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Photo-physiology of healthy-looking and diseased/health-compromised hard corals from Mauritius Island, Western Indian Ocean

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Abstract. *Jogee SY, Jeetun S, Ricot M, Taleb-Hossenkhan N, Mattan-Moorgawa S, Kaullysing D, Riemann P, Blanc L, Casareto BE, Suzuki Y, Bhagooli R. 2023. Photo-physiology of healthy-looking and diseased/health-compromised hard corals from Mauritius Island, Western Indian Ocean. Indo Pac J Ocean Life 7: 27-37.* The spatial photo-physiological responses of *in hospite* zooxanthellae in hard corals, including coenosarc and polyps, healthy-looking and affected parts in four coral diseases, namely Brown Band, Black Band, Skeletal Eroding Band and White Band on the coral *Acropora muricata*, and two health-compromised conditions such as the Pink Pigmentation Response and its differentiated morphology, the Pink Line Syndrome, on the coral *Porites* were investigated using the Imaging-PAM fluorometry. A significantly lower F_v/F_m was observed in case of Black Band, White Band, Brown Band and Pink Pigmentation Response affected parts compared to the healthy-looking parts. The F_v/F_m had the highest decline in Brown Band disease. Both the polyps and coenosarc had significantly lower F_v/F_m in White Band and Brown Band diseased parts compared to their healthy-looking parts. The $rETR_{max}$ did not change significantly between diseased/health-comprised parts and healthy-looking parts. NPQ_{max} declined significantly in White Band, Black Band and Pink Pigmentation Response cases. α and β generally did not tend to be affected in diseased/health-compromised conditions. The photo-physiology of *in hospite* zooxanthellae was least affected in Pink Line Syndrome. These findings suggest that diseased/health-compromised parts of corals behave differently in terms of their photo-physiology in different diseased and health-compromised coral conditions in important reef-building corals species such as *A. muricata* and *Porites* species, with important implications for the productivity and thus adaptive management of coral reefs in a globally warming ocean.

Keywords: Black Band, Brown Band, Imaging-PAM fluorometry, polyps, Skeletal Eroding Band, White Band disease

INTRODUCTION

Spatial heterogeneity of photosynthesis in corals and other autotrophic reef-associated organisms is a common phenomenon (Ralph et al. 2002; Hill et al. 2004), with light availability and quantity being strongly altered by the light-matter interactions which can occur at the meso (millimeter to meter) or microscale (micrometer to millimeter) (Anthony and Hoegh-Guldberg 2003). At the mesoscale, spatial heterogeneity occurs between the polyp and coenosarc, which has been observed to display contrasting photosynthetic capacities (Ralph et al. 2002). The light exposure patterns of zooxanthellae can explain the differences in the photosynthetic capacities between the polyp and the coenosarc in these different types of tissues; the zooxanthellae cells inside the coenosarc are constantly exposed to direct and high light illumination, whereas the zooxanthellae cells inside the polyp's endodermal layer are more shade-adapted as they can be retracted at high irradiances (Brown et al. 1994).

The spatial heterogeneity between the polyp and the coenosarc is also apparent under stressful conditions such as thermal bleaching (Hill et al. 2004) or light stress (Ralph et al. 2002). Short-term exposure to high temperatures (33°C) has yielded different photo-physiological responses from the polyp and coenosarc of *Acropora nobilis* and *Cyphastrea serailia* (Hill et al. 2004). The *A. nobilis* also exhibited differential photophysiological responses between its polyp and coenosarc following short-term exposure to high irradiances (1000 µmol photons m^{-2} s^{-1}) (Ralph et al. 2002). Coral diseases and other compromised coral health conditions, such as pigmentation responses, are an example of biotic stressors that can induce physiological alterations in the affected hosts (Rosenberg and Ben-Haim 2002; Roff et al. 2008; Burns et al. 2013). Diseases on marine invertebrates have been on a constant rise over the past several years and are widespread (Harvell et al. 2007), not sparing Mauritian seas (Bhagooli and Klaus 2014; Bhagooli et al. 2017; Mattan-Moorgawa et al. 2017; Bhagooli and Kaullysing 2019; Bhagooli et al. 2021a,b). Given the importance s of Symbiodiniaceae for the subsistence of reef-building corals, it is critical to study the effects of coral diseases on the photo-physiology of affected hosts. The disruption of the coral-algal symbiosis

by coral diseases greatly reduces the productivity of coral reefs since zooxanthellae account for around 50-70% of global benthic reef production (Douglas 2009). By compromising the photo-physiology of the *in-hospite* zooxanthellae, coral diseases inhibit the translocation of photosynthate from the photosynthetic zooxanthellae to the coral host, under healthy-looking conditions satisfies more than 95% of the host nutritional requirements (Muscatine et al. 1984). Coral diseases such as Black Band disease (Roff et al. 2008), White Syndrome (Roff et al. 2008), Skeletal Eroding Band (Roff et al. 2008), White Patch Syndrome, Growth Anomalies (Burns et al. 2013), Brown Band Disease (Ulstrup et al. 2007), and White Band and White Plague (Mattan-Moorgawa et al. 2017) have been reported to compromise the photo-physiology of reef-building corals.

While most of the above studies have assessed the gross spatial heterogeneity in the photo-physiological responses of diseased and health-compromised corals, no studies look at the finer scale differences between the polyp and coenosarc of affected hosts. This study aimed at characterizing and comparing the photo-physiology of healthy and diseased/health-compromised corals and the spatial heterogeneity in chlorophyll fluorescence at the affected hosts' coenosarc and polyp of dominant coral diseases from Mauritius Island, including Skeletal Eroding Band, Brown Band, Black Band, White Band in *Acropora muricata*, and health-compromised conditions like the Pink Pigmentation Response and its differentiated morphology, Pink Line Syndrome in *Porites* species.

