community, change species range shift and mortality (Jentsch et al. 2007).

Red Coralline Algae (RCAs) are classified in the division Rhodophyta and form part of a distinctive order Corallinales. The deposition of calcium carbonate around and inside the algal thalli and the presence of calcium carbonate in the wall give the thalli a hard and rigid construction which is the main feature of the coralline algae (Richmond 1997). Globally spread, RCAs are considered major components of coastal ecosystem structure and function (Basso 1998). However, few studies have been conducted around Mauritius and its adjacent islands and waters on RCA distribution with species such as *Hydrolithon* sp. and *Renouxia* sp. (Ballesteros and Afonso-Carrillo 1995; de Clerck et al. 2004).

The ecological importance of RCAs varies from playing an essential function as ecosystem engineers of greatly heterogeneous communities (Foster 2001) to being the favored surface for settlement for invertebrate larvae (Williams et al. 2008). Key ecological processes affecting the distribution pattern and abundance of associated species are widely recognized as biotic interactions involving RCAs (Seabra et al. 2019). This interaction can derive from the structure and persistence of communities within a benthic ecosystem (Nelson 2009). Globally, several studies have characterized the significant role of RCAs in the marine ecosystem, for instance, foundation species (Steneck and Dethier 1994), reef frameworks (Adey 1978; Richards and O'Leary 2015), coral larval preference for

RCAs (Elmer et al. 2018) and community structure (Kennedy et al. 2017; Lei et al. 2018; Schoenrock et al. 2018). RCAs strengthen the skeletal structure of the non-living coral and seal fissure in the reef substratum, thus sustaining topographic complexity and decreasing reef erosion (Fabricius and De'ath 2001). RCA can be primary reef builders that provide a substrate for settlement for additional organisms (Elmer et al. 2018). RCAs are characteristically believed to improve recruitment or trigger metamorphosis of larvae of further species through contributing biochemical cues (O'Leary et al. 2012) or by offering enough structural heterogeneity. These strategies are vital for the invertebrate communities' diversity in the tropic and temperate regions (McCoy and Kamenos 2015).

However, with an increase in temperature, calcification and growth rate of RCAs rise within the array of normal environments (Basso 2012) and above these optimal thermal levels, heating is harmful and causes narcosis and death. Some studies have explored the effect of temperature on RCA where one study carried out showed that after being kept at 32°C for 7 days, RCAs clearly showed signs of bleaching and the makeup of biofilm on the surface of the RCAs had significantly changed (Webster et al. 2011). Despite various studies demonstrating that RCAs are sensitive to rise in temperature, no study has defined the upper, lower and optimal photosynthetic temperature of tropical RCAs. Moreover, no study has documented the effect of steadily increasing temperature on non-geniculate RCAs, under current and predicted climate change scenarios. It is noteworthy that limited studies on RCAs have been conducted around Mauritius in the Western Indian Ocean, though studies on other macroalgae of the Republic of Mauritius have been documented (Bolton et al. 2012; Somanah et al. 2012; Mattio et al. 2013; Ramah et al. 2014, 2021a,b; Kaullysing et al. 2016; Bhagooli and Kaullysing 2019; Gopeechund et al. 2020; Bhagooli et al. 2021a,c,d; Narrain et al. 2023). To explore the effect of temperature on the photo-physiology of non-geniculate RCAs, two species were used to assess the photo-physiological thermal tolerance in laboratory-based experiments.

Despite the importance of RCAs, their sensitivity to increasing temperature is unclear (Martin et al. 2013). Therefore, it is worth understanding the biological response of climate-sensitive organisms to short-term change (Jentsch et al. 2007). The study's objectives were to expose the two fresh acclimated species of RCA to short temperature stress to test their tolerance and to use a Pulse Amplitude Modulated (PAM) fluorometer to determine the effective photosynthetic yield of photosystem II (Φ_{PSII}). The temperature was ramped up from 27°C to 33°C to get an insight into its impact on the photosynthetic activity due to heat stress.

MATERIALS AND METHODS

Distribution of RCAs and corals

The study was carried out at three zones, namely, near-coast, lagoon and reef at four sites, Belle Mare (BM), Trou aux Biches (TB), Flic en Flac (FEF) and Flat Island (FI) around Mauritius (Figure 1). The water depth ranged from 1-1.7 m at low tide. Three transects each of 20 m length were laid parallel to the reef at the near-coast, lagoon and reef zones. Quadrats of 50 cm x 50 cm were placed at random intervals on the left and right of the line transect of 20 m and RCAs and corals were recorded using video transect method (Leujak and Ormond 2017). Video recording at a speed of 7 m/minutes at an angle of 45° and in situ photos of the RCAs were captured using a digital Olympus TG5 camera by snorkeling. The percentage of RCA cover, dead and live coral cover were determined through the video survey.

