Variable photo-physiological performance of macroalgae and seagrasses from Saya de Malha and Nazareth Banks, Mascarene Plateau

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

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

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

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

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

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

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

Abstract

The photosynthetic performance of macroalgae and seagrasses related to their body parts, depth and colours from the poorly-studied Saya de Malha and Nazareth Banks on the Mascarene Plateau was investigated in this study. Two seagrass (*Thalassodendron ciliatum* and *Halophila decipiens*) and seven macroalgae species (*Caulerpa cupressoides, Acrosorium ciliolatum*, *Dictyosphaeria cavernosa*, *Halimeda opuntia*, *Ulva* sp., *Udotea orientalis* and *Udotea palmetta*) were collected using the five Van Veen grabs attached to the Video-Assisted Multi-Sampler (VAMS) from 29-79 m depths in May during the FAO EAF-Nansen Research Programme 2018. The photosynthetic performance was measured using a Diving-Pulse-Amplitude-Modulated (D-PAM) fluorometer and the parameters included effective quantum yield at photosystem II (PSII) (Φ_{PSII}), relative maximum electron transport rate (rETR$_m$), photosynthetic efficiency (α), photoinhibition (β), saturating light level (E$_k$), and maximum non-photochemical quenching (NPQ$_{max}$). All photo-physiological parameters varied significantly in *T. ciliatum* and *C. cupressoides* across their body parts. However, variation with seawater depths was not significant for NPQ$_{max}$ and β in the seagrass, and Φ_{PSII}, rETR$_m$ and β in the macroalgae. Photo-physiological functioning of the leaf of *T. ciliatum* was optimal at 40 m. The photosynthetic performance of the frond and stolon of *C. cupressoides* decreased and remained unchanged, respectively, at 79 m when compared to that at 29 m. The whitish lobes of *H. opuntia* at 31 m exhibited significantly lower photosynthetic performance, in terms of Φ_{PSII}, rETR$_m$, α and E$_k$, than the greenish lobes. These findings provide a first insight of seaplant body parts-, depth- and colour-related photo-physiological performance from the Mascarene Plateau.

Keywords: macroalgae, Nazareth, PAM, photo-physiology, Saya de Malha, seagrass

Introduction

Seagrasses and macroalgae from the Saya de Malha and Nazareth Banks on the Mascarene Plateau have received very little scientific attention to date (Fredericq *et al.*, 1999; Hagan and Robinson, 2001; Gullstrom *et al.*, 2002; Hilbertz and Goreau, 2002; Milchakova *et al.*, 2005; Vortsepneva, 2008). Three species of seagrasses, namely, *Thalassodendron ciliatum*, *Halophila decipiens* and *Enhalus acroides* have been reported at the Saya de Malha Bank (Hilbertz and Goreau, 2002; Vortsepneva, 2008). Reported macroalgae include species of Rhodophyta *Kappaphycus cottonii*, *Neogoniolithon*,

http://dx.doi.org/10.4314/wiojms.si2021.2.7

Hydrolithon, *Sporolithon*, *Mesophyllum*, *Lithophyllum* (Fredericq *et al*., 1999 cited in Vortsepneva, 2008), and calcareous encrusting and branching red algae, soft green alga *Microdictyon* sp. and calcareous green alga *Halimeda opuntia* from the Ritchie Bank (Hilbertz and Goreau, 2002). These are important primary producers which exhibit photo-physiological plasticity with respect to the prevailing light regimes.

Though light is essential for photosynthesis to take place, light limitation or excess irradiance may trigger multiple responses in photosynthetic marine organisms. Responses to light limitation in seagrasses usually include increased photosynthetic efficiency, lowered maximum electron transport rate, and a decline in the saturating irradiance (Ralph, 1999; Ralph and Gademann, 2005), while responses to increased irradiance entail decreased effective and maximum quantum yield at photosystem II (Durako and Kunzelman, 2002; Ralph and Gademann, 2005). In contrast, no photosynthetic responses to change in light regime or along a light gradient have been reported (Major and Dunton, 2000; Olesen *et al*., 2002). Solar irradiation, in particular short wavelengths (UVB, 280-315 nm), may change photo-physiological performance and protective mechanisms in plants (Bischof *et al*., 2006) and cause DNA damage (van de Poll *et al*., 2001), which in turn slows growth (Aguilera *et al*., 2002). Elevated light levels enhance the production of reactive oxygen species, which if not soaked up by antioxidant activities, may cause cellular damage and photosynthetic dysfunctioning. Phenolic compounds, such as coumarins, with their high UV absorption properties, prevent light-induced damage in green macroalgae such as *Caulerpa* and *Dasycladus* (Aguilera *et al*., 2002; Bischof *et al*., 2006). Macroalgae in the intertidal environment adapt physically and physiologically to changing irradiance, and thus optimise their photosynthetic performance (Davison and Pearson, 1996). Similarly, light-induced stress leads to reduced photosynthetic activity as a photo-physiological adaptation to elevated irradiance (Schagerl and Möstl, 2011). Seagrasses and macroalgae occurring in the waters of the Mascarene Plateau at depths greater than 20 m may be more likely exposed to a light-limited environment and more so on their different body parts, like stem or stolon, thus warranting investigation of the photo-physiological responses of their different photosynthetically active body parts.

Although the leaves of seagrasses or fronds of macroalgae have mainly been used in photosynthetic investigations, other body parts like the stem and stolon are yet to be photo-physiologically explored. The different body parts of some seagrass and macroalgal species appear green in colour, potentially indicating the presence of the green photosynthetic pigment, and consequently may be photosynthetically active. Several plants have either specialized/modified or different body parts that perform photosynthesis. Examples include the roots of the epiphytic orchids, *Taeniophyllum* (Chinese Herbs Healing, 2020), the roots of the flowering plant, *Podostemon* (Cook and Rutishauser, 2007), the adventitious roots and succulent stem of the aquatic plant, *Tecticornia pergranulata* (Rich *et al*., 2008), and the leaves and roots of water chestnut *Trapa bispinosa* Roxb (Ishimaru *et al*., 1996). It is noteworthy that re-oxygenation effectiveness in marine plant tissues in different body parts may be reduced due to the lower solubility and about a thousand-fold slower oxygen diffusion rate in water than in air (Grable, 1966). Though the photosynthetic adventitious roots in some aquatic plants like *Tecticornia pergranulata* occur in very light-limited environment, they may reduce the internal oxygen deficit (Rich *et al*., 2008). Similarly, the different body parts of seagrasses and marine macroalgae may possibly avoid internal oxygen deficit through limited photosynthetic activities despite occurring in low light regimes or in deeper waters. Given these possibilities, future investigations may be necessary; first exploring the photo-physiological activities and any photo-acclimatory capacity in seagrass and macroalgal body parts using non-destructive chlorophyll fluorescence techniques. A similar approach may also be applied to investigate the decolouration process in green coralline macroalga like *Halimeda*, which usually whitens and degrades to produce sand.

Apart from light, temperature, substratum type and hydrodynamics act as major determinants of marine macrophytes spatial distribution (Riss and Hawes, 2003; Koch *et al*., 2006; Infantes *et al*., 2011). Seagrasses and macroalgae attach firmly to consolidated substrata such as rocks, which provide a stable and non-motile surface, and colonise unconsolidated substrata like sand, which requires root-like structures to stabilize unstable and mobile surface. Seagrases have true roots while some macroalgae have root-like rhizoids to colonise sediment particles on unconsolidated substrata, which may be mobilized by waves and currents leading to erosion or accretion and thus negatively impacting marine macrophytes through uprooting or burial (Fonseca and Kenworthy, 1987; Cabaco *et al*., 2008).

Though most macroalgae colonise consolidated substratum, some species of order Caulerpales grow on unconsolidated substrata, where the creeping stolons have rhizoids that may bind with sediment particles (Taylor, 1960; Chisholm and Moulin, 2003) and thus anchor in sandy sediments (Klein and Verlaque, 2008). *Caulerpa* species may inhabit both consolidated and unconsolidated substrata (Thibaut *et al.*, 2004). Some *Caulerpa* species appear to tolerate sediment deposition and burial to a certain extent (Glasby *et al.*, 2005; Piazzi *et al.*, 2005) as reflected by macroalgae cover persistence (Infantes *et al.*, 2011). However, photo-physiological tolerance of the creeping stolon to temporary burial by sandy sediment has yet to be investigated.