MATERIALS AND METHODS

Study site and sample collection

This study was undertaken in the lagoon of Belle Mare, which is located on the east side of the Island of Mauritius (20°11'33.85"S, 57°46'37.04"E) and in the lagoon of Flic en Flac, which is located on the west side of the island (20°16'24.74"S, 57°22'5.14"E) (Figure 1). The depth of the lagoon at Belle-Mare varies from 0-3 m, and the distance from shore to the reef is approximately 850 m (Sadally et al. 2014). Due to heavy precipitation, belle-Mare also experiences algal blooms when fertilizers and sewage washes into the lagoon (Ramessur 2002). In addition, belle-Mare is subjected to higher wind intensity from the South East Trade Winds, as it is located on the Island's east coast. The study area at Belle Mare supported diverse coral assemblages mostly dominated by large branching colonies of *A. muricata*. At Flic en Flac, the lagoon is shallower (0-2 m) and is also dominated by large stands of branching *Acropora* corals in some areas. There is also the presence of underground water seepage at Flic En Flac, which discharges freshwater, nutrients and other land-based chemicals into the lagoon (Ramessur et al. 2011). Coral fragments (n=5 per disease/health-compromised condition) of an affected coral host with different types of lesions (skeletal eroding band, brown band, white band, black band in *A. muricata*, and pink line syndrome and pink pigmentation response in *Porites* sp.) were collected using either a plier or a hammer and a chisel. The lesions were identified on the field using coral disease identification guides such as those in Beeden et al. (2008).

Gross morphological description of coral diseases and compromised coral health conditions

The gross morphology of the coral diseases and compromised health conditions were systematically characterized using the framework proposed by Work and Aeby (2006). This included providing information on the distribution of the lesion (focal, multifocal, multifocal to coalescing, diffuse), the location of the lesion on the colony (central, peripheral, basal, medial, apical), the edges of the lesion (distinct, indistinct), the margins of the lesion (serrated, undulating, smooth, serpiginous), the shape of the lesion (circular, oblong, pyriform, cruciform, linear, lanceolate, irregular), the relief of the lesion (umbonate, bosselated, nodular, exophytic and fimbriated), the color of the lesion, and the texture of the lesion (smooth, rugose). The morphologic diagnosis of the diseases and compromised health conditions was also performed using the framework by Work and Aeby (2006), and additional information on the extent of the lesion (mild (1-20%), moderate (21-50%), severe (51-100%), time (acute, subacute and chronic), lesion (tissue loss, discoloration, growth anomaly) and structures affected (polyp, coenosarc, and skeleton) (Figure 2). Time, herein, refers to the time taken for the development of the disease, and the categories include acute (ranging from hours to days), subacute (weeks to develop), and chronic (months or years to develop).

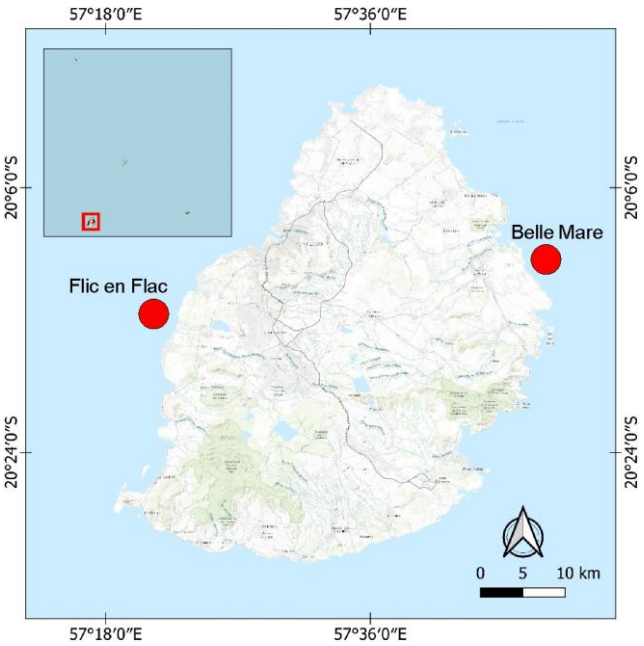


Figure 1. A. Location of Mauritius Island (20^0 34'84'' S, 57^0 55'22''E) in the Indian Ocean, B. Location of Flic en Flac and Belle Mare around Mauritius Island

Figure 2. Examples of (A) Acute disease (Brown Band) with a clear, denuded white skeleton and not overgrown by algae, (B) Sub-acute disease (Skeletal Eroding Band) with denuded skeleton overgrown with filamentous algae and (C) Chronic disease (Pink Pigmentation Response) with no apparent loss of tissue or algal overgrowth

Chlorophyll *a* fluorescence

Chlorophyll *a* fluorescence was measured using an Imaging Pulse-Amplitude-Modulated (I-PAM) fluorometer [Maxi-PAM, M Series, Waltz]. Measurements, through the addition of multiple areas of interest (diameter-5mm), were taken from both diseased and health-compromised and the healthy-looking coral parts. Chlorophyll fluorescence measurements were taken at the lesion and in apparently healthy-looking coral tissues located at least 2 cm from the lesion. By reducing the size of the areas of interest, measurements were also taken on individual polyp and on the coenosarc of close to the lesions and of the healthy-looking coral part. It is noteworthy that three main chlorophyll fluorescence parameters (F_v/F_m, $rETR_{max}$, NPQ_{max}) have been widely used in photo-physiological stress studies in marine organisms (Bhagooli et al. 2021c) and this study focused on these parameters. F_v/F_m represents the maximum quantum yield of Photosystem II (PSII) and it provides and indication of the photosynthetic efficiency of the PSII when all reaction centers are open. $rETR_{max}$ is the maximum relative electron transport rate and it is used to measure the rate of electron transport through the reaction centers in the PSII. NPQ_{max} is the maximum non-photochemical quenching parameter and it gives an indication of the ability of a photosynthetic organism to dissipate excess radiation through non-damaging heat emissions (Bhagooli et al. 2021c).