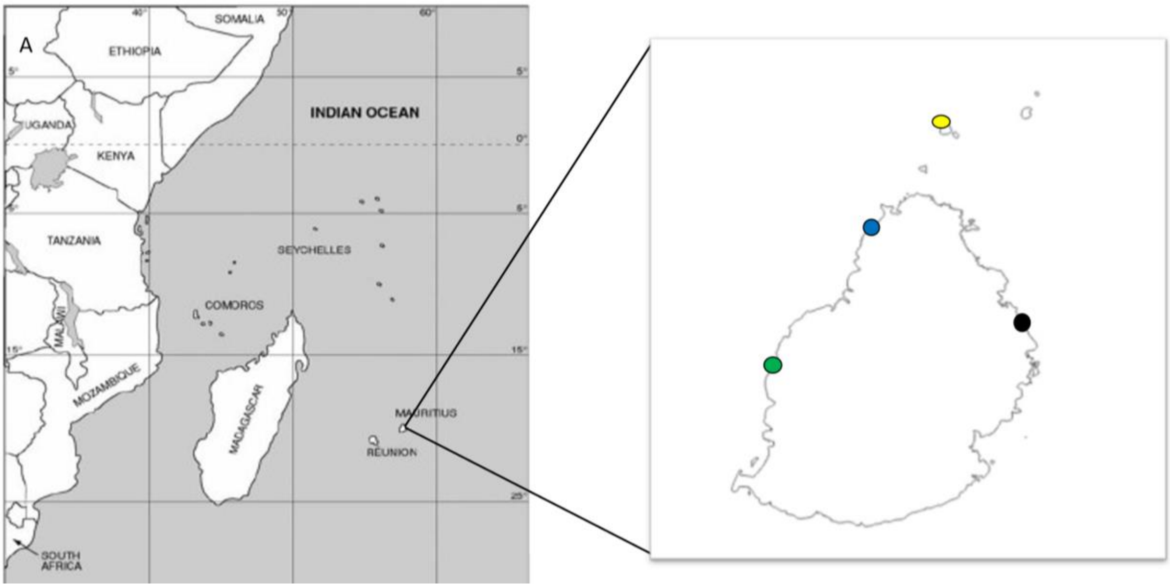

Figure 1. A. map of Indian Ocean showing location of Mauritius. B. Map showing studied areas: Belle Mare (*black*), Trou aux Biches (*blue*), Flic en Flac (*green*), and Flat Island (*yellow*)

Field surveys were carried out in October and November 2019, and January and February 2020. The lagoon and reef zones are rather flat, with similar exposure to light and RCA samples were harvested in-depth ~ 1.2 m in lagoon and ~ 1 m in reef zone using hammer and chisel and/or handpicked from the four sites while snorkeling. The samples were preserved in seawater from the station during transportated to the laboratory. RCA samples were preserved at-20°C for subsequent identification under a light microscope according to Woelkerling et al. (1993).

Sampling of RCAs for thermal experimentation

Fragments from two species of RCAs, namely, *Lithophyllum incrustans* (Philippi, 1837) and *Hydrolithon onkodes* ((Heydrich) D.Penrose & Woelkerling), known to attract coral larvae, were collected on the same day during early hours using a blade at depths not exceeding 1.5 m at BM. Following collection, the two species of RCAs were inserted in a clear plastic bag with seawater and were maintained in ambient collection conditions by placing them in a covered container filled with seawater while transportation to the laboratory. The two RCAs were transferred to aquaria in the laboratory within one hour of collection and were acclimated for 24 hours with continuous air supply.

Laboratory thermal stress experiment

The effect of temperature on photosynthetic yield of photosystem II (Φ_{PSII}) of the two RCAs were experimentally investigated. Nine aquaria were used and were arranged in a set of three rows labelled with temperature 27°C (control), 30°C and 33°C. Both species were placed in all aquaria containing seawater at a salinity 34 ppm and the temperatures were ramped up to 30°C and 33°C within 3 hours. The temperature of each aquarium was controlled constantly using thermostats 50W aquarium heater (Eco-therm, aquarium system). The temperature was checked regularly and monitored using a hand-held thermometer. Each aquarium was aerated to maintain a constant oxygen and a homogeneous temperature condition. The control was set at room temperature (~27°C) and the treatments were set at 30°C and 33°C, and after that a constant temperature was maintained in the respective aquaria.

