Physiological responses of scleractinian corals in marginal habitat

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Abstract. *Polapa FS, Werorilangi S, Ali SM, Jompa J. 2021. Physiological responses of scleractinian corals in marginal habitat. Biodiversitas 22: 4011-4018.* This study aims to analyze physiological differences in corals in marginal habitats. Under different conditions, the production/respiration (P/R) ratio and photobiology of various coral genera were compared. Samples were taken from three coral reef zones representing typical reef habitats and from the mangrove ecosystem as a marginal habitat. Surveys revealed two coral genera surviving in extreme conditions (marginal habitat). The P/R ratio measurements indicated that corals living in the mangrove ecosystem tend to be heterotrophic. This was supported by observations of colonies with tentacles extended from the corallites. Furthermore, *Porites* living in the mangrove habitat consume more O^2 directly than saving it for other purposes, such as growth. The genus *Dipsastraea* exhibited elevated zooxanthellae density in the mangrove ecosystem, whereas *Porites* exhibited similar densities in both ecosystems.

Keywords: Coral reef, Mangrove, P/R ratio, photobiology, physiology

INTRODUCTION

Understanding the ability of corals to withstand high environmental pressures is not as advanced as knowledge regarding the important role of coral reefs. Coral reefs provide habitats for many marine organisms, and are a major source of income through subsistence, commercial, cultural and recreational fishing activities as well as dive-based tourism and the recreation industry (Weijerman et al. 2016).

Despite their recognized importance, coral reefs are under threat. Several coral species are categorized as Endangered (EN) in the IUCN Red List (IUCN 2021). Coral reefs are directly affected by anthropogenic activities through pollution and overfishing (Hughes et al. 2019) in addition to indirect impacts from increasing carbon dioxide emissions (Masson-Delmotte et al. 2018), rising temperatures (Rooke et al. 2017), and decreasing seawater pH (Chan and Connolly 2013). Recognizing the severity of these threats, much research has been devoted to seeking solutions.

Several studies have found corals that can survive in conditions outside the limits considered "normal", in habitats referred to as "marginal" (Yamano et al. 2011; Beger et al. 2014; Yates et al. 2014; Camp et al. 2016; Camp et al. 2018). Marginal habitats have been proposed as one alternative type of future refugia for coral reefs (Yamano et al. 2011). Marginal reefs can also be categorized as extreme reefs with their own unique ecological aspects (Yamano et al. 2011; Camp et al. 2018), composed of ecologically and functionally distinct reef communities (Soares 2020).

In many tropical waters, coral reef ecosystems coexist or are associated with seagrass and mangrove ecosystems. Although mangroves are often considered unsuitable for coral growth due to high sedimentation, lack of substrate for coral attachment and unsuitable water quality for recruitment and coral growth, Yates et al. (2014) found coral species living in a mangrove ecosystem; these corals were able to survive in harsh or marginal habitat conditions including relatively low pH levels with fluctuations in temperature and light.

Understanding how corals can withstand high environmental pressures can help to predict how things will be in future coral reef ecosystems (Camp et al. 2016). Furthermore, marginal habitats may provide coral species or strains selected to survive in future conditions, and thus help with efforts to ensure the survival of coral reefs (Morikawa and Palumbi 2019; Schoepf et al. 2019). Hoga Island and Kaledupa Island, located within the Wakatobi Marine National Park, Southeast Sulawesi, Indonesia, have extensive coral reef and mangrove ecosystems, making this area appropriate as a site for studying marginal corals. Therefore, the purpose of this study was to analyze physiological differences between corals found in typical coral reef habitats and in the mangrove ecosystem (a marginal habitat); determine the distribution of corals in different natural conditions; and examine the adaptation processes of corals living in mangrove habitat.

MATERIALS AND METHODS

Study area

The research was conducted from 27 June to 31 July 2018 on Wakatobi District, Southeast Sulawesi Province, Indonesia; i.e. (i) the coral reef slopes off Hoga Island (123°45'20.68"E /5°28'6.76"S); and (ii) a nearby mangrove ecosystem of Kaledupa Island (123°43'26.87"E /5°28'17.32"S) (Figure 1). Laboratory tests were conducted at the Operation Wallacea Research Centre (OPWALL) Wet Laboratory on Hoga Island.