However, photo-physiological variations among species of macroalgae and seagrasses, and in relation to environmental gradients such as depth, are unchartered on the Saya de Malha and Nazareth Banks, Mascarene Plateau. This study aimed at investigating the variations in the photo-physiological performance, using a diving fluorometer, in two seagrass and seven macroalgae species. The variability in photo-physiological performance of selected seaplants with respect to their body parts, whitening, seawater depth and sand burial was assessed.

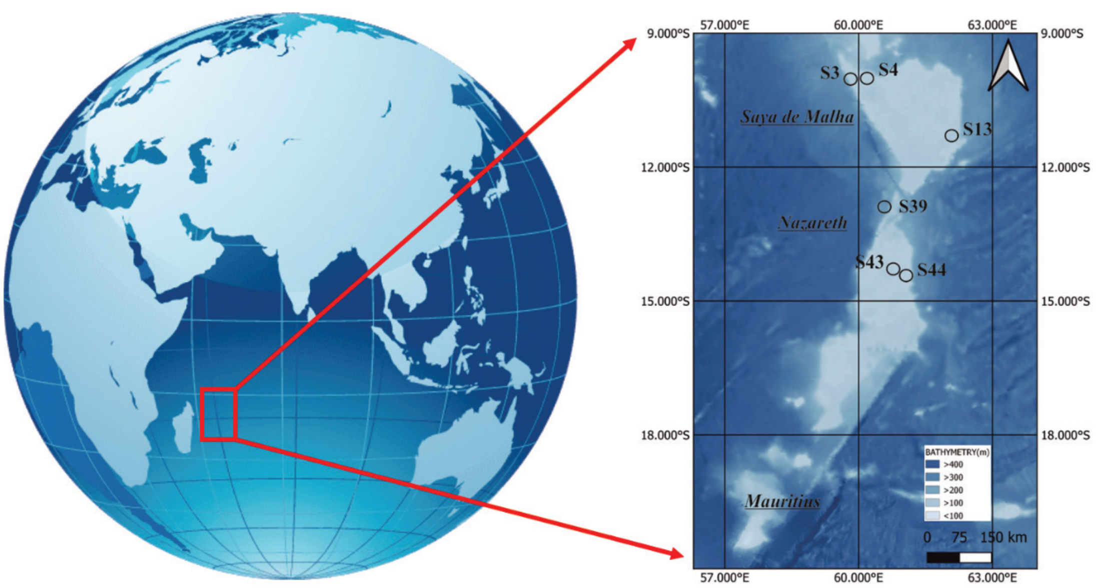

Figure 1. Map of Mascarene Plateau indicating the sampling locations at Saya de Malha (S3, S4, S13 and S39) and Nazareth Banks (S43 and S44).

Rapid light curves (RLCs) generated by Pulse-Amplitude-Modulated (PAM) fluorometry (Beer and Bjork, 2000; Beer *et al.*, 2000; Beer and Axelsson, 2004; Campbell *et al.*, 2008) provide chlorophyll *a* fluorescence parameters such as effective quantum yield at photosystem II (Φ_{PSII}), initial slope (α), photoinhibition (β), maximum relative electron transport rate ($rETR_m$), and maximum non-photochemical quenching (NPQ_{max}). These act as a proxy indicating natural variations and stress responses in marine plants including seagrasses and macroalgae (Li *et al.*, 2010, 2014; Bhagooli *et al.*, 2021). Diving-PAM fluorometry is a non-destructive method to estimate photosynthetic activities in seaplants (Beer *et al.*, 2001) and symbiotic marine invertebrates (Bhagooli *et al.*, 2021).

Material and methods

Study sites

Grab sites for this study included S3, S4, S13 and S39 at the Saya de Malha Bank, and at S43 and S44 at the Nazareth Bank (Fig. 1). Sampling was conducted in the month of May 2018 during the Nansen research expedition to the Mascarene Plateau. The seagrass and macroalgal samples were collected using Van Veen grabs on the Video-Assisted Multi-Sampler (VAMS) deployed at respective study sites. The samples were kept in seawater from the respective sites and the chlorophyll fluorescence measurements were performed within 1-1.5 hours following collection.

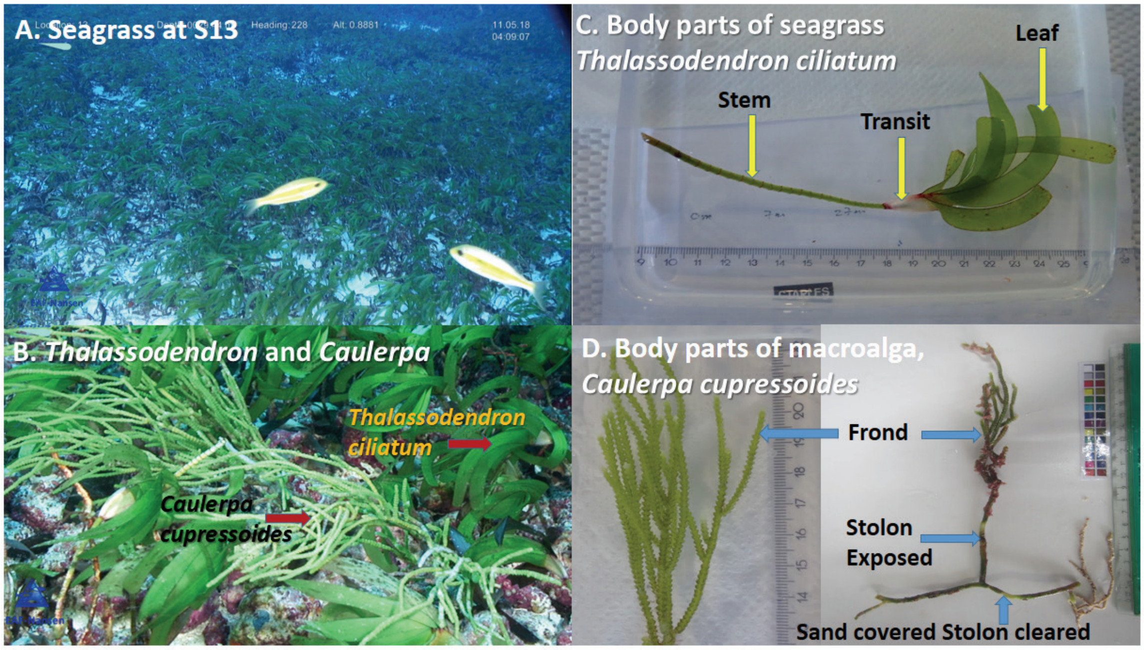

Figure 2. A. Seagrass at SMB location S13 at a depth of 29 m. B. Close up image of the seagrass, *Thalassodendron ciliatum* and the macroalga, *Caulerpa cupressoides,* both indicated by red arrows. C. Stem, transit and leaf body parts of the seagrass, *Thalassodendron ciliatum* (indicated by yellow arrows) for measurement of chlorophyll fluorescence. D. Frond, Exposed stolon and cleared stolon covered with sand as body parts of the macroalga *Caulerpa cupressoides* (indicated by blue arrows) for measurement of chlorophyll fluorescence.

Light intensity, salinity and temperature measurements at study sites

CTDs were deployed at all study sites, except for S39. Light intensity and salinity were recorded through the CTD at depths of 66 m, 22.2 m, 21 m, and 25 m for S3, S4, S13, and S43/44, respectively. For temperature measurements, records from the VAMS were used for the specific collection depths.

Seagrass and macroalgae identification

Seagrasses and macroalgae were identified based on morphological features related to their leaves, stems and roots, and the thallus/fronds, respectively (Oliveira *et al*., 2005).