Chlorophyll-*a* fluorescence measurement

The effective quantum yield at photosystem II (Φ_{PSII}) was determined using a Diving-Pulse-Amplitude-Modulated (PAM) fluorometer (Bhagooli et al. 2021b). A saturating pulse of 4000 μmol quanta m^{-2} s^{-1} was applied by placing a 5 mm fiber optic probe on the thallus and a weak light emission of <1 μmol quanta m^{-2} s^{-1} was used to measure the maximum (F_m) and minimum (F_t) fluorescence, respectively. The Φ_{PSII} was then calculated as follows (Genty et al. 1989):

$$\Phi_{PSII} = (F_m - F_t)/F_m = \Delta F/ F_m$$

Initial observations were made and readings taken (T_0) prior to the RCAs being placed in the respective treatments. Further readings were taken after 3 (T_3), 6 (T_6) and 19 (T_{19}) hours after exposure to the thermal conditions.

Statistical analysis

Statistical analysis was conducted in SPSS. First, all data were tested for normality using the Shapiro-Wilk test (data was normally distributed P value>0.05). One-way ANOVA and Post Hoc Tests were performed to determine whether zones influenced growth form distribution at each site studied. One-way ANOVA was also carried out to investigate the effect of temperature and exposure period on the effective quantum yield of the two species of RCA. Finally, Principal Component Analysis (PCA) was performed on the data related to species distribution of RCA found occurring at the study sites in Mauritius to investigate their correlation.

RESULTS AND DISCUSSION

Distribution of substrate, corals, and RCAs around Mauritius

The coastal substrate was dominated by live coral (65.9±4.55%) at BM and coral rubble was at 5.00±0.29% (Figure 2A). The same tendency was found in the lagoon with 26.0±1.45% live coral and 1.40±0.8% coral rubble. On the reef, sand dominated by 15.2±1.64% and dead coral stand was the least at 3.4±0.74%. At FEF, the dominant substrate at the coastal zone was sand at 35.5±6.09% and the coral rubble was the lowest at 14.1±1.31%. Sand was dominant in the lagoon with 11.5±6.09% and dead coral stand with macroalgae (DCS+MA) the least at 3.20±1.88%. On the reef there was a dominance of DCS+MA with 14.9±3.32% and DCS was lower at 4.20±2.72%. Coastal substrate at TB was dominated by sand at 28.0±4.31% and DCS+MA was least at 1.40±0.73%. Live coral had the highest percentage cover of 16.7±9.53% in the lagoon and DCS was the lowest at 0.90±0.62%. Data indicated a dominance of live coral cover at the reef with 22.2±6.69% and DCS was the lowest at 0.80±0.40%. Flat Island coastal zone was dominated by sand with a percentage cover of 26.0±5.25% and live coral the lowest at 5.6±3.70%. In the lagoon, sand had the highest percentage cover with 9.0±3.82% and DCS+MA was at 4.37±4.0%. The reef substrate was dominated by sand at 10.7±1.91% and DCS+MA was at 5.4±0.78%.

PCA results indicated that *L. kotschyanum*, *L. incrustans* and *Phymatolithon purpureum* were most dominant at TB (Figure 2B, Table 1). The *H. gardineri* was most dominant at FEF but least dominant at BM. The *H. onkodes* was most dominant at FI. The RCAs were higher in the lagoon and reef sites compared to the coastal zones at all the four study sites (Figure 3A). The RCAs varied in composition among the sites with a single species occurring at the coast of BM and six species at the lagoon of FEF and TA out of the total of 11 species of RCAs observed around Mauritius (Figure 3B). Only one species of non-geniculate RCA, *H. onkodes* was found growing in near-coast at BM. Four Species were recorded in the lagoon, namely, *H. gardineri*, *H. onkodes*, *L. incrustans* and *P. purpureum*, and six species were recorded on the reef: *H. gardineri*, *H. onkodes*, *L. incrustans*, *L. kotschyanum*, *L. cabiochae* and *P. purpureum*. From the five genera, seven species of RCAs were recorded at Flic en Flac. Four species were identified in the near-coast zone: *P. purpureum*, *L. incrustans*, *H. onkodes* and *H. gardineri*. Five species, namely, *H. gardineri*, *H. onkodes*, *L. incrustans*, *L. kotschyanum* and *Phymatolithon* were found occurring in the lagoon and reef zones. At TA, four species, *H. gardineri*, *H. onkodes*, *L. incrustans* and *P. purpureum*, were recorded at the near-coast zone. Six species were observed in both lagoon and reef zones at TB. Six species were observed at the reef zone at FI: *H. gardineri*, *H. onkodes*, *L. incrustans*, *L. kotschyanum*, *P. purpureum*, and *L. laevigatum*.