Data collection

Coral distribution

Data were collected from four habitats, three representing the reef ecosystem (Reef Slope, Reef Crest and Reef Flat) and one representing the mangrove ecosystem, using SCUBA diving equipment in the reef ecosystem and snorkeling equipment in the mangrove ecosystem. Coral distribution data were collected with taxonomic identification to genus level using a modified belt transect method. Each belt transect was 20 m long x 2 m wide with five replicates placed 10 m apart at each survey location (habitat). For the photography data collection using a Canon G7x camera. Measurement using a 1 x 1 m square placed on each side of the centerline of the transect with 40 replicates of each 20x2 transect. each coral in quadrant is identified to genus level using well-known coral identification guide (Veron and Pichon 1982). The data were then analyzed to determine which genera were found in all of the observed habitats.

Surface area measurement

Colonies of the genera found in all habitats were measured to examine the variation in coral colony size between the two ecosystems. Some aspects of the physical and biological processes of a coral colony can be determined by measuring the area of the colony (Veal et al. 2010). These data were obtained by measuring the length, width and height of each coral colony. Measurements were also collected using 20 x 2 belt transects with five replicates per habitat.

P/R ratio

Physiological parameters were measured to examine the differences in coral physiological responses between the two different ecosystems. In this study, the parameters measured were the production/respiration (P/R) ratio and photobiology (zooxanthellate density). Coral samples were collected using a hammer and chisel. The research targeted larger coral colonies to provide specimens with a minimum area of 10 cm^2. A minimum of five colonies from each genus was collected from each ecosystem. The mangrove habitat samples were collected at a depth of around 1m and the coral reef habitat samples were collected from the reef slope at a depth of around 7m.
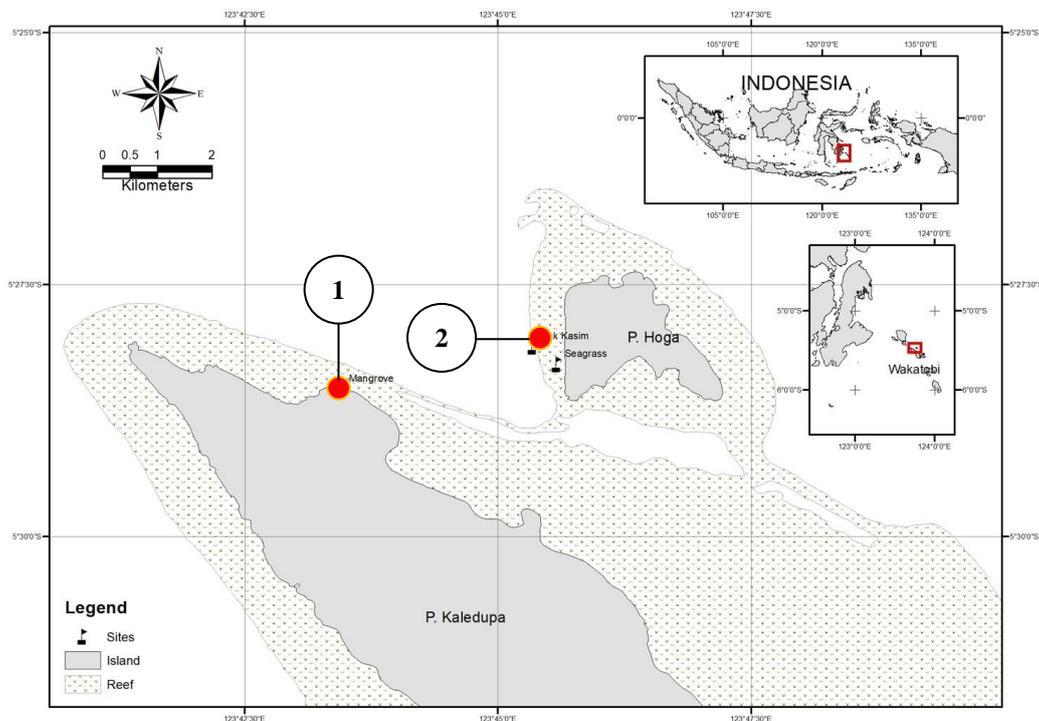

Figure 1. Map of Hoga Island and Kaledupa Island, Wakatobi District, Southeast Sulawesi Province, Indonesia showing the study sites: 1. Mangrove site; 2. Coral site

Each coral sample was placed in a container filled with sterile seawater. Net primary production (NPP) and respiration (R) values were obtained through measuring oxygen levels using dissolved oxygen (DO) vernier optode (Make, model) placed into each container together with a Magnetic Stirbar to ensure homogenous conditions around the sensor. DO was measured every 16 seconds for 40 minutes. The NPP value was obtained from measurements made in light conditions, while the value of R was obtained from measurements made in dark conditions through analyses performed in Microsoft Excel 2019.

