Variations in abundance, diversity, photo-physiology and estimated productivity of micro-phytoplankton with depth at the Saya de Malha Bank, Mascarene Plateau

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Abstract

The variations in micro-phytoplankton abundance, diversity, photo-physiology, chlorophyll *a* (Chl*a*) concentration and estimated productivity were assessed at depth ranges of 0-4, 5-10, and 11-29 m with 100, 28 and 11% of irradiance, respectively, in Saya de Malha waters. The total micro-phytoplankton abundance (TMPA) differed significantly ($P < 0.001$) with depth ranges, and between day and night samples. Out of the 34 genera identified, 27 showed a decrease in abundance of over 40% with depth. *Chaetoceros*, *Coscinodiscus*, *Navicula*, *Nitzschia* and *Ceratium* were most dominant. The Shannon-Wiener (H') diversity index did not differ among depth ranges and between samples collected during day and night, but diatoms were more diverse than dinoflagellates. The effective quantum yield (Φ_{PSII}) and the light-use efficiency factor (α) tended to decrease, while the maximum relative electron transport rate (rETR$_{max}$), the photo-inhibitory factor (β) and the maximum non-photochemical quenching (NPQ$_{max}$) varied insignificantly from morning to afternoon sampling points at all depth ranges studied. The estimated productivity, rETR$_{max}$ and Chl*a* concentration decreased with depth ranges. The higher diversity of diatoms, better photosynthetic performance in the morning hours and higher near-surface estimated productivity provide new insights into micro-phytoplankton dynamics and productivity in Saya de Malha waters.

Keywords: estimated productivity, micro-phytoplankton, photo-physiology, water column, Saya de Malha, Mascarene Plateau

Introduction

Phytoplankton form the base of the marine food chain and are one of the most important biological components that regulate life in the ocean. In the open ocean, there are several parameters that influence the diversity, distribution and photo-physiological state of phytoplankton. The variation of phytoplankton is less affected by anthropogenic activities in the open ocean compared to the coastal regions. The abundance and distribution of phytoplankton in the open ocean is mostly governed by mixing processes, more specifically vertical mixing which eventually promotes changes in the light and nutrient availability, and influence the growth performance of the micro-algae

(Diehl, 2002). At a depth where there is limited light, even if there is high nutrient flux from the deeper waters, the phytoplankton density will remain low due to the lower photosynthetic activity (Bode *et al.*, 1996). Moreover, species-wise, Margalef (1978) demonstrated that resilient vertical mixing is more advantageous for diatom dominance compared to dinoflagellates where the dinoflagellates were found to choose to migrate towards more stratified water columns. The locomotive advantage of the dinoflagellates provides them with the ability to swim to zones rich in nutrients and light (Glibert, 2016; Smayda and Reynolds, 2003).

Being a primary producer, the phytoplankton is consumed by the zooplankton. During night-time, there is absence of light and thus, the primary productivity decreases and zooplankton tends to move to the upper water layer to graze on the free floating phytoplankton (Roman *et al.*, 1988). This migration of zooplankton, which is at the same time an escape from larger predators in the deep waters, has been well studied by Shaw and Robinson (1998). The grazing capacity of the zooplankton will impact the density and abundance of certain species of phytoplankton. Moreover, Goldyn and Kowalczewska-Madura (2007) have demonstrated that a high density of zooplankton tends to cause a significant decrease in the phytoplankton community.

The photo-physiological state of all photosynthetic organisms depends mainly on the availability of irradiance. McMinn *et al.* (2003) reported the dependence of the variability of maximum relative electron transport rate (rETR$_{max}$) on irradiance, but at the same time stated that the observation varied due to the changing weather conditions in the Antarctica, and in the natural environment, the change in intensity of light is not consistent. Excess irradiance causes harm to the photosystem of photosynthetic organisms (Aro *et al.*, 1993). In order to prevent this damaging effect, photosynthetic organisms have established a defense mechanism which disperses excess light energy as heat. This process is called non-photochemical quenching (NPQ) which is identified as a decrease in chlorophyll fluorescence (Guidi *et al.*, 2019; Krause and Weis, 1991). The diatom dissipates thermal energy via the xanthophyll cycle (Kashino and Kudoh, 2003). This is why diatoms have rapidly-inducible NPQ, and sustain high photochemical activities through a wide range of light intensities (Buck *et al.*, 2019; Derks and Bruce, 2018). The Western Indian Ocean is among the regions that have been least studied during the past years with very

few studies conducted on phytoplankton (Armance *et al.*, 2019; Sadally *et al.*, 2012; Sadally *et al.*, 2014a, 2014b; Sadally *et al.*, 2015; Sadally *et al.*, 2016; Sandooyea *et al.*, 2020; Schlüter *et al.*, 2011; Soondur *et al.*, 2020).