Table 1. PC loading for the PCA

	RCA species				
Sites	***H. gardineri***	***H. onkodes***	***L. incrustans***	***L. kotschyanum***	***P. purpureum***
BM_C	0.00	100.00	0.00	0.00	0.00
BM_L	6.90	65.52	17.24	0.00	6.90
BM_R	17.78	33.33	24.44	2.22	6.67
FEF_C	49.15	11.86	22.03	0.00	16.95
FEF_L	25.71	17.14	28.57	5.71	17.14
FEF-R	26.32	18.42	26.32	5.26	21.05
TB_C	7.55	24.53	41.51	0.00	26.42
TB_L	10.87	19.57	28.26	8.70	23.91
TB_R	8.62	20.69	39.66	5.17	15.52
FI_C	7.14	42.86	21.43	3.57	25.00
FI_L	6.02	45.78	26.51	2.41	19.28
FI_R	6.45	41.94	33.87	1.61	12.90

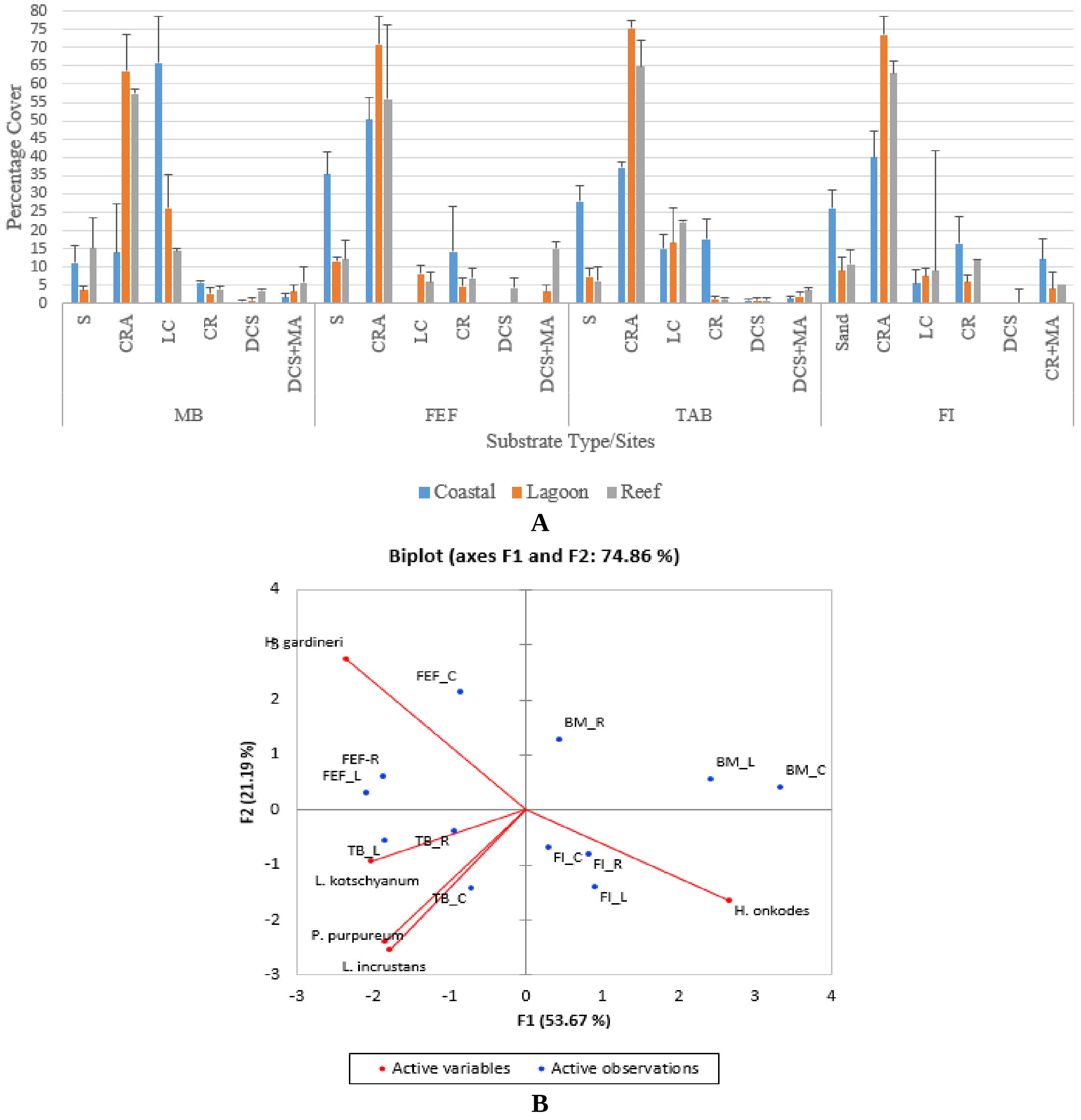

Figure 2. A. Distribution of substrate and biota at Belle Mare (BM), Flic en Flac (FEF), Trou aux Biches (TAB), and Flat Island (FI) around Mauritius. Coralline red algae (CRA), live coral (LC), Coral rubble (CR), Dead coral stand (DCS) and dead coral stand with macroalgae (DCS+MA). B. Principal Component Analysis (PCA) for RCAs for four sites around Mauritius Island