Photobiology

Photobiology data were obtained by calculating the density of zooxanthellae in each colony. Zooxanthellae were sampled by spraying coral samples with filtered seawater using an airbrush (Make, model). Samples were observed under a microscope (make, model) with the help of a hemocytometer (make, model). The density of zooxanthellae was obtained from the sampled area, the volume of seawater and the hemocytometer count. The area sampled was measured using the Image J application (add reference).

Environmental parameters

The environmental parameters measured in this study were temperature and light intensity, with data being collected by HOBO pendant temperature/light loggers. Placed in each ecosystem. In each ecosystem, the loggers were placed at the location where the coral colony samples were collected (at a depth of 7 m on the coral reef slope and 1 m in the mangrove habitat). Data were automatically collected by the loggers every 15 minutes over an 8 day observation period.

Data analysis

The data were tabulated and analyzed descriptively. Differences between habitats (ecosystems) were evaluated using the Student's t-test at the 95% confidence level ($\alpha = 0.05$). Analyses were implemented in Microsoft Excel 2016.

RESULTS AND DISCUSSION

Coral distribution

We found 39 genera of coral across the 4 habitats, with a total of 2722 colonies recorded (Table 1). In the three reef habitats, 2671 colonies were found, comprising all 39 genera. 1645 colonies from 36 genera were found in the reef crest habitat, while 983 colonies from 39 genera were found on the reef slope, and 43 colonies from 8 genera on the reef flat. *Porites* and *Montipora* were the dominant genera across all three reef habitats. In the mangrove habitat, 51 colonies were found, representing just 2 genera: *Dipsastraea* and *Porites*. *Dipsastraea* was the dominant genus found in the mangrove habitat, while only 3 *Porites* colonies were recorded. These two genera were the only genera found across all study sites, with *Porites* being the most common genus in reef habitats, with 843 colonies

across the three reef zones. A review by Yates et al. (2014) found 30 species of coral reported from mangrove habitats in the Virgin Islands. These included four species of *Porites* but no *Dipsastraea*; the latter is an Indo-pacific genus (Huang et al. 2014) and is therefore not found in the Caribbean.

Surface area

Coral colonies of two genera were found in both reef and mangrove ecosystems: *Porites* and *Dipsastraea*. Most *Porites* colonies in the research area measured less than 75 cm^2 in area (Figure 2). In the mangrove ecosystem, all three *Porites* had an area below 50 cm^2. Colony size ranged from small (0-25 cm^2) to large (11,792 cm^2) colonies in the coral reef habitat. The most commonly occurring colony size class was 26-50 cm^2, with 89 colonies recorded.

Table 1. Coral colonies recorded by genus and habitat

Coral genus	Slope	Crest	Reef flat	Mangrove
Porites	225	604	14	3
Dipsastraea	46	137	1	48
Acropora	61	30		
Astreopora	3	5	3	
Caulastrea	1	1		
Coeloseris	14	56		
Cyphastrea	6	26	1	
Diplostrea	12	16		
Echinophyllia	8	5		
Echinopora	7	5		
Euphyllia	1	1		
Favia	31	54		
Fungia	32	107		
Galaxea	31	13		
Gardineroseris	1	1	5	
Goniastrea	12	19		
Goniopora	31	54		
Hydnophora	1			
Isopora	1			
Leptastrea	11	15		
Leptoseris	12	13		
Lobophylia	3	2		
Merulina	3	14		
Millepora	23	3		
Montastrea	7	9	4	
Montipora	229	188	13	
Mycedium	8	18		
Oxypora	2	2		
Pachyseris	11	26		
Pavona	63	128		
Pectinia	5	12		
Physogyra	5	5		
Platygyra	12	19		
Plerogyra	1	1		
Pocillopora	41	38	2	
Psammocora	1			
Stylophora	13	4		
Symphyllia	7	5		
Turbinaria	2	9		
Totals number of genera	39	36	8	2

Dipsastraea colony size class distributions were similar for the two ecosystems, with most colonies below 150 cm^2 in area (Figure 3). In the mangrove habitat, the largest *Dipsastraea* colony was in the 451-475 cm^2 class, while the maximum colony size in the coral reef habitat was 375 cm^2. The 26-50 cm^2 class had the largest number of colonies for the mangrove (n=10) and coral reef (n=23) habitats.