Studies on phytoplankton and their photo-physiology are limited in the Saya de Malha region, which is a fishing bank that is considered to be among the world's largest fishing areas covering over 44,130 km², and is conjointly managed by the Republic of Mauritius and the Republic of Seychelles. An indicative decrease in total fish catch from 2010 to 2011 of nearly 6 tonnes has been reported at the bank. In 2011, around 1,472 tonnes of frozen fish were caught from the region of Saya de Malha which highlights its importance for the fisheries sector. Over 80% of fish are caught from depths of 15-50 m (Bhagooli and Kaullysing, 2019). Given the known relationship between productivity and fish catch, studies on productivity and micro-phytoplankton in the water column of this region are imperative. The present study aimed at determining the change in species composition and abundance of micro-phytoplankton and their photo-physiological features, together with the estimated productivity across different depth ranges in the Saya de Malha region. The objectives were to: 1) investigate the spatial and depth variation of micro-phytoplankton abundance and diversity; 2) compare the abundance of micro-phytoplankton between samples collected during the day and night; and 3) investigate the general trend in the variation of Chl*a*, estimated productivity and photo-physiological parameters in response to different depth ranges for samples collected during the day.

Methodology
Study site, stations and sampling strategy
This study was conducted in May 2018, during the southern hemisphere winter which is a low rainfall period, on board the R/V Dr Fridtjof Nansen during the Indian Ocean Research Expedition 2018l in the region of the Saya de Malha Bank located in the Southern Indian Ocean (Fig. 1a). A CTD was used for seawater sample collection and sensors to record light intensity. For the determination of the micro-phytoplankton density and abundance, *in-situ* Chl*a* concentration and estimated productivity, samples were collected at three different depth ranges: 0-4 m; 5-10 m; and 11-29 m at seven stations during the day (391, 394, 397, 400, 401, 404 and 408) and six stations during the night (393, 396, 398, 403, 412 and 416) (Fig. 1b). All samples were collected in triplicates. Level 3 satellite sea surface Chl*a* (MODIS-Aqua

MODISA_L3m_Chl*a*_8d_4km vR2019.0) and sea surface temperature (MODIS-Aqua MODISA_L3m_SST_8d_4km vR2019.0) data were extracted from AquaMODIS and processed on GIOVANNI version 4.35 (https://giovanni.gsfc.nasa.gov/giovanni/).

Micro-phytoplankton and Chl*a* sampling, preservation and analysis

The CTD was deployed at each station and samples were collected from the Niskin bottles at respective depths, and 10 L of sea water were filtered through a plankton net of 5 μm mesh size. The filtrate containing the micro-phytoplankton was then preserved using 1% Lugol's solution and stored at 4°C on board the vessel. The samples were later processed in the laboratory where they were centrifuged at 3500 rpm for 10 min-

filtered through Whatman® glass fiber filters of pore size 0.45 μm using an electrical pump. Then, Chl*a* pigment extraction was conducted in 10 ml of 90% acetone. The extract in the liquid acetone was read under a spectrophotometer (Spectronic® GenesysTM 8) at wavelengths 630, 647, 664 and 750 nm after 24 hours. The Chl*a* concentration was determined using the formula:

Chlorophyll a = (11.85* (E_{664} – E_{750}) – 1.54* (E_{647} – E_{750}) – 0.08 (E_{630} – E_{750})) *V_e/L*V_f