A double exponential decay function (Platt et al. 1980) was used to fit curves to the Rapid Light Curves (RLCs) and quantitatively compare the parameters such as Alpha (α) (initial slope of the RLC before the onset of saturation), Beta (β) (slope of the RLC after saturation) and $rETR_{max}$ between the healthy-looking and diseased or health-compromised coral parts. $rETR_{max}$, α and β values were obtained after curve fitting through Sigmaplot (Version 12.0).

Statistical analyses

Data were transformed, if necessary, using arcsine-square root transformation to meet the assumptions of normality and equal variance for use of parametric statistical tests. A one-way ANOVA test was used to determine differences (α=0.05) of photo-physiological parameters (F_v/F_m, $rETR_{max}$, NPQ_{max}, α and β) between the diseased or health-compromised lesions and the adjacent healthy-looking parts of the corals. One-way ANOVA was conducted to determine differences (α=0.05) of photo-physiological parameters (F_v/F_m, $rETR_{max}$, NPQ_{max}, α and β) in the polyp and the coenosarc between the healthy-looking and the diseased/health-compromised coral parts. Variations in mean values of photo-physiological parameters (F_v/F_m, $rETR_{max}$, NPQ_{max}, α and β) were analysed, using one-way ANOVA, between the polyp and coenosarc in the disease-affected or health-compromised coral parts.

RESULTS AND DISCUSSION

Morphological description of diseases and health compromised conditions

Four coral diseases (Brown Band, Skeletal Eroding Band, White Band and Black Band) were observed on *A. muricata* and 2 compromised coral health conditions (Pink Pigmentation Response and Pink Line Syndrome) were observed on *Porites* sp. The morphological description of the lesion characteristics of the coral diseases and compromised coral health conditions is summarized in Table 1.

Spatial variation in the photo-physiology of coral diseases

All the coral diseases assessed showed substantial variation in their photosynthetic responses between the healthy-looking part and the diseased lesion (Figure 2). The spatial heterogeneity in the photosynthetic parameters between the healthy-looking part and the diseased part can be observed by the differences in the false-colour images generated by the Imaging-PAM. Within each area of interest chosen, the pixel value of each photosynthetic parameter was automatically averaged and allowed for comparison between the healthy-looking and the diseased coral part. For the Brown Band Disease on *A. muricata*, a 39.3% significant decrease [($F(1, 25) = 252.603$, $p=0.000$] was observed in F_v/F_m in the diseased part compared to the healthy-looking coral part. F_v/F_m was observed to be significantly higher in the polyp [($F(1, 25) = 119.573$, $p= 0.000$]and coenosarc [($F(1, 25) = 124.308$, $p= 0.000$] of the healthy-looking coral part compared to the diseased coral part. For the Skeletal Eroding Band Disease on *A. muricata*, a 13.3% significant decline ($p<0.01$) in NPQ_{max} was observed in the diseased part, compared to the healthy coral part. Significantly lower α ($p<0.01$) was observed in the polyp from the healthy-looking part compared to the diseased part. For White Band disease, a 20.1% and 41.9%

significant decline in F_v/F_m and NPQ_{max}, respectively, was recorded in the diseased coral part compared to the healthy-looking part. F_v/F_m ($p<0.001$) and NPQ_{max} ($p<0.01$) was observed to be significantly higher in the healthy-looking part compared to the diseased part. α was significantly higher in the coenosarc over the White Band-affected coral part compared to the healthy-looking part. However, β was found to be significantly higher in the coenosarc over the healthy-looking part compared to over the diseased part. For the Black Band Disease, a 7.8% significant ($p<0.05$) decrease in F_v/F_m was recorded in the diseased part of the affected coral compared to the healthy-looking part. For NPQ_{max}, a 34.2% significant decrease ($p<0.01$) was observed in the diseased part of the coral compared to the healthy-looking part. F_v/F_m, NPQ_{max} and β was significantly greater ($p<0.01$, Figure 4) in the polyps from the healthy-looking part compared that in the Black Band-affected part.

Spatial variation in the photo-physiology of compromised coral health conditions

The compromised coral health conditions also showed considerable variation in the photosynthetic responses between the health-compromised part and the healthy-looking coral part, as it can be observed from the Imaging-PAM images (Figure 2). For the Pink Pigmentation Response on *Porites lutea*, an 11.6% and a 26.7% significant decline ($p<0.001$) in F_v/F_m and NPQ_{max}, respectively, was recorded in the health-compromised part, compared to the healthy-looking part of the coral. NPQ_{max} was observed to be significantly higher ($p<0.001$) in both the polyp and coenosarc from the healthy-looking part compared to the pigmentation response part. β also was significantly ($p<0.05$) much higher in the coenosarc of the healthy-looking part as opposed to in the Pink Pigmentation Response. No gross scale difference was apparent between the healthy-looking part and the health-compromised part of Pink Line Syndrome, however, slightly lower β was recorded in the coenosarc from the healthy-looking part compared to the Pink Line Syndrome.