P/R ratio

Gross Production (GP) is the total amount of oxygen (O^2) generated by the photosynthesis process. Respiration (R) is amount of O^2 used for the respiratory process. This is expressed as mg O^2/hour. Net Primary Production (NPP) is the amount of oxygen (O^2) generated by the photosynthesis process after subtracting the O2 used in respiration (NPP = GP - R). The mean values of NPP and R were found to be higher in *Dipsastraea* than in *Porites* (Figure 4). Colonies from the mangrove habitat had a P/R ratio below 1, as did *Dipsastraea* colonies from the coral reef habitat, while *Porites* colonies from the coral reef habitat had P/R ratios close to or higher than 1 (Figure 5).

The P/R ratio is used to evaluate the effectiveness of key biological processes within organisms, especially those that co-exist with animal symbionts (McCloskey and Muscatine 1984). If the ratio is higher than one, the organism is considered to be an active net producer and effective autotroph. The results show corals found in both habitats had values below 1, except for the *Porites* colonies from the coral reef ecosystem. Although symbiont-produced energy can be altered substantially to meet the variable demands of a shifting environment (Burmester et al. 2018), these low P/R values suggest that the corals sampled tend to be heterotrophic.
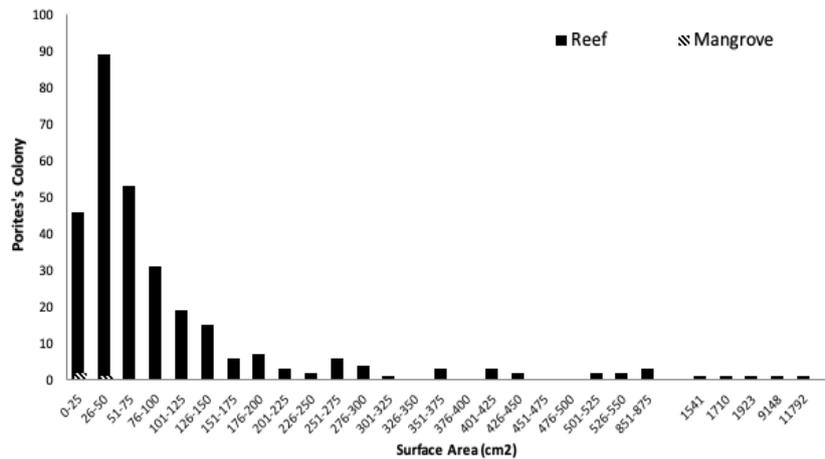

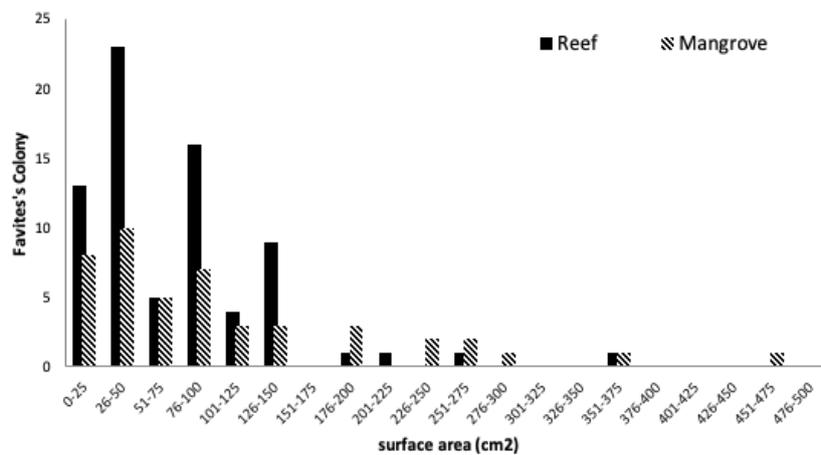**Figure 2**. Surface area of *Porites* colonies recorded in coral reef and mangrove habitats