Photo-physiology of seagrass and macroalgae – Chlorophyll *a* fluorescence measurement

Following collections using the Van Veen grabs, the seagrasses and macroalgae were kept shaded to provide dark conditions for a maximum of one hour prior to being exposed to saturating pulses using a Diving-PAM fluorometer (WALZ, Germany) for measurement of chlorophyll fluorescence parameters such as effective quantum yield at photosystem II (Φ_{PSII}), relative electron transport rate (rETR), photosynthetic efficiency (α), photoinhibition (β), saturating light level (E_k). ETR_m and NPQ_{max} were determined from the rapid light curves. rETR was computed as half the product of photosynthetically active radiation (PAR) and Φ_{PSII}. The effective quantum yield, $\Delta F/F_m'$ (Φ_{PSII}), which is unitless, was determined as the ratio of change in maximum fluorescence (F_m') and minimum fluorescence (F) to F_m', where F and F_m' were measured by applying a weak and saturating light, respectively (Genty *et al*., 1989; Serôdio *et al*., 2007). NPQ was calculated as $(F_m - F_m')/F_m'$ (Bilger and Bjorkman, 1990). Samples were exposed to a series of rapidly (10 s) increasing light climates (0, 110, 150, 300, 400, 500, 800, 1000, 1325 µmol quanta m^{-2} s^{-1}) from the D-PAM to generate the Rapid Light Curves (RLCs) (Ralph *et al*., 1999). Using the RLCs the rETR and NPQ were estimated at each irradiance. The ETR and NPQ curve fitting was done using the equation of Platt *et al*. (1980) on SigmaPlot 12.0 (Systat Software Inc, USA) to determine $rETR_m$ (µmol electron m^{-2} s^{-1}) and NPQ_{max}, α and β, which are unitless. E_k (µmol quanta m^{-2} s^{-1}) was determined as $rETR_m/\alpha$. Gain was set to 3 for all samples, except for the cleaned sand-covered stolons of *C. cupressoides* and the whitish lobes of *Halimeda opuntia* whereby gains were set to 6 and 12, respectively, to get reliable fluorescence signals.

For the seagrass, *Thalassodendron ciliatum* (Fig. 2A, B), the photo-physiological performance of three different parts of the plant were measured: 1) leaf; 2) transition part between leaf and stem (transit); and 3) stem (Fig. 2C). For the other seagrasses tested, measurements were taken on the leaves only. In the case of the macroalga *Caulerpa cupressoides* (Fig. 2B), chlorophyll fluorescence measurements were carried out at two parts: 1) frond; and 2) stolon (Fig. 2D). For the *C. cupressoides* stolons, exposed and sand-covered were also compared, with the sand on the stolon physically removed prior to measurements (Fig. 2D). Upon collection, some stolons were exposed (not-covered) and others were covered by sand. Prior to PAM measurements, sand-covered stolons were cleaned after collection and thus both exposed and sand-covered (but cleaned) stolons were measured in a similar manner for reliable comparison. For the other macroalgae studied, measurements were taken on the frond. For the macroalga *Halimeda*, measurements were taken on the green and white lobes to test the effect of discolouration.

Statistical analyses

Photo-physiological parameters such as Φ_{PSII}, $rETR_m$, NPQ_{max}, α, β, and E_k were analysed using the software PASW Statistics 18. The data was expressed as mean±SD from three replicates (n=3). The raw data was Arcsine square root transformed prior to ANOVA tests. The two-way ANOVA was employed to test the effect of seawater depth on body parts in terms of photo-physiological parameters in *T. ciliatum* and *C. cupressoides*. The one-way ANOVA was used to test for the effect of exposure of stolon (exposed vs covered with sand) on photo-physiological parameters in *C. cupressoides* and the effect of colour (greenish vs whitish) on photo-physiological parameters in *H. opuntia*.

Results and discussion

Seagrass and macroalgae identification

Two seagrass species, namely, *Thalassodendron ciliatum* and *Halophila decipiens*, and seven macroalgae species, namely, *Caulerpa cupressoides*, *Acrosorium ciliolatum*, *Dictyosphaeria cavernosa*, *Halimeda opuntia*, *Udotea orientalis, Udotea palmetta*, and *Ulva* sp. were collected from different depths (Table 1).

Photo-physiology of different parts of *T. ciliatum* and *C. cupressoides*

T. ciliatum and *C. cupressoides* from S13 and S39 at Saya de Malha and S44 at Nazareth, respectively, were used for assessing the variation in photo-physiology of the parts of these seaplants. All the photo-physiological parameters investigated differed significantly across the body parts for *T. cilatum* (Table 2). The mean Φ_{PSII}, $rETR_m$, NPQ_{max}, α, β and E_k of the seagrass *T. ciliatum* ranged from 0.77 to 0.84, 4.81 to 28.31, 0.44 to 1.07, 0.27 to 0.96 0.02 to 0.05 and 18.31 to 74.43, respectively (Fig. 3A-F). Φ_{PSII} was highest in the leaf of *T. ciliatum* (Fig. 3A), while the $rETR_m$ was highest in the transit part at NZB and in the stem at SMB (Fig. 3B). The NPQ_{max} was highest in leaf part of *T. ciliatum* (Fig. 3C). Photosynthetic efficiency (α) was higher in transit and stem for SMB, while it was lowest in the transit part at NZB (Fig. 3D). Photo-inhibition (β) was highest in the transit part in samples from NZB (Fig. 3E). The light saturation (E_k) was highest in transit and stem parts for NZB and SMB samples, respectively (Fig. 3F).

Both the frond and stolon of the macroalga *C. cupressoides* exhibited significantly variable photosynthetic performance (Table 3). The mean Φ_{PSII}, $rETR_m$, NPQ_{max}, α, β and E_k ranged from 0.55 to 0.81, 3.68 to 13.60, 0.09 to 7.37, 0.10 to 0.99, 0.00 to 0.47 and 3.72 to 25.77, respectively (Fig. 4A-F).

Table 1. Species of seagrasses and macroalgae collected from Saya de Malha and Nazareth Banks and used for chlorophyll fluorescence measurements. For light and salinity, data were available at the specified depths in brackets at respective locations.

Location	Depth of collection (m)	Temp (oC)	Light (µmol quanta m-2 s-1)	Salinity (PSU)	Seagrass species	Macroalgal species
SMB-S3	79.0	23.3	10.81 (at 66 m)	35.1 (at 66 m)	-	*Caulerpa cupressoides, Acrosorium ciliolatum*
SMB-S4	31.0	28.4	27.2 (at 22 m)	34.4 (at 22 m)	-	*Dictyosphaeria cavernosa; Halimeda opuntia*
SMB-S13	29.0	28.3	21.1 (at 21 m)	34.3 (at 21 m)	*Thalassodendron ciliatum*	*Caulerpa cupressoides*
SMB-S39	33.0	28.1	-	-	-	*Caulerpa cupressoides*
NB- S43	44.0	27.3	15.1 (at 25 m)	34.3 (at 25 m)	*Halophila decipiens*	*Udotea orientalis, Udotea palmetto, Caulerpa cupressoides*
NB-S44	40.0	27.1	15.0 (at 25 m)	34.1 (at 25 m)	*Thalassodendron ciliatum*	*Udotea orientalis, Ulva* sp.

Table 2. Two-way ANOVA for the effect of depth (29 m and 40 m) and plant parts (leaf, transit and stem) on photo-physiological features of *Thalassodendron ciliatum*. Asterisks ***, ** and * represent significant differences at $P<0.001$, $P<0.01$ and $P<0.05$, respectively.