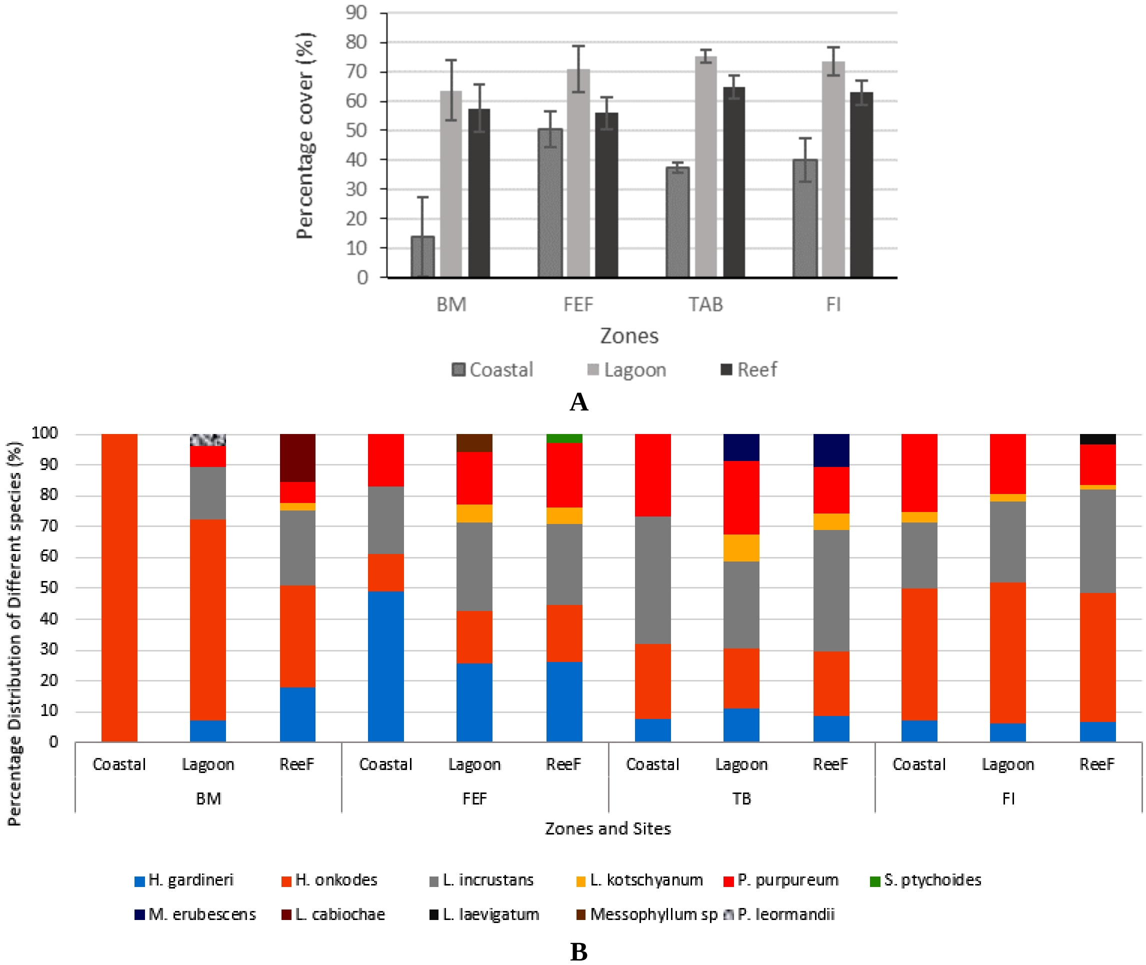

Figure 3. A. Distribution of Red Coralline Algae (RCAs) in terms of percentage cover (Mean ± SD, n=3) and B. RCA species at the four studied sites around Mauritius Island

Chlorophyll-*a* fluorescence thermal responses of *H. onkodes* and *L. incrustans*

The effective quantum yield at PSII (Φ_{PSII}) decreased significantly after 6 hours (P=0.0027) and 19 hours (P=0.002) at both 30°C and 33°C treatments in *H. onkodes* when compared to 27°C treatment, which remained unchanged during this exposure period (P>0.05) (Figure 4A). While in *L. incrustans*, Φ_{PSII} decreased significantly only at 33°C after 19 hours (P= 0.044) of treatment (Figure 4B). Relative changes indicated insignificant changes in 27°C treatment (P>0.05) for both RCAs throughout the experimental period (Figure 5A). At 30°C, only Φ_{PSII} in *H. onkodes* decreased by approximately 20% (Figure 5B), while at 33°C after 19 hours, Φ_{PSII} decreased by 20% and 98% in *L. incrustans* and *H. onkodes*, respectively (Figure 5C).