Discussion

This study reveals variable photo-physiological responses of diseased/health-compromised coral parts, including comparing the coenosarc and polyps among four coral diseases in *A. muricata* and two health-compromised conditions in *Porites*. In addition, a comparison of photo-physiological effects of diseases on corals from the published literature and this study (Table 2) indicates the varied responses observed.

A pathogenic ciliate causes brown Band Disease from the class Oligohymenophorea, subclass Scuticociliatia (Bourne et al. 2008), which can ingest zooxanthellae cells and harness the photosynthate from the still-photosynthetically competent microalgae (Ulstrup et al. 2007). The significant reduction of Fv/Fm in the diseased coral part compared to the healthy-looking coral part can be explained by the reduction of zooxanthellae density, commonly reported in this disease (Ulstrup et al. 2007). This observation is in contradiction with the findings of Ulstrup et al. (2007) and Roff et al. (2008), whom both recorded no significant difference in Fv/Fm values between the brown band lesion and the healthy-looking coral part of *A. muricata* and *A. nobilis*, respectively (Figure 3). No difference was also observed in the photo-physiological responses of the polyp and coenosarc between the diseased and healthy-looking coral parts. The higher Fv/Fm in the polyp and coenosarc of the healthy-looking part compared to the diseased part can be attributed to the higher zooxanthellae density and higher concentration of photosynthetic pigments in these zooxanthellae cells in both tissue types in that part of the coral (Ulstrup et al. 2007). No difference was observed, however, between the polyp and coenosarc in the Brown Band lesion, and the lack of significant alterations can explain this observation to the coral skeleton and polyp or coenosarc structure affected by the Brown Band Disease and the motility of the ciliates and their ability to migrate across the coral skeleton and to form lesions with varying width and densities which covers both the polyp and coenosarc (Boyett 2006; Lobban et al. 2011). Although differences in the oxygen concentration and Heat Shock Proteins (Hsp) 60 levels have been reported between the healthy part of *A. muricata* and the Brown Band affected part, with relatively lower oxygen concentration and higher Hsp60 levels in the lesion as opposed to the healthy coral part (Ulstrup et al. 2007; Seveso et al. 2015), no fine-scale measurement over the polyp and coenosarc has been recorded so far to be able to explain any spatial heterogeneity in photosynthesis.

The Skeletal Eroding Band is another coral disease caused by the pathogenic ciliate, *Halofolliculina corallasia*. This ciliate is known to disrupt the coral tissues and erodes the coral skeleton of the affected host through the spinning movement of the ciliates and the secretion of chemicals during the formation of the ciliate-housing loricae (Page and Willis 2008). Significant reductions in NPQmax were recorded in the diseased part compared to the healthy-looking coral part of *A. muricata*. Some of this study's observations are in accordance with the findings of Roff et al. (2008), who did not record any significant difference in Fv/Fm or rETRmax of between the healthy-looking and Skeletal Eroding Band-affected parts of *Pocillopora damicornis*. However, a decline in NPQmax was also observed in this study, which contradicts the results of Roff et al. (2008), who did not make such observations. The lack of difference in Fv/Fm can be explained by the presence of photosynthetically competent zooxanthellae, which has also been found to occur in large densities inside the pathogenic ciliates (Cróquer et al. 2006). However, the drop in NPQmax in the diseased coral part might suggest some level of damage to the photosynthetic apparatus of the zooxanthellae. Such damage can be explained by the aggressive movement of the ciliates, which disrupt the coral tissue and *in-hospite* zooxanthellae cells. The higher α value in the diseased part can be explained by the erosion of the coral skeletal structures of the affected coral part, causing potential alterations to the light scattering and diffusion patterns and the availability and efficiency of use of incoming irradiance by the engulfed zooxanthellae. No major difference in the photo-physiological responses of

the polyp and coenosarc was observed across the diseased part. The lack of difference can be explained by the photosynthetically competent zooxanthellae, which are engulfed by the ciliates and which have been observed to embed themselves in both the polyp and coenosarc tissues (Cróquer et al. 2006; Page and Willis 2008). This observation can also be explained by the overgrowth of epiphytic turf algae, which overgrows the dead coral polyp and coenosarc faster than the pathogenic ciliates (Page and Willis 2008), which inhibits the differentiation of the photo-physiological responses between polyp and coenosarc of the affected areas.

White Band Disease is caused by *Vibrio* and *Rickettsiales* bacteria (Ritchie and Smith 1998; Kline and Vollmer 2011). The decline in Fv/Fm and NPQmax in both the polyp and coenosarc of the diseased coral part, compared to the healthy-looking coral part, suggests significant damage to the photosystem of the zooxanthellae in both tissue types. A similar observation, but at a more gross scale, was made by Mattan-Moorgawa et al. (2017), which also reported reduced Fv/Fm and NPQmax in White Band-affected *A. muricata*. The observation made in this study can be explained by the tissue-penetrating action of the pathogenic bacteria associated with this disease. Bacterial penetration inside the tissues of the affected hosts, including both polyp and coenosarc (Croquer et al. 2003), can disrupt the tissue structure and integrity and cause the loss of the *in-hospite* zooxanthellae (Sussman et al. 2009). The putative pathogens of this disease have also been found to have algicidal properties and can cause enzymatic processes (Sunagawa et al. 2009; Silva-Lima et al. 2021), which degrade the coral tissue and cause the loss of the endosymbionts. The bacteria have also been found to inhibit the nitric oxide signaling regulators, which subsequently compromises the coral-algal symbiosis process. All these factors can contribute to causing damage to the photosynthetic function of the zooxanthellae. The lack of difference in the other photo-physiological parameters of the polyp and coenosarc can be associated with the no major structural alteration of the coral skeletal structures and, subsequently, no major changes to the light diffusion and availability patterns in both affected and non-affected coral parts. Higher α in the coenosarc of the diseased part can be explained by the loss of zooxanthellae cells and the higher scattering of light by the less opaque and rugged coral skeleton (Enríquez et al. 2005). Higher β in the coenosarc of the healthy-looking tissues, compared to the diseased part, indicates the presence of photosynthetically competent zooxanthellae in that part which can effectively dissipate the excess irradiances.