	Source of Variation	SS	df	MS	F	P-value
Φ_{PSII}	Depth	0.008	1	0.008	25.570	0.000^{***}
	Plant parts	0.042	2	0.021	65.698	0.000^{***}
	Depth x Plant parts	0.014	2	0.007	21.723	0.000^{***}
$rETR_m$	Depth	0.001	1	0.001	8.821	0.012^{*}
	Plant parts	0.003	2	0.002	10.326	0.002^{**}
	Depth x Plant parts	0.021	2	0.011	62.398	0.000^{***}
NPQ_{max}	Depth	0.003	1	0.003	0.864	0.371
	Plant parts	0.029	2	0.015	5.033	0.026^{*}
	Depth x Plant parts	0.003	2	0.002	0.591	0.569
α	Depth	0.976	1	0.976	58.198	0.000^{***}
	Plant parts	0.496	2	0.248	14.774	0.001^{**}
	Depth x Plant parts	0.642	2	0.321	19.128	0.000^{***}
β	Depth	0.055	1	0.055	4.198	0.063
	Plant parts	0.242	2	0.121	9.246	0.004^{**}
	Depth x Plant parts	0.231	2	0.115	8.814	0.004^{**}
E_k	Depth	0.018	1	0.018	52.740	0.000^{***}
	Plant parts	0.025	2	0.013	35.801	0.000^{***}
	Depth x Plant parts	0.052	2	0.026	74.496	0.000^{***}

These results suggest that the leaf, transit part and stem of the seagrass *T. ciliatum* and the frond and stolon of the macroalga *C. cupressoides* were comparably photosynthetically competent. This study highlights the photo-physiological performance of the stem of *T. ciliatum* and the stolon of *C. cupressoides* as also being photosynthetically active and functional. Studies on photo-physiology of seagrasses and macroalgae using the chlorophyll fluorescence technique focus mostly on the leaves and the fronds, respectively, and the conventional methods may use leaves or fronds or parts of entire seaplant communities enclosed in bottles (Beer and Bjork, 2000; Beer *et al.*, 2001; Beer and Axelsson, 2004). Further studies on the relative photosynthetic contributions of the different parts of seagrasses and macroalgae to the whole respective

Table 3. Two-way ANOVA for the effect of depths (29 m, 44 m, and 79 m) and plant parts (frond and stolon) on photo-physiological features of *Caulerpa cupressoides*. Asterisks ***, ** and * represent significant differences at $P<0.001$, $P<0.01$ and $P<0.05$, respectively.

	Source of Variation	SS	df	MS	F	P-value
Φ_{PSII}	Plant parts	0.111	2	0.055	42.426	0.000^{***}
	Depth	0.000	1	0.000	0.359	0.560
	Plant parts x Depth	0.026	2	0.013	9.933	0.003^{**}
$rETR_m$	Plant parts	0.007	2	0.004	27.511	0.000^{***}
	Depth	0.000	1	0.000	3.623	0.081
	Plant parts x Depth	0.003	2	0.001	11.194	0.002^{**}
NPQ_{max}	Plant parts	0.968	2	0.484	180.613	0.000^{***}
	Depth	0.423	1	0.423	157.847	0.000^{***}
	Plant parts x Depth	0.707	2	0.353	131.847	0.000^{***}
α	Plant parts	2.003	2	1.001	153.223	0.000^{***}
	Depth	1.867	1	1.867	285.747	0.000^{***}
	Plant parts x Depth	0.670	2	0.335	51.260	0.000^{***}
β	Plant parts	0.528	2	0.264	40.562	0.000^{***}
	Depth	0.026	1	0.026	3.965	0.070
	Plant parts x Depth	0.443	2	0.222	34.056	0.000^{***}
E_k	Plant parts	0.032	2	0.016	36.752	0.000^{***}
	Depth	0.048	1	0.048	109.678	0.000^{***}
	Plant parts x Depth	0.019	2	0.010	22.203	0.000^{***}

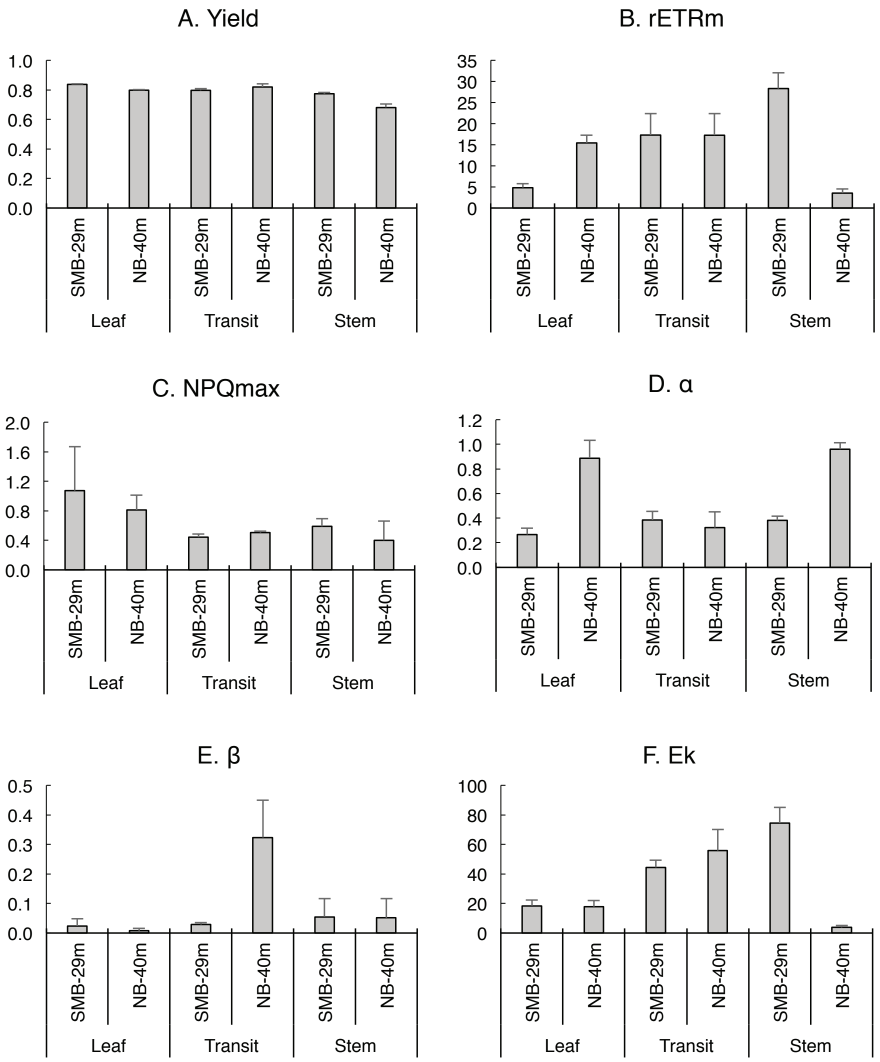

Figure 3. Photo-physiological performance of the seagrass *Thalassodendron ciliatum* from Saya de Malha (SMB) and Nazareth Banks (NB) at 29 m (white bars - S13) and 40 m (black bars - S44), respectively. A. Yield (unitless); B. rETRm (µmol electron m^{-2} s^{-1}); C. NPQmax (unitless); D. α (unitless); E. β (unitless); F. Ek (µmol quanta m^{-2} s^{-1}). Three parts of the plant were measured: 1) leaf; 2) transit part between leaf and stem; and 3) stem. Bars represent Mean±SD (n=3).

individual would help understand these primary producers more thoroughly.