Where, L = Cuvette light-path in centimeters; V_e = Extraction volume in milliliters; V_f = Filtered volume in liters; and concentrations were in mgm^{-3} (Jeffrey and Humphrey, 1975).
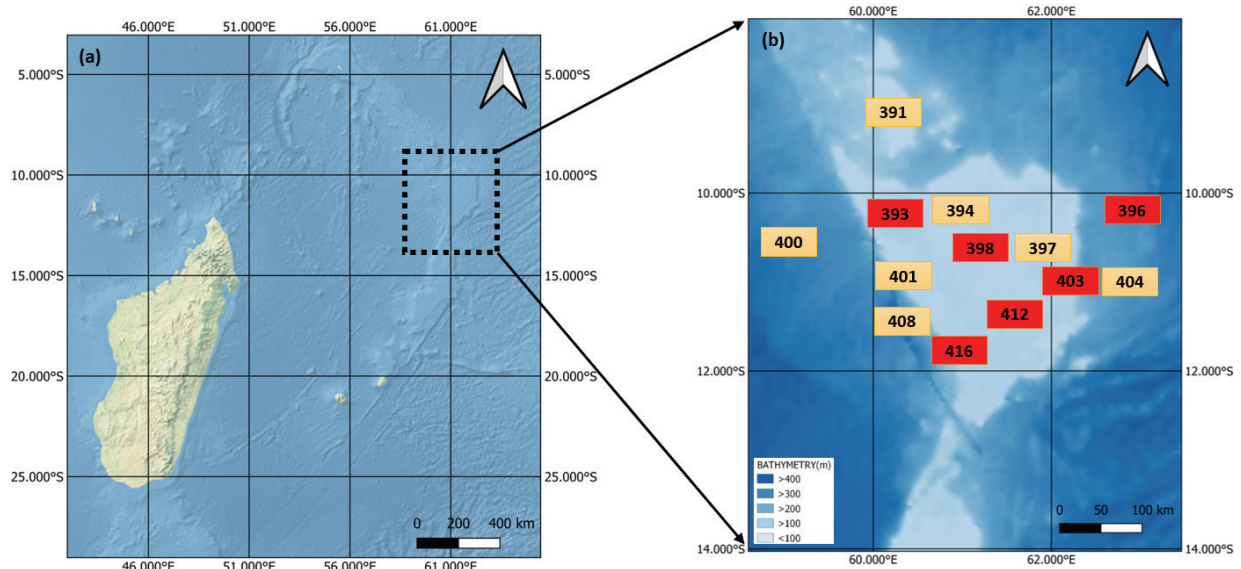

Figure 1. (a) Southern Indian Ocean; and (b) Region of Saya de Malha with yellow and red boxes indicating daytime and night-time sampling stations, respectively, and the blue color indicating the bathymetry data in meters. The CTD station numbers are shown in the boxes.

utes to further concentrate the sample to 1 ml (Mukherjee *et al.*, 2014; Sadally *et al.*, 2014; Zarauz and Irigoien, 2008). The samples were analysed according to Woelkerling *et al.* (1976). The 1 ml micro-phytoplankton sample was loaded on a Sedgwick Rafter counting chamber and quantification was carried out under a light microscope (Devassy and Goes, 1991; Sadally *et al.*, 2014). Furthermore, the species and genera of the micro-phytoplankton were identified according to Tomas (1996).

The sea water samples for Chl*a* analysis were collected from the CTD at respective depths and stations. From the Niskin bottle, 500 ml of water were

Photo-physiology and estimated productivity

The photo-physiology and estimated productivity were assessed only for samples that were collected during daytime. The Diving Pulse Amplitude Modulator (D-PAM) fluorometer (Submersible Photosynthesis Yield Analyzer, Walz, Germany) was used to assess the photo-physiology of micro-phytoplankton by measuring the fluorescence of Chl*a*, thus determining the relative electron transport rate (rETR) and non-photochemical quenching (NPQ) when exposed to a series of rapidly (10 s) changing light climates (RLC) (McMinn *et al.*, 2005, 2012). Phytoplankton were adsorbed on filter papers by filtering seawater samples collected using the CTD at different depths
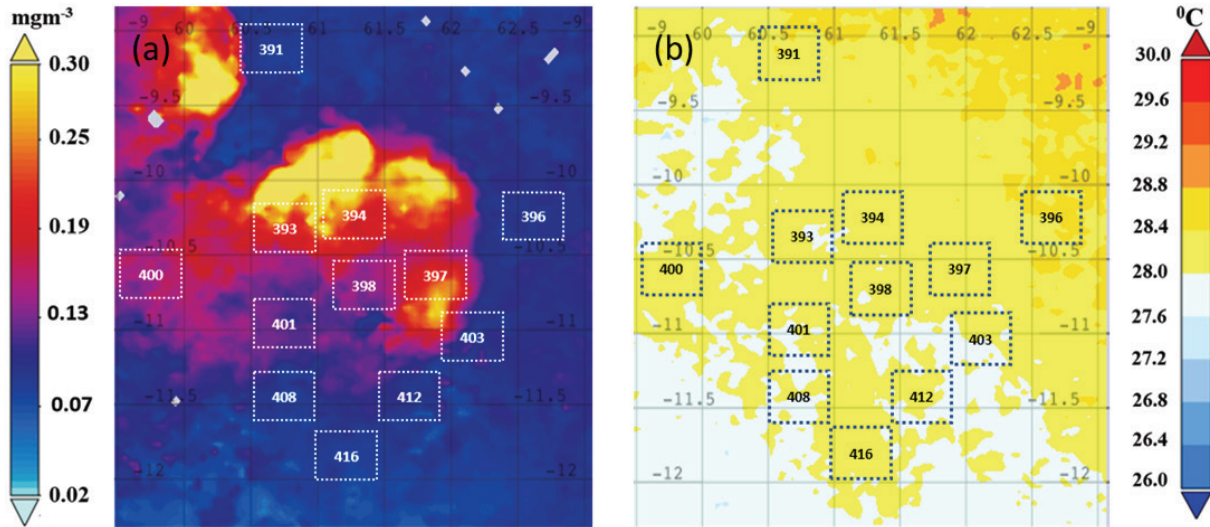
Figure 2. Average satellite AquaMODIS data for: (a) sea surface Chl*a* concentration and (b) sea surface temperature for the region of Saya de Malha for May 2018. The CTD numbers indicated in white colour represent the sampling locations.