A rapidly advancing band characterizes the Black Band Disease, black or deep-reddish brown, separating healthy-looking tissues from the dead and algae-covered skeleton. This black band comprises mostly of a cyanobacterial mat dominated by the *Phormidium corallyticum* species and other groups of sulfate-reducing bacteria, creating an anoxic condition that ultimately kills the coral tissues (Edmunds 1991; Kuta and Richardson 1996; Barneah et al. 2007). The cyanobacteria which constitute the black band are autotrophs which can perform photosynthesis and thus influence chlorophyll fluorescence. Significantly lower Fv/Fm in the Black Band lesion, particularly in the polyps, can be explained by the ability of *P. corallyticum* to create hypoxic conditions for the zooxanthellae occurring near the band (Richardson and Kuta 2003). The observation of this study is to the findings of Roff et al. (2008), who observed significantly reduced Fv/Fm at the interface of the black band lesion and the healthy-looking tissues. Roff et al. (2008) also observed lowered Fv/Fm at the disease interface. Roff et al. (2008) also observed higher NPQmax at the disease interface and hypothesized photoinhibition in the zooxanthellae before the lesion. The lower NPQmax observed at the disease lesion and in the polyps in this study can be explained by considerable damage to the photosynthetic apparatus of the zooxanthellae found close to the lesion. The greater impact on the polyp compared to the coenosarc can be explained by the boring action of the cyanobacteria associated with the Black Band Disease, which has been observed to migrate towards the center of the coral polyp (Miller et al. 2011). The absence of significant differences between the photo-physiological responses between the polyp and coenosarc in the diseased part can be explained by the structure of the cyanobacterial mat, which is commonly associated with the Black Band lesion. The mat's extensive, thick, and diffuse properties hinder the exact estimation and differentiation of the photo-physiological responses between the affected polyp and coenosarc.

Pink Pigmentation Response is one morphological form of Pigmentation Responses and is characterized as brightly colored pink or purple lesions which can be focal or multi-focal or sometimes coalescing on the surface of mostly massive coral colonies. The lesion has been associated with excessive melanin levels inside the coral tissues. Significantly lower Fv/Fm and NPQmax photo-physiological responses were observed in the health-compromised areas compared to the healthy-looking areas of the massive *Porites* coral fragments used in this study. This observation contradicts the findings of Roff et al. (2008), who did not find such significant differences between the affected and non-affected coral parts. The presence of non-fluorescent chromoproteins can explain this difference, but green fluorescent proteins, which have been associated with the Pink Pigmentation Response lesions and are believed to have photo-protective properties for the stressed corals (D'Angelo et al. 2012; Yucharoen 2016). Significant differences were also observed in the NPQmax of the polyp and coenosarc and β in the coenosarc only between the health-compromised and healthy-looking parts of the coral and this can be linked to the morphological changes to the host's skeleton and histological properties. Pink Pigmentation Response lesions are often characterized by thickened corallite walls and loss in coral hardness in the upper margins of the corallites (Yucharoen 2016; Zakaria et al. 2021) with swollen polyps (Thangaradjou et al. 2016), which can influence the light scattering properties over the polyp and coenosarc in the health-compromised part.

Table 1. Morphologic description of the coral diseases or health-compromised coral conditions

Disease name	Species	Distribution of lesions	Location on colony	Edges	Margins	Shapes	Colour	Texture	Extent	Time	Lesion	Structure affected	Mean lesion size (cm)
BBD	*A. muricata*	Diffuse	Central	Annular	Undulating	Circular	Black	Smooth	Severe	Acute	Tissue loss, discoloration	Polyp, coenosarc	0.4±0.1
SEB	*A. muricata*	Diffuse	Medial, basal	Distinct	Smooth	Linear	Grey, black	Smooth	Mild	Acute, sub-acute	Tissue loss	Polyp, coenosar, skeleton	1.8±1.6
WB	*A. muricata*	Diffuse	Medial, basal	Distinct	Smooth	Linear	White	Smooth	Mild	Sub-acute	Tissue loss	Polyp, coenosarc	2.4±1.5
BrB	*A. muricata*	Diffuse	Medial	Distinct	Smooth	Linear	Brown	Smooth	Mild	Acute, sub-acute	Tissue loss, discoloration	Polyp, coenosarc	1.1±0.9
PPR	*P. lutea*	Focal, multifoca, multifocal to coalescing	Colony-wide	Irregular	Undulating	Irregular	Pink, purple	Rough	Mild, moderate	Chronic	Discoloration	Coenosarc	3.6±2.7
PLS	*P. lutea*	Focal, multifoca, multifocal to coalescing	Colony-wide	Irregular, annular	Undulating	Circular, oblong, irregular	Pink	Rough	Mild, moderate	Chronic	Tissue loss, discoloration	Polyp, coenosarc	0.2±0.3