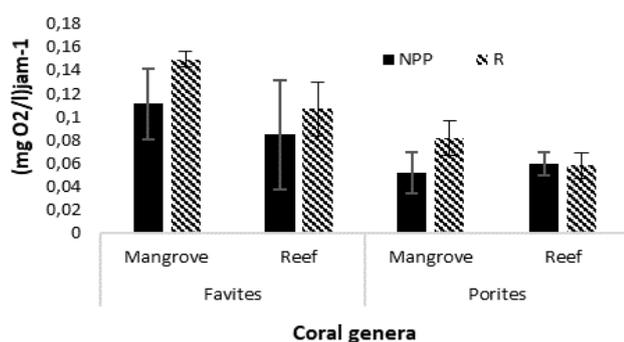**Figure 3**. Surface area of *Dipsastraea* colonies recorded in coral reef and mangrove habitats

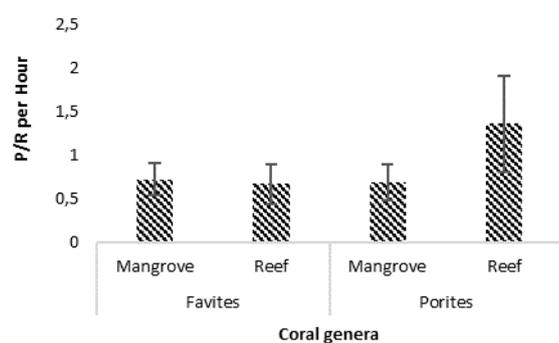**Figure 4.** Ratio NPP and R of *Porites* and *Dipsastraea*

Figure 5. Ratio P/R of *Porites* and *Dipsastraea*

Zooxanthellae density

Corals with symbiotic zooxanthellae can obtain their energy source in various ways. For example, when energy is obtained from photosynthesis they function as autotrophs, whereas if they obtain energy through predation they function as heterotrophs (Fine et al. 2002). Photosynthesis by the zooxanthellae can generally provide all or most of the energy needed by corals (Palardy et al. 2008). Of the two observed genera from two habitats, *Dipsastraea* from the mangrove habitat had a higher density of zooxanthellae than congeners from the coral reef habitat, while Porites had similar mean densities of zooxanthellae in both habitats (Figure 6).

Dipsastraea colonies in mangrove ecosystems had higher densities of zooxanthellae but relatively similar P/R ratios. Conversely, *Porites* from the two habitats had similar densities of zooxanthellae but higher P/R ratios in the coral reef habitat than in the mangrove habitat.

Changes in environmental conditions may cause an organism to adapt to the new conditions. In particular, corals that live in marginal environments (e.g. mangroves) may have different responses (Keshavmurthy et al. 2020). The results indicate that one form of adaptation adopted by corals in marginal conditions can be to increase the number or density of zooxanthellae present in the coral tissue. Furthermore, during this study corals living in the mangrove habitat were observed with tentacles extended from the corallites during the daytime, a behavior that was not observed in the reef habitats.

Parameters

Light intensity

Light is an important factor in the coral-zooxanthellae symbiosis because it is related to the photosynthesis processes carried out by zooxanthellae (Schutter et al. 2012; Wijgerde et al. 2012; Rocha et al. 2013). The result of photosynthesis is one of the main energies for coral life (Hoogenboom et al. 2006). Measurement of light intensity (Figure 7) was carried out every 15 minutes for 8 days at two locations (coral reefs and mangroves). The data shows that the temperature of mangroves has high fluctuations, ranging from 26°C to 30°C, the temperature of coral reefs is more stable, ranging from 27°C to 28°C.

Temperature

Temperature observations recorded every 15 minutes for 8 days in the coral reefs and mangrove habitats (Figure 8) show that temperature ranged from 26°C to 30°C in the mangrove habitat and 27°C to 28°C in the coral reef habitat.

Research on species adaptation to environmental changes has been carried out, particularly on temperature fluctuations above or below the survival threshold (Wernberg et al. 2016). Temperature fluctuations cause stress for corals and damage the symbiosis between coral hosts and their symbionts (Coles and Jokiel 1977; Brown 1997).