through the Whatman® glass fiber filters of pore size 0.45 µm, and immediately analyzed using the D-PAM on-board the research vessel (Bhagooli and Hidaka, 2003; Bhagooli, 2010; Bhagooli *et al.*, 2021). Using the RLCs, the rETR and NPQ were estimated at each irradiance. At each irradiance, the respective relative electron transport rate (rETR) was calculated using the formula rETR= 0.5 x Φ_{PSII} x PAR, where PAR is the photosynthetically active radiance. The different PAR used were 110, 150, 300, 400, 500, 800, 1000 and 1325. The NPQ was calculated based on the formula NPQ = $(F_m-F_m')/F_m'$. The maximum rETR and NPQ WERE calculated using sigma plots (Platt and Jassby, 1976). Furthermore, other photophysiology parameters calculated were Ek ($rETR_{max}/\alpha$) which is the minimum saturating irradiance, and α (light-use efficiency factor measured as the initial slope of the light curve before the onset of saturation) and β (the slope of the light curve beyond the onset of photo-inhibition) was determined from the rETR curve. Estimated relative productivity for each sample at respective sites was calculated using the formula for Estimated productivity, P, defined as P = ($rETR_{max}$× Chl*a*) (McMinn and Hegseth, 2004; McMinn *et al.*, 2005; McMinn *et al.*, 2010).

Statistical analysis

The software PASW Statistics 18 was used to analyze the data. The data was first tested for normality before any further statistical analyses. Non-normally distributed data were transformed via log_{10} or Arcsine. The one-way ANOVA was used to determine any significant differences between the CTD stations, and two-way ANOVA was used to determine significant

differences for the micro-phytoplankton in terms of depth and time. Moreover, a Principle Correspondence Analysis (PCA) was generated to reveal the relationship between all the different parameters analyzed. Shannon-Wiener, Equitability, and Evenness diversity indices were used to determine the variability of the different micro-phytoplankton genera at different depth ranges.

Results

AquaMODIS sea surface Chl*a*, sea surface temperature, light variation with depth, and associated hydrographic data

The average sea surface Chl*a* concentration for the period May 2018 to early June 2018 revealed the oligotrophic characteristic of the region of Saya de Malha. The satellite Chl*a* showed an average concentration below 0.3 mgm⁻³. Using the Chl*a* concentration as an index for phytoplankton biomass, the highest biomass was around stations CTD 393, CTD 394, CTD 397, CTD 400 and CTD 401 (Fig. 2a). The variation in sea surface temperature was low, where CTD 396 showed the highest temperature (> 28.8⁰C), while lower temperatures were apparent (< 28.0⁰C) at CTD 408, CTD 412 and CTD 416 (Fig. 2b).