Visual observations of thermally treated RCAs

Both RCAs at 27°C showed no signs of visual bleaching and the healthy color was maintained throughout the experiment. At 30°C, *H. onkodes* exhibited a change in color from grey-white to an uneven pale-purple across all specimens in the aquaria after approximately 10 hours of exposure, whereas after only six hours of continuous exposure to 33°C, a change in color was observed in all specimens of *H. onkodes*. After 19 hours of exposure, specimens of *H. onkodes* in both 30°C and 33°C had visible signs of visual bleaching where a pale-purple color was observed in all specimens (Figure 6). On the other hand, *L. incrustans* showed a slight change in color at 33°C after 19 hours of exposure and no apparent changes in specimens exposed to 27°C and 30°C conditions (Figure 7).

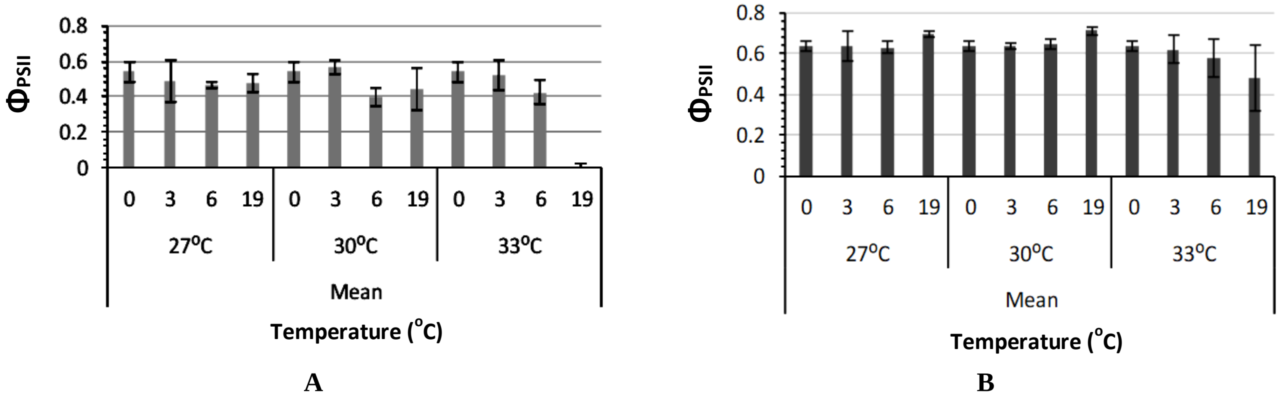

Figure 4. Effective quantum yield at PSII (Φ_{PSII}) in *Hydrolithon onkodes* (A) and *Lithophyllum incrustans* (B) exposed at 27°C, 30°C and 33°C for a period of 19 hours

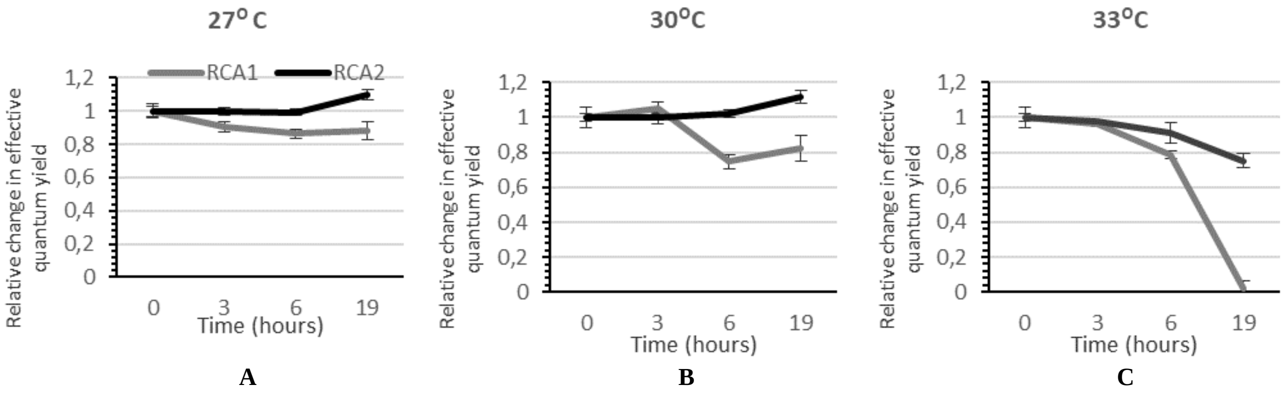

Figure 5. Relative (to initial) changes in Φ_{PSII} in *H. onkodes* (RCA1) and *L. incrustans* (RCA2) at 27°C, 30°C and 33°C exposures (Mean ±SD, n=3)