Note: BBD: Brown Band Disease, SEB: Skeletal Eroding Band; WB: White Band; BrB: Black Band; PPR: Pink Pigmentation Response: PLS: Pink Line Syndrome

Table 2. Summary of the photo-physiological impacts of coral diseases and health-compromised conditions, compared to the findings of this study

Coral disease	Coral species	Location	Photo-physiological impact in diseased/health-compromised part compared to healthy-looking part	Sources
Brown Band Disease	*Acropora muricata*	Davies Reef, Great Barrier Reef, Australia	Higher F_v/F_m, Lower α	Ulstrup et al. (2007)
		Mauritius Island	Lower F_v/F_m	This study
	A. nobilis	Heron Reef, Great Barrier Reef, Australia	Lower ETR_{max}, Lower α	Roff et al. (2008)
Skeletal Eroding Band	*Pocillopora damicornis*	Heron Reef, Great Barrier Reef, Australia	No significant change	Roff et al. (2008)
	A. muricata	Mauritius Island	Lower NPQ_{max}	This study
White Band	*A. muricata*	Mauritius Island	Lower F_v/F_m, $rETR_{max}$ and NPQ	Mattan-Moorgawa et al. (2017)
			Lower F_v/F_m and NPQ_{max}	This study
Black Band	*Cyphastrea microphthalma*	Heron Reef, Great Barrier Reef, Australia	Reduced F_v/F_m, Higher NPQ_{max}	Roff et al. (2008)
	A. muricata	Mauritius Island	Lower F_v/F_m, Lower NPQ_{max}	This study
Pink Pigmentation Response	*Porites* species	Heron Reef, Great Barrier Reef, Australia	No significant change	Roff et al. (2008)
		Mauritius Island	Lower F_v/F_m, Lower NPQ_{max}	This study
Pink Line Syndrome	*Porites* species	Mauritius Island	No significant change	This study