It is noteworthy that there is a tendency to consider mostly the leaves of seagrasses and fronds of macroalgae as being involved in photo-physiological studies. For instance, Campbell *et al.* (2007) using the chlorophyll fluorescence to study photo-physiological variations in seagrasses such as *Thalasodendron ciliatum* and *Halophila decipiens* among other species in tropical Queensland at depths of 2-7 m reported values within the range found for the parameters used in this study. The mean values of Φ_{PSII}, $rETR_m$, α and E_k for *T. ciliatum* were 0.66, 103.9, 0.30, and 365.5 at 2 m and 0.65, 42.6, 0.20, 221.6, respectively. In the case of *H. decipiens*, the mean values of Φ_{PSII}, $rETR_m$, α and E_k were 0.59, 58.5, 0.22 and 294.9, respectively. Olsen *et al.* (2017) documented photo-physiology of macroalgae, in particular *Halimeda* and *Caulerpa* species at depths of 3-5 m around Browse Island off the north-western coast of Western Australia. In October 2017 the mean Φ_{PSII}, $rETR_m$, α, and E_k for *Halimeda* sp. were 0.546, 34.8, 0.36, and 101.1, while for *Caulerpa* sp. the mean values were 0.687, 80.8, 0.41, and 203 for respective parameters. Driscoll (2004) reported photo-physiological performance of three *Caulerpa* species, namely *C. racemosa*, *C. sertularioides*, and *C. mexicana*, at less than 15 m depth from Florida Keys and Tampa Bay, South Florida. For *in-situ C. racemosa* the mean $rETR_m$, NPQ, α, and E_k reported were 4.0-4.4, 0.083-0.098, 0.370-.390, and 27.9-28.4, while

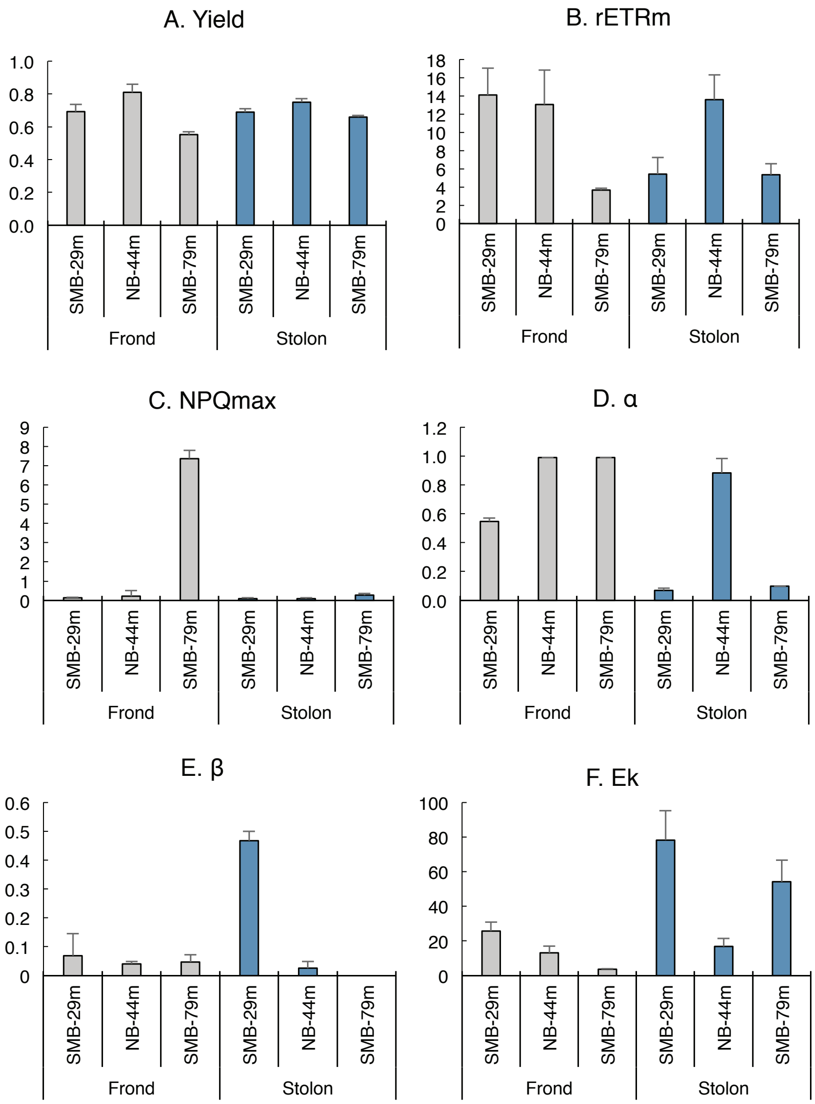

Figure 4. Photo-physiological performance of the macroalgae *Caulerpa cupressoides* from Saya de Malha (SMB) at 29 m (white bars - S13) and 79 m (black bars - S3) and Nazareth (NZB) Banks at 44 m (blue bars - S43). A. Yield (unitless); B. rETRm (µmol electron m^{-2} s^{-1}); C. NPQmax (unitless); D. α (unitless); E. β (unitless); F. Ek (µmol quanta m^{-2} s^{-1}). Two parts of the macroalga were measured: 1) frond; and 2) stolon. Bars represent Mean±SD (n=3).

for *in situ C. sertularioides* the mean values for rETR$_m$, α, and E$_k$ were 7.2-12.8, 0.217-0.257, and 30.3-56.8, respectively. The range of values for the chlorophyll fluorescence parameters seem to be within similar range for the macroalgae tested in the present study. Due to the environmental variability in which these seagrasses and macroalgae were studied and the variability in the values of chlorophyll fluorescence parameters tested, it is difficult to make direct comparison of these values among studies. The present study adds the first report of chlorophyll fluorescence photo-physiological features of seagrasses and macroalgae at depths of ≥29 m deep, with new insights into the photosynthetic performance of the different body parts, including leaf, stem, frond and stolon.

Variation in photo-physiology of *T. ciliatum* and *C. cupressoides* with depth

Availability of samples of the seagrass *T. ciliatum* from depths of 29 m at SMB-S13 and 40 m at NB-S44 (Fig. 3), and macroalga *C. cupressoides* from depths of 29 m at SMB-S13, 44 m at NB-S43 and 79 m at SMB-S3 (Fig. 4) allowed for depth-related photo-physiological performance comparison for the seagrass and macroalga. Significant variation in photo-physiology with seawater depth was noted except for NPQ$_{max}$ and β for the seagrass (Table 2), and Φ_{PSII}, rETR*m* and β for the macroalga (Table 3). It is noteworthy that the interaction between depth and body parts was found to be significant (Table 2). The depth at which samples were collected did reflect variations in light levels (Table 1) and thus different body parts of *T. ciliatum* and *C. cupressoides* may have differential photo-acclimatory capacities. However, in this study pigment analyses were not conducted and this aspect warrants future investigation.

In the case of *T. ciliatum* (Fig. 3A-F), the leaf had slightly reduced Φ_{PSII}, higher $rETR_m$ and α, and similar β and E_k at 40 m in comparison to 29 m, suggesting higher photosynthetic activity at 40 m. The transit part between leaf and stem (transit) exhibited slightly higher Φ_{PSII} and E_k, higher β and similar $rETR_m$ and NPQ_{max} at 40 m relative to 29 m, implying similar photosynthetic activity at these two depths. The stem had a significantly lower Φ_{PSII}, $rETR_m$ and E_k, similar NPQ_{max} and higher α at a depth of 40 m compared to those parameters at 29 m. This may be indicative of reduced photosynthetic activity and lower light saturation levels. Thus, these results generally indicate that the photosynthetic activity increased in the leaf, decreased in the stem and was similar in the transit part of *T. ciliatum* in deeper waters. One possible explanation for this may be that leaves are the most important photosynthetic part of the seagrass and may adjust to lower light levels at a depth of 40 m. In other words, the conditions at this depth may be optimal for photosynthesis in the leaf part of *T. ciliatum*.

For *C. cupressoides* (Fig. 4A-F), with reference to the values at 29 m in the frond, the Φ_{PSII} increased at 44 m but decreased at 79 m; $rETR_m$ was similar at 44 m but decreased at 79 m; NPQ_{max} was similar at 44 m and increased at 79 m; α increased at both 44 m and 79 m; β remained similar, and E_k decreased with depth. In the stolon part, Φ_{PSII} increased at 44 m but decreased at 79 m; $rETR_m$ increased at 44 m but remained unchanged at 79 m; NPQ_{max} remained unchanged at 44 m but increased slightly at 79 m; α increased at 44 m but remained unchanged at 79 m; β decreased with depth; and E_k decreased at a higher level at 44 m. The results may indicate that the frond of *C. cupressoides* may perform equally well photosynthetically at 44 m but not at 79 m when compared to that at 29 m. While the stolon of *C. cupressoides* may perform equally well photo-physiologically at 79 m and better at 44 m compared to that at 29 m.

Photo-physiology of *C. cupressoides* stolons exposed vs covered by sand

The stolon covered by sand and that not covered by sand was compared At S39. The covered stolon had significantly lower $rETR_m$ (Table 4) and slightly lower Φ_{PSII}, similar NPQ_{max} and β but slightly higher β (Fig. 5A-F). This indicates that the stolon of *C. cupressoides* that burrowed under the sand may be slightly affected in terms of electron transport rate and was not chronically damaged, implying the possibility of maintaining its photo-physiological functioning though temporarily covered by sand at this station.