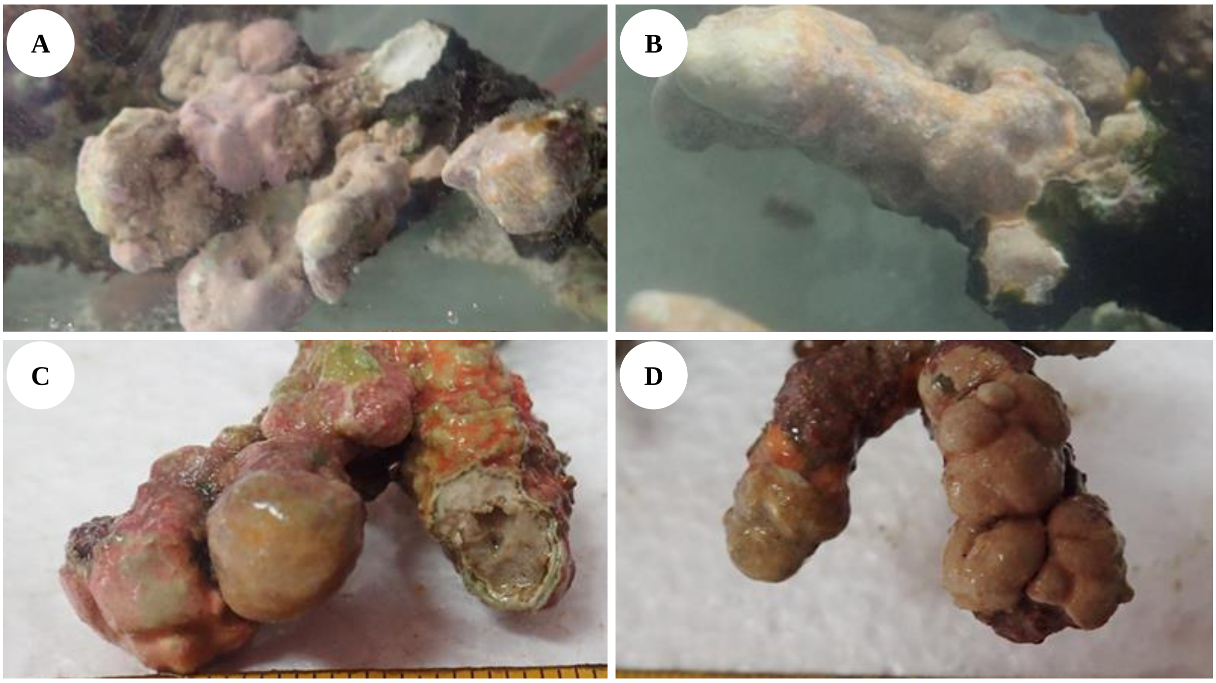

Figure 6. Visual observation of colors before and after thermal experimental trials on RCA *H. onkodes*. Color observed: (A) Healthy color before experiment, color following 19 hours treatment at (B) 27°C, (C) 30°C and (D) 33°C

Figure 7. Visual observation of colors before and after thermal experimental trials on RCA *L. incrustans*. Color observed: (A) Healthy color before experiment, color following 19 hours treatment at (B) 27°C, (C) 30°C and (D) 33°C

Discussion

Distribution of Red Coralline Algae around Mauritius Island

Historically, research on RCAs in the Republic of Mauritius has been overlooked. Nevertheless, some work has been carried out on Mauritius's main island, for instance, by Ballesteros and Alfonso-Garrillo (1995). In the present study, non-geniculate RCAs that lack a non-calcified segment in the middle of the calcified segment were the most abundant species on hard substrate in all zones. Results indicated that areas covered by sand were most common in the near-coast zone of all studied sites and lagoon zones. Consequently, poor distribution of RCAs was observed in these zones, owing to loose substrate type. A similar observation was made by Lei et al. (2018), showing the influence of the sand substrate on the distribution of RCAs. All the species identified in Mauritius occur either on dead coral (broken and dead stand) or as epizoic (on dead or living gastropods). *Hydrolithon* has been found as epiphytes on seagrass in the lagoon area at BM. This supports the finding of several authors (Bramwell and Woelkerling 1984; Payri et al. 2001; Woelkerling et al. 1993) who have reported species of *Hydrolithon* to be common epiphytes on seagrasses in various regions worldwide. Lagoon and reef zones of almost all studied sites were observed with good live coral cover and coral rubble, thus, the distribution of RCAs was higher due to substrate type. Consequently, RCAs were widely distributed at the lagoon and reef zones at all studied sites with abundant hard substrates. Kroeker et al. (2013) reported a similar observation, demonstrating the importance of hard substrate availability for growth and distribution.