Samplings at stations CTD 391, CTD 400 and CTD 401 were carried out on cloudy days resulting in low absolute light intensity with the highest values recorded at CTD 404 and CTD 408 (Fig. 3a). The average absolute light intensity was highest at the 0-4 m surface layer (236.2 ± 211.9 µmol quanta m⁻² s⁻¹) followed by 5-10 m (75.4 ± 69.0 µmol quanta m⁻² s⁻¹) and by 11-29 m (30.8 ± 30.4 µmol quanta m⁻² s⁻¹). Considering the near-surface
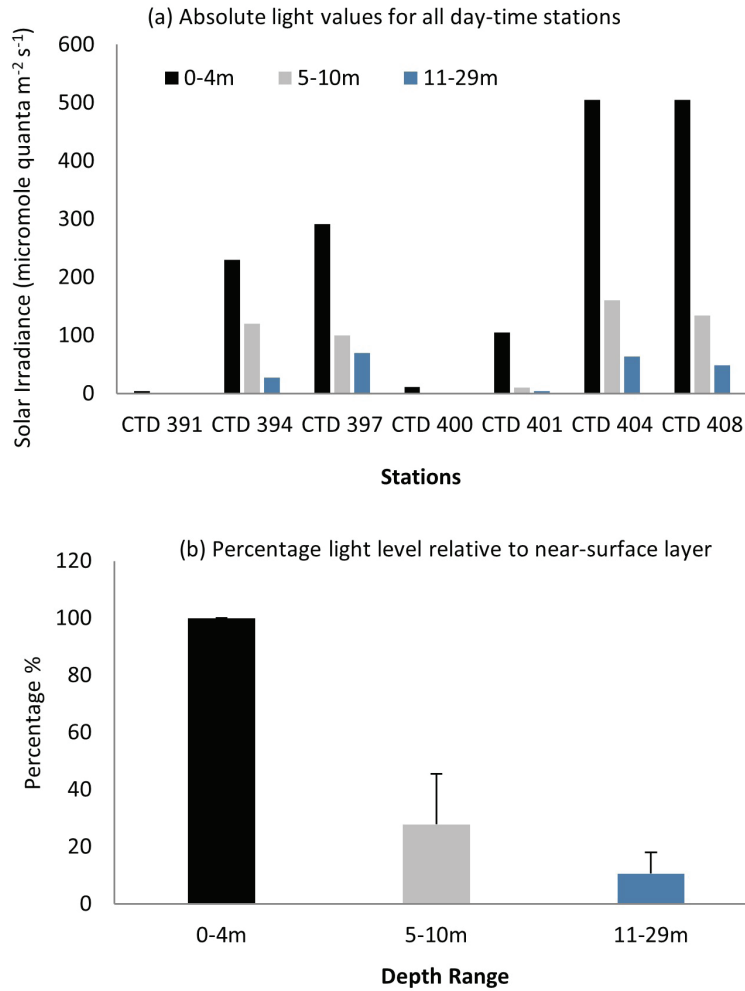
Figure 3. Absolute light values (a), and percentage light level relative to near-surface layer (b) for all daytime stations.

layer of 0-4 m to have 100% of solar irradiance, then the layer of 5-10 m had around 28% light which was a decrease of 72%. At a depth range of 11-29 m, the solar irradiance was 11% which was a decrease of 89% from the 0-4 m layer (Fig. 3b). Thus, there was a noticeable decrease in the light intensity reaching the layers between 5 and 29 m depth. Additionally, Table 1 gives an overview of the maximum depth at each station with minimum depth at stations CTD 403 (29 m) and maximum depth at CTD 396 (2172 m).

Table 1. Time, CTD station, and maximum depth at respective stations where samples were collected.

Sampling time	CTD Station	Max depth (m)
Day	391	135
	394	31
	397	68
	400	51
	404	2123
	408	-
Night	393	79
	396	2172
	398	60
	403	29
	412	2068
	416	1309

Micro-phytoplankton abundance at different depth ranges

The highest TMPA during daytime was recorded at CTD 397 ($5.51 \pm 0.54 \times 10^4$ cells L^{-1}) and at night-time at CTD 398 ($3.86 \pm 0.21 \times 10^4$ cells L^{-1}) at a depth range of 0-4 m. These two CTD stations also maintained their highest abundances of TMP at depth ranges of 5-10 m and 11-29 m among the stations. During daytime, the highest TMPA was $3.12 \pm 0.12 \times 10^4$ cells L^{-1} at CTD 397 at depth 5-10 m, and at depth 11-29 m