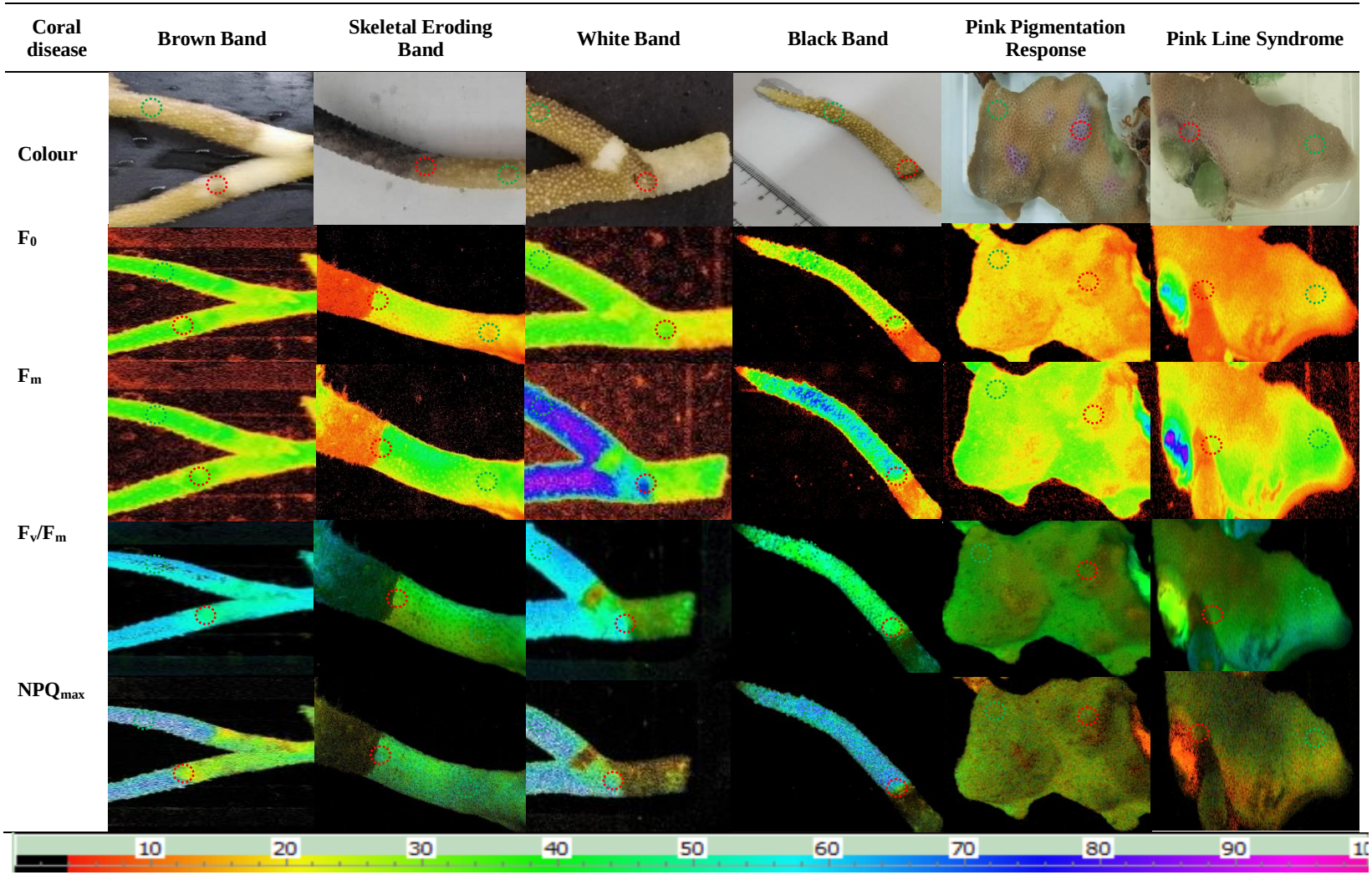
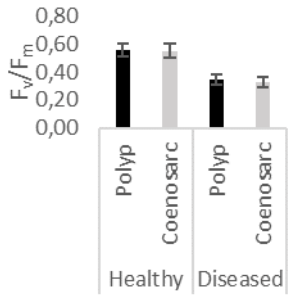
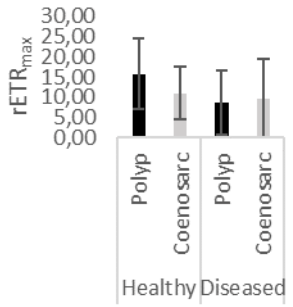
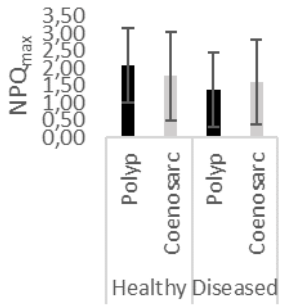
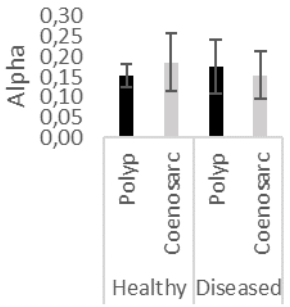
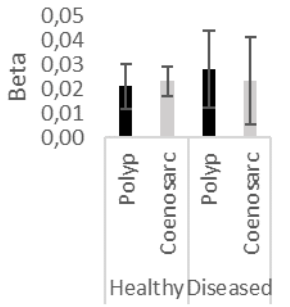
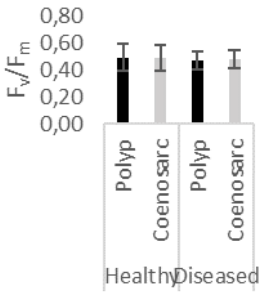
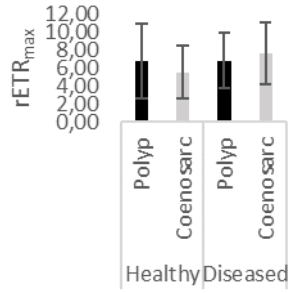
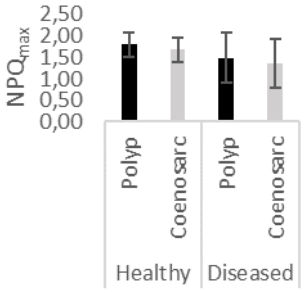
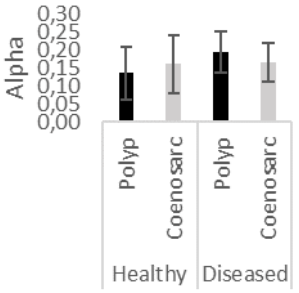
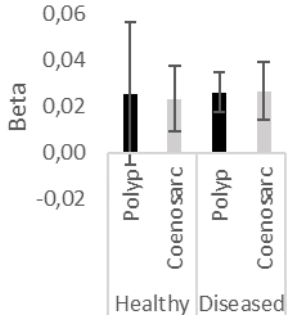
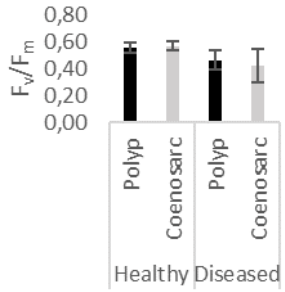
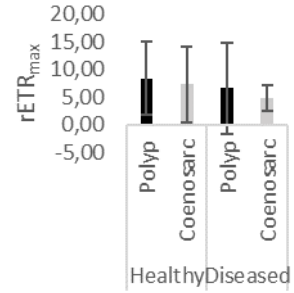
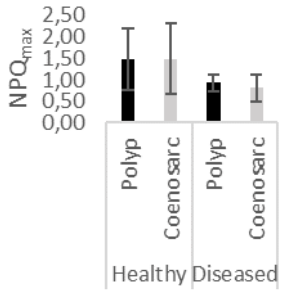
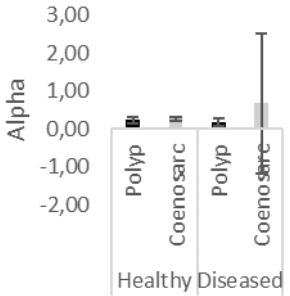
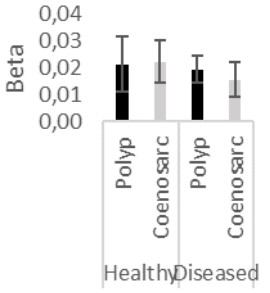


Figure 3. Colour, F_0, F_m, F_v/F_m, NPQ_{max} images of brown band, skeletal eroding band, white band, black band and pink pigmentation response, pink line syndrome (Red circles indicate measurement point for diseased or health-compromised part and green circle indicate measurement point for healthy-looking part). The false colour scale shows the relative values ranging from 0 to 1