Discussion

The results of this study showed variations in the number of coral genera found in four habitats. The highest genus-level diversity (39 genera) was found on the reef slope, and the lowest (2 genera) in the mangrove habitat. This indicates that habitat characteristics limit the distribution of coral genera. The coral genera found in the mangrove area were *Dipsastraea* and *Porites*. *Porites* has been reported in mangrove habitat in the Caribbean and the Indo-Pacific (Yates et al. 2014; Camp et al. 2016), while *Dipsastraea* has also been reported in Indo-Pacific mangrove habitats (Camp et al. 2016). these genera can survive in environmental conditions that are considered extreme for coral life, so further measurements are carried out.
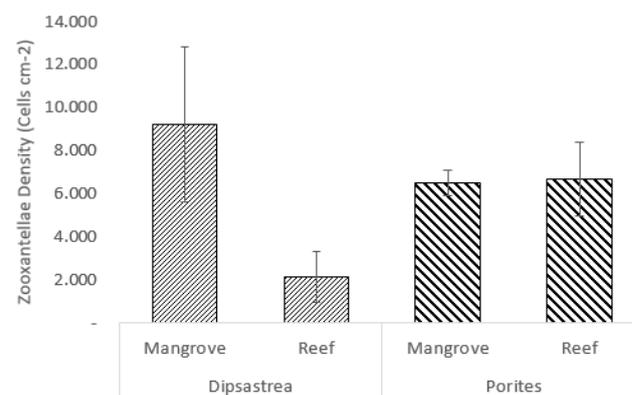

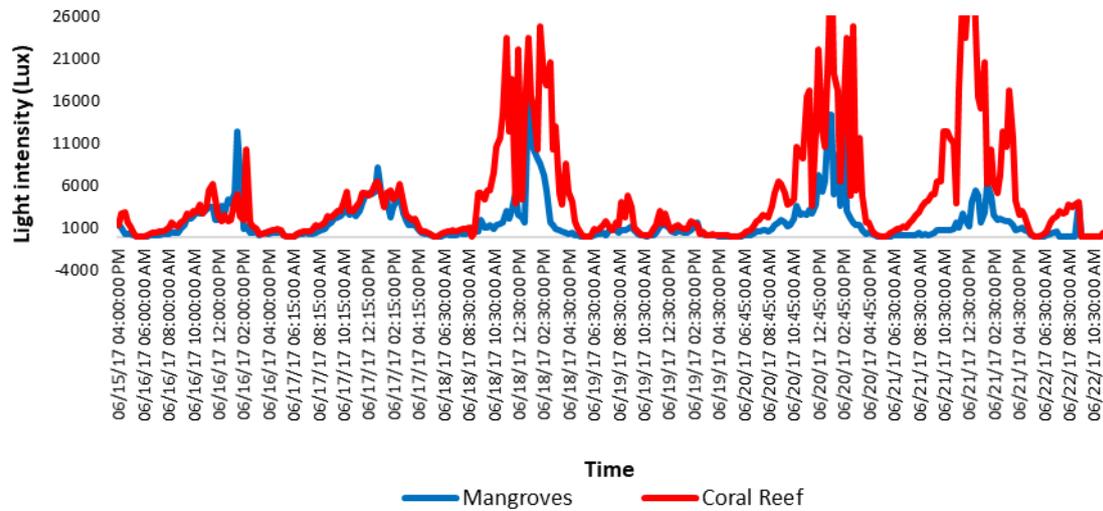**Figure 6.** Density of Zooxanthellae in *Porites* and *Dipsastraea*