Photo-physiology of greenish and whitish *Halimeda opuntia* lobes

Both greenish and whitish lobes of *H. opunitia* from 31 m deep from S39 at Saya de Malha Bank were examined for their photo-physiological functioning (Fig. 6). The whitish lobes of *H. opuntia* at 31 m exhibited significantly lower photosynthetic performance, in terms of Φ_{PSII}, $rETR_m$, α and E_k, than the greenish lobes. The Φ_{PSII} and E_k almost halved; $rETR_m$ decreased seven-fold; NPQ_{max} increased about 40-fold; α decreased by about six-fold; and β increased six-fold in the whitish compared to the greenish lobes. These results suggest that in the whitish condition, the photo-physiology of *H. opuntia* lobes declined drastically. The whitish lobes may be due to either of two processes, namely, sexual reproduction and/or chloroplast movement. It is understood that when *Halimeda* segments reproduce, the edges become whitish while the reproductive cells expel the protoplasmic contents of their spores through a process called holocarpy (Drew and Abel, 1988). These segments die and disintegrate after turning white. The photo-physiology of *Halimeda* under these

Table 4. One-way ANOVA for the effect of exposed or covered stolon on photo-physiological features of *Caulerpa cupressoides*. Asterisk (*) represents significant difference at $P<0.05$.

Parameters	SS	df	MS	F	P-value
Φ_{PSII}	0.013	1	0.013	2.479	0.190
$rETR_m$	0.002	1	0.002	8.547	0.043*
NPQ_{max}	5.386E-06	1	5.386E-06	0.041	0.849
α	0.001	1	0.001	1.733	0.258
β	0.033	1	0.033	1.619	0.272
E_k	0.024	1	0.024	3.342	0.142

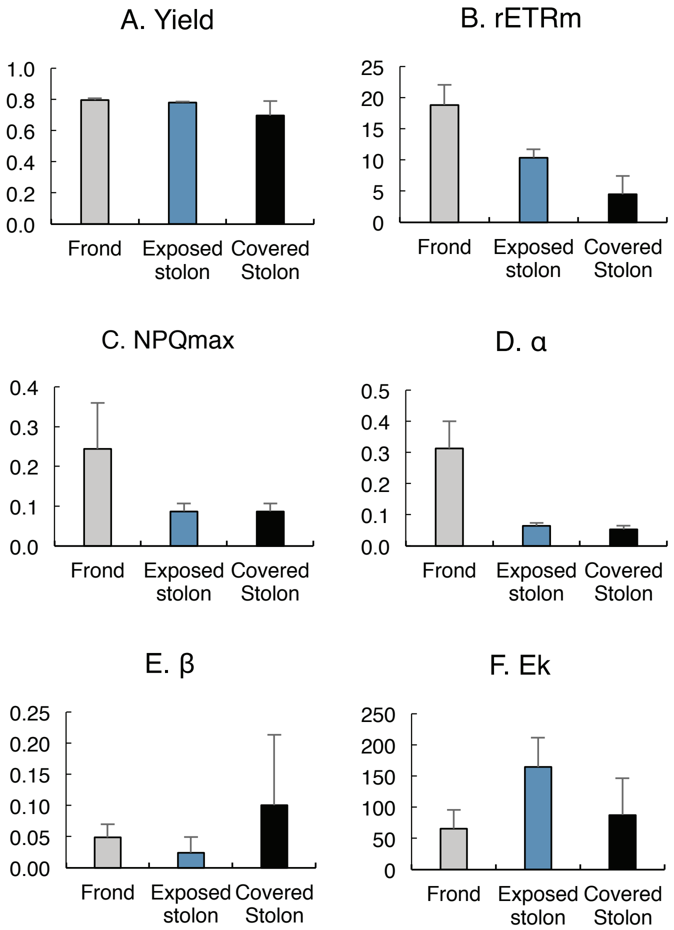

Figure 5. Photo-physiological performance of the macroalgae *Caulerpa cupressoides* from Saya de Malha (SMB) at 33 m (S39). A. Yield (unitless); B. rETRm (µmol electron m^{-2} s^{-1}); C. NPQmax (unitless); D. α (unitless); E. β (unitless); F. Ek (µmol quanta m^{-2} s^{-1}). The parts of the macroalga measured were: 1) frond (white bars); and 2) exposed stolon (not burrowed under sand – blue bars); and 3) covered stolon (mostly burrowed under sand – black bars). Bars represent Mean±SD (n=3).

conditions is not known. The gametogenesis process is known to occur seasonally in *Halimeda* spp. on the Great Barrier Reef (Drew and Abel, 1988).

Chloroplast redistribution in *Halimeda* leads to changes from a greenish to a whitish colour. This occurs because *Halimeda* is coenocytic, where the branching filamentous structure lacks crosswalls, and thus allows mass movement of the chloroplasts into the medullary filaments below the calcium carbonate deposits from the utricles at the segment surface (Drew and Abel, 1990). Mass migration of chloroplasts in *Halimeda* has been shown to be rhythmic (Drew and Abel, 1992). The photo-physiology of *Halimeda* under these migrations conditions is not thoroughly understood. However, the photo-physiology of greening in *Halimeda*

Table 5. One-way ANOVA for the effect of greenish or whitish conditions on photo-physiological features of *Halimeda opuntia*. Asterisks ***, ** and * represent significant differences at *P<0.001*, *P<0.01* and *P<0.05*, respectively.

Parameters	SS	df	MS	F	P-value
Φ_{PSII}	0.182	1	0.182	597.553	0.000***
$rETR_m$	235.978	1	235.978	45.855	0.002**
NPQ_{max}	6.045	1	6.045	1.629	0.271
α	0.175	1	0.175	24.036	0.008**
β	0.014	1	0.014	0.904	0.396
E_k	471.263	1	471.263	8.900	0.041*

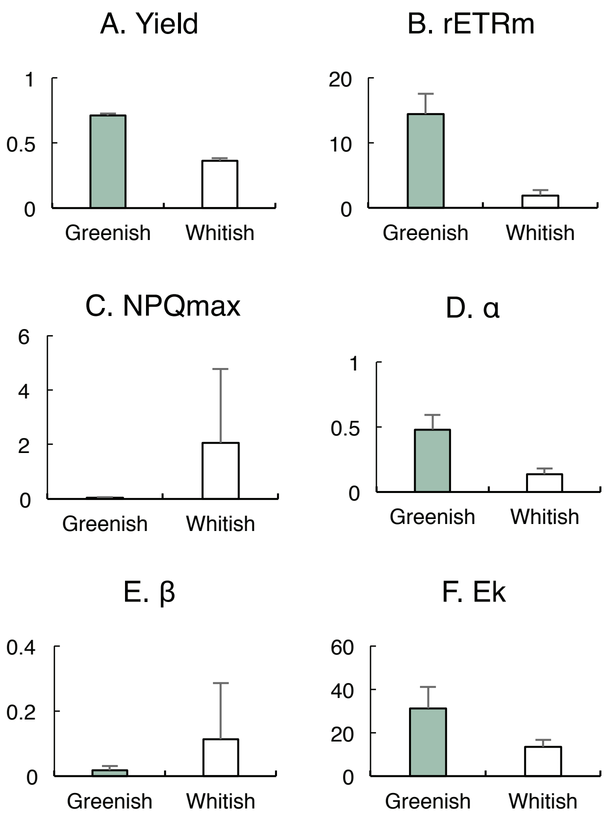

Figure 6. Photo-physiological performance of the greenish (green bars) and whitish (white bars) lobes of the macroalga *Halimeda opuntia* from a depth of 31 m at S4 at Saya de Malha. A. Yield (unitless); B. rETRm (µmol electron m^{-2} s^{-1}); C. NPQmax (unitless); D. α (unitless); E. β (unitless); F. Ek (µmol quanta m^{-2} s^{-1}). Bars represent Mean±SD (n=3).