Disease/compromised health condition	Maximum Quantum Yield (Fv/Fm)	Maximum Relative Electron Transport Rate (rETRmax)	Maximum Non-Photochemical Quenching (NPQmax)	Alpha (α)	Beta (β)
Brown Band Disease					
Skeletal Eroding Band Disease					
White Band Disease					

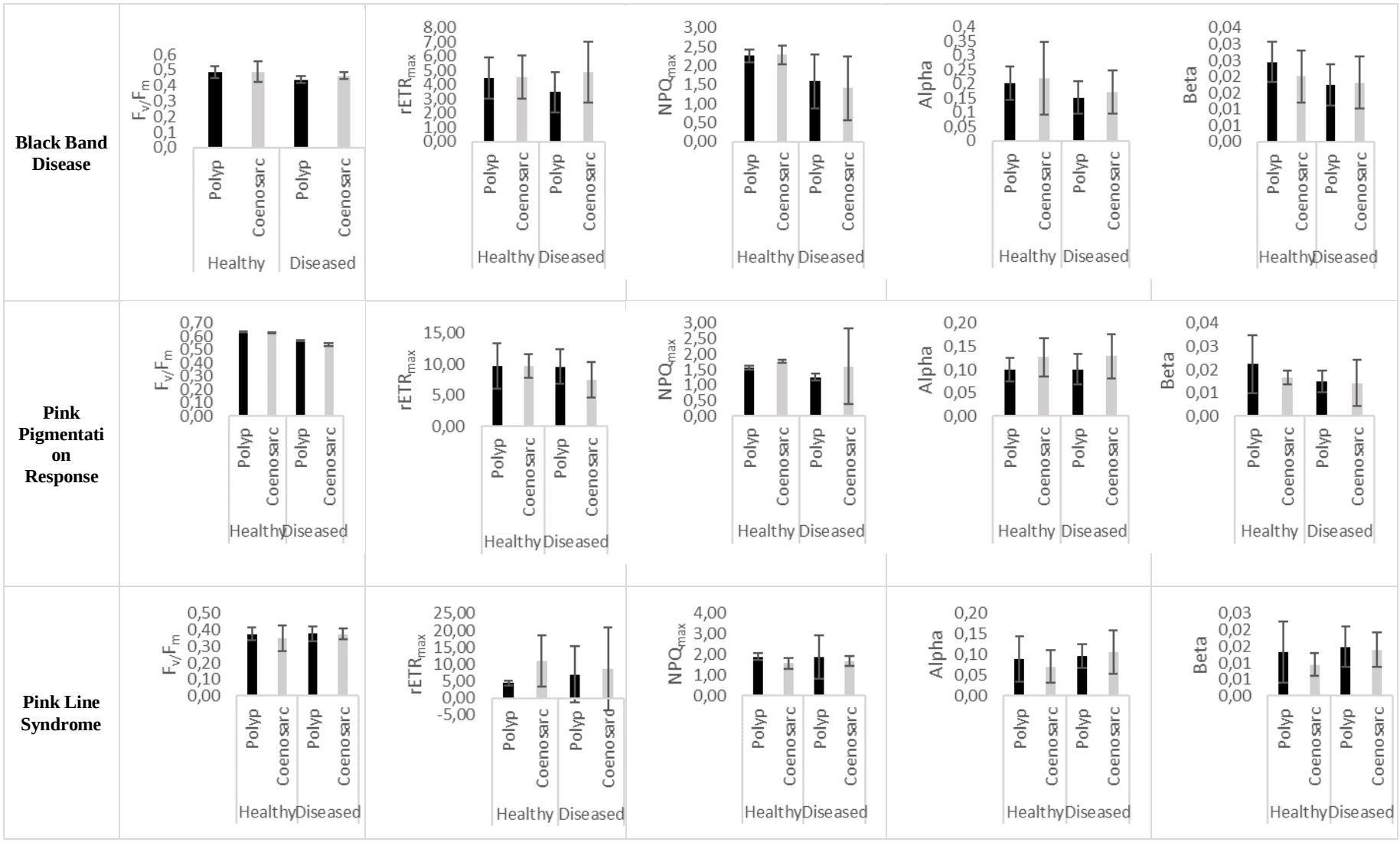


Figure 4. F_v/F_m, $rETR_{max}$, NPQ_{max}, α and β of the polyp and coenosarc of diseased-affected and health-compromised and healthy-looking coral part. Bars represent mean ± SD

The Pink Line Syndrome, a differentiated morphology of Pink Pigmentation Response, is characterized by a brightly pigmented and inflamed pink-colored line separating healthy-looking coral tissues from the dead and algae-covered dead coral skeleton. Pink Line Syndrome has been associated with a cyanobacterium, *Phormidium valderianum*, penetrating the coral tissues and disrupting their integrity (Ravindran and Raghukumar 2002). However, in this study, no significant difference in the photo-physiological responses was observed between the healthy and health-compromised coral parts, similar to another study by Roff et al. (2008), who also did not find any photo-physiological differences between pigmentation responses and the healthy-looking coral part.

The findings of this study show differential spatial heterogeneity in the gross (between the healthy-looking part and the diseased/health-compromised part) and fine-scale (between the polyps and coenosarc) photo-physiological responses among different coral diseases and compromised health conditions on dominant reef-builders found around the island of Mauritius. The findings of this study will have serious implications for the mitigation and management of coral diseases and compromised coral health conditions, given the importance of the photo-physiology of reef-building corals as a critical and proactive indicator of coral health. However, with global climate change, further research is warranted to assess the fine- and gross-scale temporal changes related to the spatial heterogeneity in the photophysiological responses of coral diseases and health-compromised conditions.

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