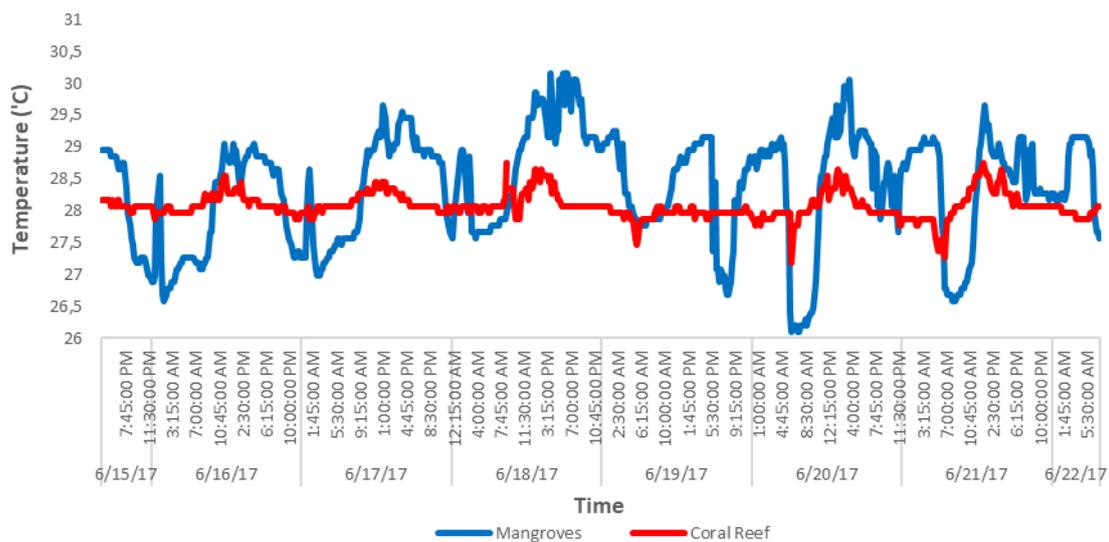**Figure 7.** Light intensity measurements over 8 days

Figure 8. Temperature graph for 8 days

Measurement of coral biomass and photobiology can provide an overview of important processes in coral reef ecology (Rocha et al. 2013; Iluz and Dubinsky 2015). This study found the size of *Porites* colonies ranged between 6-11792 cm^2 in coral reef habitat and between 17-45 cm^2 in mangrove habitat. *Dipsastraea* colony size varied considerably, ranging between 9-454 cm^2 in the coral reef habitat and 6-369 cm^2 in the mangrove habitat. This indicates that the Dipsastrean colony can adapt well to the mangrove environment.

The corals from the mangrove habitat had higher NPP and R values than corals from the coral reef. For *Dipsastraea* colonies from both habitats, respiration (R) was higher than the net primary productivity (NPP). The genus *Porites* used more oxygen for the respiration process ($\approx$ 60% of total O^2 produced) in mangrove habitat; in

contrast, NPP and R values were similar for *Porites* from coral reef habitat. This is consonant with the colony measurements, where the *Porites* colonies found in coral reefs reached much larger sizes than those in mangrove habitats. The results lead to the assumption that *Porites* living in the mangrove habitat consume more O^2 directly rather than saving it for other purposes, for example for growth. When under environmental pressure, corals are able to provide a variety of molecular responses (Kenkel and Matz 2017) and display physiological plasticity (Fox et al. 2019) to cope with such stresses. but the timing of these changes is unpredictable (Rooke et al. 2017).

Overall, the results indicate that the two genera found in marginal mangrove habitats display different adaptation mechanisms. The P/R ratios of corals from both habitats were below 1, except for *Porites* in the coral reef habitat.

Such low ratios suggest that the corals sampled tend to be heterotrophic (Burmester et al. 2018). Heterotrophic feeding in corals can supplement the energy supply from symbiotic zooxanthellae (Lesser et al. 2010). The density of zooxanthellae differed between the two habitats in the genus *Dipsastraea*. This difference could be related to the expanded polyps observed in coral colonies found in mangrove habitat, which could provide more room for the zooxanthellae to reproduce compared to the closed polyps in the coral reef habitat (Ismail et al. 2010). Combined with the lack of difference in P/R ratios between habitats, this indicates that one form of coral adaptation under marginal conditions adopted by *Dipsastraea* is to increasing the number of symbiotic zooxanthellae. The genus *Porites* displayed no significant difference in zooxanthellae density between the two habitats but did have a lower P/R ratio in the mangrove habitat. It seems likely that *Porites* can adapt to this marginal habitat through heterotrophy.

Further research needs to be done to see whether the role of mangrove habitat in the coral growth system. Approaches to the relationship between coral biomass and the mangrove environment also need to be explored more deeply to see to what extent mangroves can become refugia for coral reefs in the future.

ACKNOWLEDGEMENTS

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