Table 6. Photo-physiological performance of other seagrass (leaf) and macroalgal (frond) species collected from Saya de Malha Bank (SMB) and Nazareth Bank (NZB).

Species	Bank-Location-depth (m)	Photo-physiological parameters					
		Φ_{PSII}	$rETR_m$	NPQ_{max}	α	β	E_k
Seagrass							
Thalassodendron ciliatum	SMB-S13-29	0.84±0.00	4.81±1.00	1.07±0.60	0.27±0.03	0.02±0.03	18.31±4.00
	NZB-S44-40	0.80±0.00	15.42±1.79	0.81±0.20	0.89±0.15	0.01±0.01	17.84±4.33
Halophila decipiens	NZB-S43-44	0.63±0.00	2.94±0.43	0.46±0.12	0.99±0.00	0.01±0.01	2.97±0.43
Macroalgae							
Caulerpa cupressoides	SMB-S13-29	0.96±0.04	14.11±2.92	0.14±0.02	0.55±0.02	0.06±0.08	25.77±5.20
	NZB-S43-44	0.81±0.50	13.06±3.78	0.22±0.30	0.99±0.00	0.04±0.01	13.20±3.81
	SMB-S3-79	0.55±0.02	3.68±0.21	7.37±0.42	0.99±0.00	0.05±0.02	78.23±0.21
Halimeda opuntia	SMB-S39-31 (green lobes)	0.71±0.01	14.42±3.08	0.05±0.01	0.49±0.11	0.02±0.01	31.23±9.79
	SMB-S39-31 (white lobes)	0.36±0.02	1.88±0.89	2.06±2.72	0.14±0.04	0.11±0.17	13.50±3.18
Acrosorium ciliolatum	SMB-S3-79	0.36±0.04	11.19±1.21	0.13±0.08	0.07±0.01	0.00±0.00	161.09±8.18
Dictyosphaeria cavernosa	SMB-S4-31	0.73±0.04	46.77±33.61	0.61±0.09	0.34±0.08	0.04±0.05	127.38±66.91
Udotea orientalis	NZB-S44-40	0.68±0.00	10.25±2.35	0.15±0.02	0.98±0.01	0.05±0.02	10.48±2.50
Ulva sp.	NZB-S44-40	0.67±0.05	28.84±10.46	0.06±0.10	0.54±0.39	0.03±0.01	79.95±54.51
Udotea orientalis	NZB-S43-44	0.73±0.01	5.53±0.67	0.17±0.02	0.99±0.00	0.06±0.01	5.58±0.68
Udotea palmetto	NZB-S43-44	0.75±0.00	25.75±7.84	0.31±0.10	0.48±0.27	0.15±0.22	64.24±6.56

macroloba, where rapid mass movement of chloroplasts occurs in newly formed fronds during the night, has been captured progressively by an Imaging-PAM (Larkum *et al.*, 2011).

Variation in photo-physiology in the other seagrass and macroalgae studied

The other seagrass studied here, *Halophila decipiens*, and macroalgae, including *Acrosorium ciliolatum*, *Dictyosphaeria cavernosa*, *Ulva* sp., *Udotea orientalis*, and *Udotea palmetta* exhibited variable photo-physiological performances (Table 6). These could be potentially used as baseline data for future works, though these measurements and chlorophyll fluorescence-derived parameters are relative values and may not be directly used for comparative purposes.

Conclusions

This is the first study to document the photo-physiology of two seagrass and seven macroalgal species from the Saya de Malha and Nazareth Banks, Mascarene Plateau. *Thalassodendron ciliatum* and *Caulerpa cupressoides* exhibited variable photo-physiology among their body parts and with depths. The photosynthetic activity increased in the leaf, decreased in the stem and was similar in the transit part between the leaf and the stem of *T. ciliatum* at 40 m compared to 29 m depth. Photo-physiological functioning of the leaf of *T. ciliatum* was optimal at 40 m. The photosynthetic performance of the frond of *C. cupressoides* was similar at 44 m but decreased at 79 m when compared to that at 29 m, while the stolon of *C. cupressoides* performed equally well at 79 m and better at 44 m compared to that at 29 m. The photosynthetic performance of the whitish lobes of *H. opuntia* at 31 m was poorer compared to the greenish ones. Variable photo-physiology among the other studied seagrass and macroalgae were also documented. These results provide a first insight into the plant part-, seawater depth- and colour-related photo-physiological performance of seaplants from the Mascarene Plateau. Future research on photo-physiology of other seagrass and macroalgal species from this region would further shed light on their photosynthetic features and their biological and ecological importance on the Mascarene Plateau.

Acknowledgments

We are grateful to the Food and Agriculture Organization (FAO) EAF-Nansen programme for supporting participation in the Indian Ocean Research Expedition 2018 (NORAD-FAO PROJECT GCP/INT/730/NOR) to the Saya de Malha and Nazareth Banks on board the “R/V Dr Fridtjof Nansen”, the Department for Continental Shelf, Maritime Zones Administration & Exploration of Mauritius for co-leading and coordinating the scientific expedition, the Joint Management Commission for their support and assistance, the Ministry of Blue Economy, Marine Resources, Fisheries and Shipping for granting the permits for sampling and the University of Mauritius for logistic support. RB is thankful to the Mauritius Research and Innovation Council for funding (K0460 and K0461) studies on macroalgae of the Republic of Mauritius. We also acknowledge the support of our fellow participants on the expedition: OA Bergstad, D Bissessur, K Sauba, J Rama, P Coopen, Y Oozeeraully, S Seeboruth, A Audit-Manna, A Nicolas, N Reetoo, D Kuyper, G Gendron, A Souffre, S Hollanda, R Melanie, J Harlay, L Caussy, K Tabachnick, M Olsen and TM Ensrud. The authors are grateful to the anonymous reviewer/s for insightful comments that have significantly improved the manuscript.

References

Aguilera J, Bischof K, Karsten U, Hanelt D, Wiencke C (2002) Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord. II. Pigment accumulation and biochemical defence systems against high light stress. Marine Biology 140 (6): 1087-1095

Beer S, Bjork M (2000) A comparison of photosynthetic rates measured by pulse amplitude modulated (PAM) fluorometry and O_2 evolution in two tropical seagrasses. Aquatic Botany 66: 69-73

Beer S, Larsson C, Poryan O, Axelsson L (2000) Photosynthetic rates of *Ulva* (Chlorophyta) measured by pulse amplitude modulated (PAM) fluorometry. European Journal of Phycology 35: 69-74

Beer S, Björk M, Gademann R, Ralph P (2001) Measurements of photosynthetic rates in seagrasses. In: Short FT, Coles R (eds) Global seagrass research methods. Elsevier Publishing, The Netherlands. pp 183-198

Beer S, Axelsson L (2004) Limitations in the use of PAM fluorometry for measuring photosynthetic rates of macroalgae at high irradiance. European Journal Phycology 39 (1): 1-7

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

Bilger W, Bjorkman O (1990) Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*. Photosynthesis Research 25 (3): 173-185

Bischof K, Gómez I, Molis M, Hanelt D, Karsten U, Lüder U, Wiencke C (2006) Ultraviolet radiation shapes seaweed communities. In: Life in extreme environments. Springer, Dordrecht, Netherlands. pp 187-212 [https://doi.org/10.1007/978-1-4020-6285-8_12]

Cabaço S, Santos R, Duarte CM (2008) The impact of sediment burial and erosion on seagrasses: a review. Estuarine, Coastal and Shelf Science 79: 354-366

Campbell SJ, McKenzie LJ, Kerville SP, Bite´ JS (2007) Patterns in tropical seagrass photosynthesis in relation to light, depth and habitat. Estuarine, Coastal and Shelf Science 73: 551-562

Campbell SJ, Kerville SP, Short F (2008) Photosynthetic responses of subtidal seagrasses to a daily light cycle in Torres Strait: A comparative study. Continental Shelf Research 28 (16): 2275-2281

Chinese Herbs Healing (2020) Plastids in root of *Taeniophyllu*m. [https://www.chineseherbshealing.com/rain-forest/roots.html]