Non-geniculate RCAs dominated all studied sites in sheltered areas and exposed reef flats except at FEF. Geniculate RCAs were higher in all near-coast zones (5.85±41.00%), lagoon (2.66±59.10%) and reef (2.25±28.10%). Similarly, Ballesteros and Alfonso-Carillo (1995) reported that non-geniculate RCAs were dominant at Trou d'Eau Douce, Mauritius, overgrowing different hard substrate types. The highest distribution of RCAs was observed on hard substrate on *Acropora*, with genera *Hydrolithon* and *Lithophyllum* being the most dominant species. The *H. onkodes* was found to be abundant on dead over-turned tabular *Acropora*, and many coral recruits were observed. This supports the finding of several authors (Adey et al. 1982) who have reported *Hydrolithon* as the main reef-building RCA.

Sessile organisms' recruitment is a vital ecological process that impacts the organization and conservation of ocean communities by effectively spreading and settling movable gametes. Therefore, larval settlement is a crucial stage in the life cycle of various invertebrates, for instance, reef-building coral. Specific compounds induce coral larval settlement, for example morphogens (Gomez-Lemos et al. 2018). Documented three decades ago, it was revealed that RCA was a crucial group of benthic communities whose chemical compounds play an imperative role as inducers for marine invertebrates larvae, including corals. Therefore, the high abundance of non-geniculate RCAs at the different studied sites clearly indicates that natural regeneration will occur. However, any disruption to interaction is of particular concern to the recruitment success of coral. Coral recruits *Hydrolithon* spp. have well been observed at many studied sites, mainly BM in Mauritius. Similar findings were reported by authors (Birrell et al. 2008; Elmer et al.

2018), who have documented coral larval settlement and recorded to enhancement rate of settlement of larvae of coral on *Hydrolithon* spp. This research provides a geographically substantial assessment of the community structure of RCA in the east, west and north of Mauritius.

Knowledge of the different non-geniculate in Mauritius sustaining the mechanisms driving coral larvae-microbe-plant interaction and the influence of RCA on initial life history processes of coral larvae will enable a sound understanding of drivers of reef retrieval succeeding disruption.

Thermal tolerance experiment coralline red algae

The RCAs respond differently to PAM fluorometry techniques compared to other algae owing to the presence of phycobilisome in their photosynthetic apparatus (Burdett et al. 2012). The *L. incrustans* and *H. onkodes* are non-geniculate RCAs essential to the coastal ecosystem and functions. The laboratory thermal study results demonstrated the adverse effect of elevated temperature on RCA photo-physiology *L. incrustans* and *H. onkodes*; the latter was more affected among the two species studied. It was observed that raised temperature gave rise to continuous photodamage build-up, evidenced by a significant progressive decrease in effective quantum yield throughout the study in the two species. No build-up of photodamage was detected in the control treatment 27°C, suggesting that the experimental seawater situations were ideal, and the two RCAs were well photo acclimated to their corresponding temperature environments.

At temperature treatment 30°C PAM measurement demonstrated a continuous increase in photo-physiology for *L. incrustans*. This can be explained as a temperature-enhanced metabolic rate through increased enzyme activity. After exposure to temperature stress 33°C for 3 hours, PAM records demonstrated significant losses in effective quantum yield associated with photodamage enhancement, which was principally noticeable for the *H. onkodes*. Thus, *L. incrustans* has more thermal adaptation than *H. onkodes*. These findings indicated that heat-induced photodamage was significantly worsened under raised heat in *H. onkodes*. This result highlights the major role of heat stress in the gravity of the effect of global warming resulting in rising seawater temperature on RCA performance, consistent with former results documented for some RCAs. However, it is not necessarily signifying that ocean warming will have an unlimited impact on all RCA species, initially, certain species are eventually more susceptible than others. At 19 hours, the *H. onkodes* was bleached to pale purple, followed by necrosis and eventually death. This finding is in line with other authors reported that bleaching causes loss of photosynthetic pigment and, in several cases, may lead to necrosis (Martone et al. 2010) and an increase of temperature 2-4°C above the seasonal maxima causes approximately 90% bleaching. However, the outcome of upcoming climate change will depend on the ability of a species to adapt or acclimatize over various generations rather than short-term responses measured in nearly all laboratory research. The outcomes of this study not only highlighted the impact of rising seawater temperature due to global warming but reinforced the importance of non-geniculate communities in contributing to coral reef ecosystem maintenance by assisting in the regeneration of disrupted areas through enhancing coral larval settlement, particularly reef-building coral.

This investigation showed that some differences exist between species living under similar depth conditions and consequences of changes in temperature of the marine environment on *H. onkodes*. These findings have implications for coral recruitment on degraded reefs and need more attention to better manage the resilience and recovery of coral reefs.

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