Chisholm JRM, Moulin P (2003) Stimulation of nitrogen fixation in refractory organic sediments by *Caulerpa taxifolia* (Chlorophyta). Limnology and Oceanography 48: 787-794

Cook CDK, Rutishauser R (2007) Podostemaceae. In: Kubitzki K (ed) Flowering plants · Eudicots. The families and genera of vascular plants, vol 9. Springer, Berlin, Heidelberg. [https://doi.org/10.1007/978-3-540-32219-1_40]

Davison IR, Pearson GA (1996) Stress tolerance in intertidal seaweeds. Journal of Phycology 32 (2): 197-211

Drew EA, Abel KM (1988) Studies on *Halimeda* II. Reproduction, particularly the seasonality of gametangia formation, in a number of species from the Great Barrier Reef Province. Coral Reefs 6: 207-218

Drew EA, Abel KM (1990) Studies on *Halimeda*. III. A daily cycle of chloroplast migration within segments. Botanica Marina 33: 31-45

Drew EA, Abel KM (1992) Studies on *Halimeda.* IV. An endogenous rhythm of chloroplast migration in the siphonous green alga, *H. distorta*. Journal of Interdisiplinary Cycle Research 23 (2): 128-135

Driscoll MD (2004) Effects of hydrodynamic regime on photosynthesis in the green alga *Caulerpa*. Graduate Theses and Dissertations. University of South Florida. 87 pp

Durako MJ, Kunzelman JI (2002) Photosynthetic characteristics of *Thalassia testudinum* Banks ex König measured *in situ* by pulse amplitude modulated (PAM). Aquatic Botany 73: 173-185

Fonseca MS, Kenworthy WJ (1987) Effects of current on photosynthesis and distribution of seagrasses. Aquatic Botany 27: 59-78

Fredericq S, Freshwater D W, Hommersand MH (1999) Observations on the phylogenetic systematics and biogeography of the Solieriaceae (Gigartinales, Rhodophyta) inferred from rbcL sequences and morphological evidence. Hydrobiologia 398/399: 25-38

Genty B, Briantais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochimica et Biophysica Acta 990 (1): 87-92

Glasby TM, Gibson PT, Kay S (2005) Tolerance of the invasive marine alga *Caulerpa taxifolia* to burial by sediment. Aquatic Botany 82: 71-81

Grable AR (1966) Soil aeration and plant growth. Advances in Agronomy 18: 57-106

Gullstrom M, de la Torre Castro M, Bandeira SO, Bjork M, Dahlberg M, Kautsky N, Ronnback P, Ohman MC (2002) Seagrass ecosystems in the Western Indian Ocean. Ambio 31 (7): 588-596

Hagan A, Robinson J (2001) Benthic habitats of the Saya de Malha Bank. Marine Science, training, and education in the western Indian Ocean. 30 Reefs, Symposium of the Zoological Society of London 28. pp 26-27

Hilbertz W, Goreau T (2002) Saya de Malha Expedition report. Lighthouse Foundation Project. 101 pp

Infantes E, Terrados J, Orfila A (2011) Assessment of substratum effect on the distribution of two invasive *Caulerpa* (Chlorophyta) species. Estuarine, Coastal and Shelf Science 91: 434-441

Ishimaru K, Kubota F, Saitou K, Nakayama M (1996) Photosynthetic response and carboxylation activity of enzymes in leaves and roots of water chestnut *Trapa bispinosa* Roxb. Journal of the Faculty of Agriculture, Kyushu University 41: 57-65

Klein J, Verlaque M (2008) The *Caulerpa racemosa* invasion: a critical review. Marine Pollution Bulletin 56: 205-225

Koch EW, Ackerman JD, Verduin J, van Keulen M (2006) Fluid dynamics in seagrass ecology - from molecules to ecosystems. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: Biology, ecology and conservation. Springer, Netherlands. pp 193-224

Larkum AWD, Salih A, Kuhl M (2011) Rapid mass movement of chloroplasts during segment formation of the calcifying siphonalean green alga, *Halimeda macroloba*. PLoS ONE 6 (7): e20841 [doi:10.1371/journal.pone.0020841]

Li W, Park J, Park SR, Zhang X, Lee K (2010) Chlorophyll a fluorescence as an indicator of establishment of *Zostera marina* transplants on the southern coast of Korea. Algae 25 (2): 89-97

Li XM, Zhang QS, Tang YZ, Yu YQ, Liu HL, Li LX (2014) Highly efficient photoprotective responses to high light stress in *Sargassum thunbergii* germlings, a representative brown macroalga of intertidal zone. Journal of Sea Research 85: 491-498

Major KM, Dunton KH (2000) Photosynthetic performance in *Syringodium filiforme*: seasonal variation in light-harvesting characteristics. Aquatic Botany 68: 249-264

Milchakova NA, Phillips RC, Ryabogina VG (2005) New data on the locations of seagrass species in the Indian Ocean. National Museum of Natural History Smithsonian Institution. Washington, DC, USA. Atoll Research Bulletin 537: 178-187

Olesen B, Enríquez S, Duarte CM, Sand-Jensen K (2002) Depth acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea. Marine Ecology Progress Series 236: 89-97

Oliveira EC, Osterlund K, Mtolera MSP (2005) In: Sporrong N, Bjork M (eds) Marine plants of Tanzania. A field guide to the seaweeds and seagrasses. Botany Department, Stockholm University, Sweden. 267 pp

Olsen YS, Bessey C, McLaughlin J, Keesing J (2017) 2017 Annual Report: Patterns in primary producers, herbivory and reef metabolism around Browse Island. Australian Institute of Marine Science and Shell Development (Australia) Pty Ltd (Shell) and INPEX Operations Australia Pty Ltd. Shell/INPEX ARP7-2 Milestone 2017 Report #2. 69 pp

Piazzi L, Balata D, Ceccherelli G, Cinelli F (2005) Interactive effect of sedimentation and *Caulerpa racemosa* var. cylindracea invasion on macroalgal assemblages in the Mediterranean Sea. Estuarine, Coastal and Shelf Science 64: 467-474

Platt T, Galleoos CL, Harrison WG (1980) Photoinhibition of photosynthesis in natural assemblages of marine photoplankton. Journal of Marine Research 38: 687-701

Ralph PJ (1999) Light-induced photoinhibitory stress responses of laboratory-cultured *Halophila ovalis*. Botanica Marina 42 (1): 11-22

Ralph PJ, Gademann R (2005) Rapid light curves: a powerful tool for the assessment of photosynthetic activity. Aquatic Botany 82: 222-237

Rich SM, Ludwig M, Colmer TD (2008) Photosynthesis in aquatic adventitious roots of the halophytic stem-succulent *Tecticornia pergranulata* (formerly *Halosarcia pergranulata*). Plant, Cell and Environment 31: 1007-1016

Riis T, Hawes I (2003) Effect of wave exposure on vegetation abundance, richness and depth distribution of shallow water plants in a New Zealand lake. Freshwater Biology 48: 75-87

Schagerl M, Möstl M (2011) Drought stress, rain and recovery of the intertidal seaweed *Fucus spiralis*. Marine Biology 158 (11): 2471-2479

Serôdio J, Vieira S, Cruz S, Coelho H (2007) Rapid light-response curves of chlorophyll fluorescence in microalgae: relationship to steady-state light curves and non-photochemical quenching in benthic diatom-dominated assemblages. Photosynthesis Research 90 (1): 29-43

Taylor WR (1960) Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor. 870 pp

Thibaut T, Meinesz A, Coquillard P (2004) Biomass seasonality of *Caulerpa taxifolia* in the Mediterranean sea. Aquatic Botany 80: 291-297

van De Poll WH, Eggert A, Buma AGJ, Breeman AM (2001) Effects of UV-B-induced DNA damage and photoinhibition on growth of temperate marine red macrophytes: habitat-related differences in UV-B tolerance. Journal of Phycology 37 (1): 30-38

Vortsepneva E (2008) Saya de Malha Bank – an invisible island in the Indian Ocean. Geomorphology, Oceanology, Biology. Moscow State University, Moscow, Russia. 44 pp