the highest TMPA was also at CTD 397 with an abundance of $1.88 \pm 0.18 \times 10^4$ cells L^{-1}. For the night-time, the abundance was $1.30 \pm 0.80 \times 10^4$ cells L^{-1} at CTD 398 at depth 5-10 m, and at depth 11-29 m, it was $1.03 \pm 0.25 \times 10^4$ cells L^{-1}. The lowest abundances of TMP during daytime was recorded at CTD 401 ($1.20 \pm 0.11 \times 10^4$ cells L^{-1}) and for night-time, at CTD 416 ($0.84 \pm 0.21 \times 10^4$ cells L^{-1}) (Fig. 4a). The highest and lowest diatom abundances followed the same trend at the same CTD stations (CTD 397 and CTD 398) as the
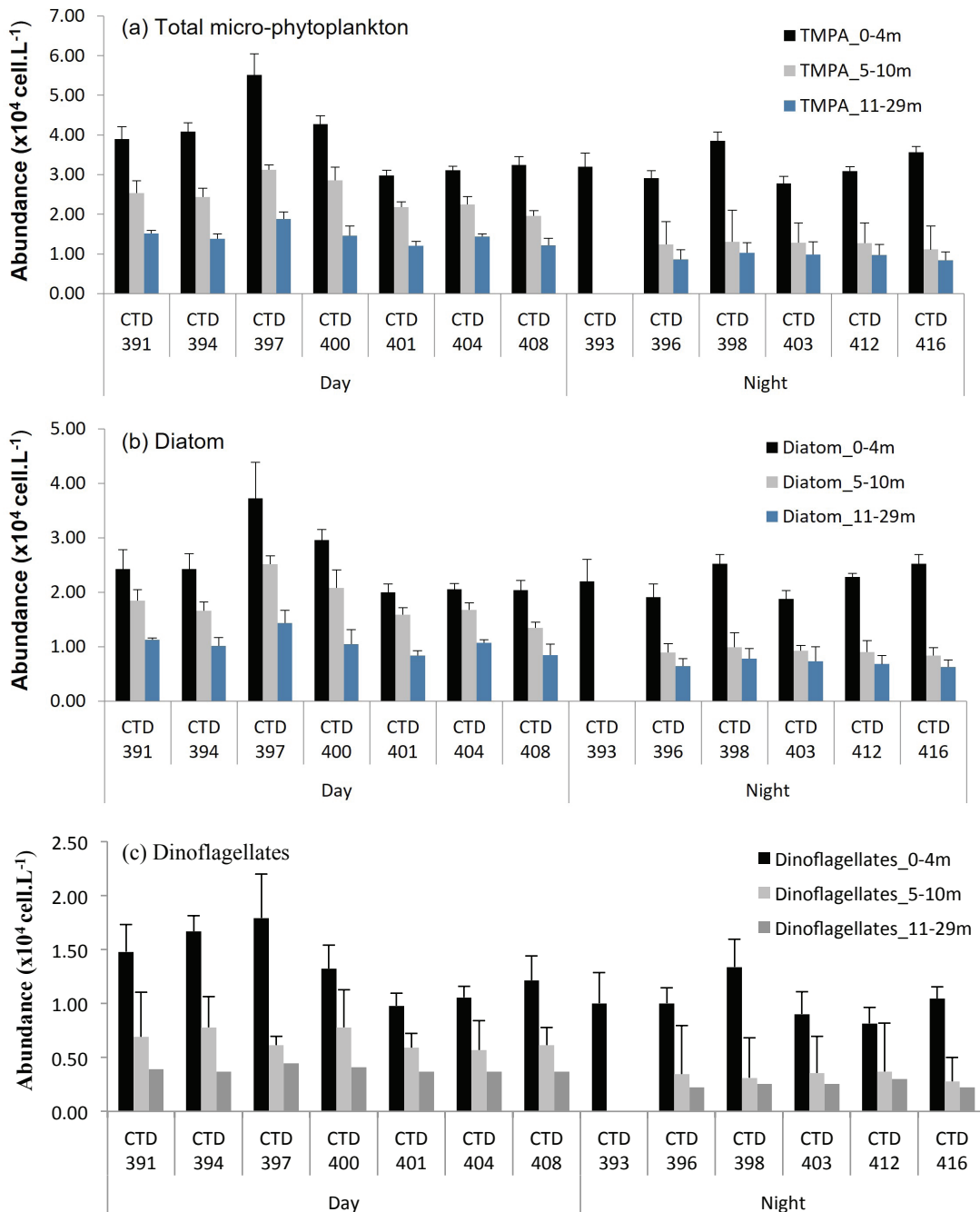

Figure 4. Abundance of total micro-phytoplankton (a), diatom (b), and dinoflagellates (c) during day- and night-time at different CTD stations at three depth ranges of 0-4 m, 5-10 m and 11-29 m.
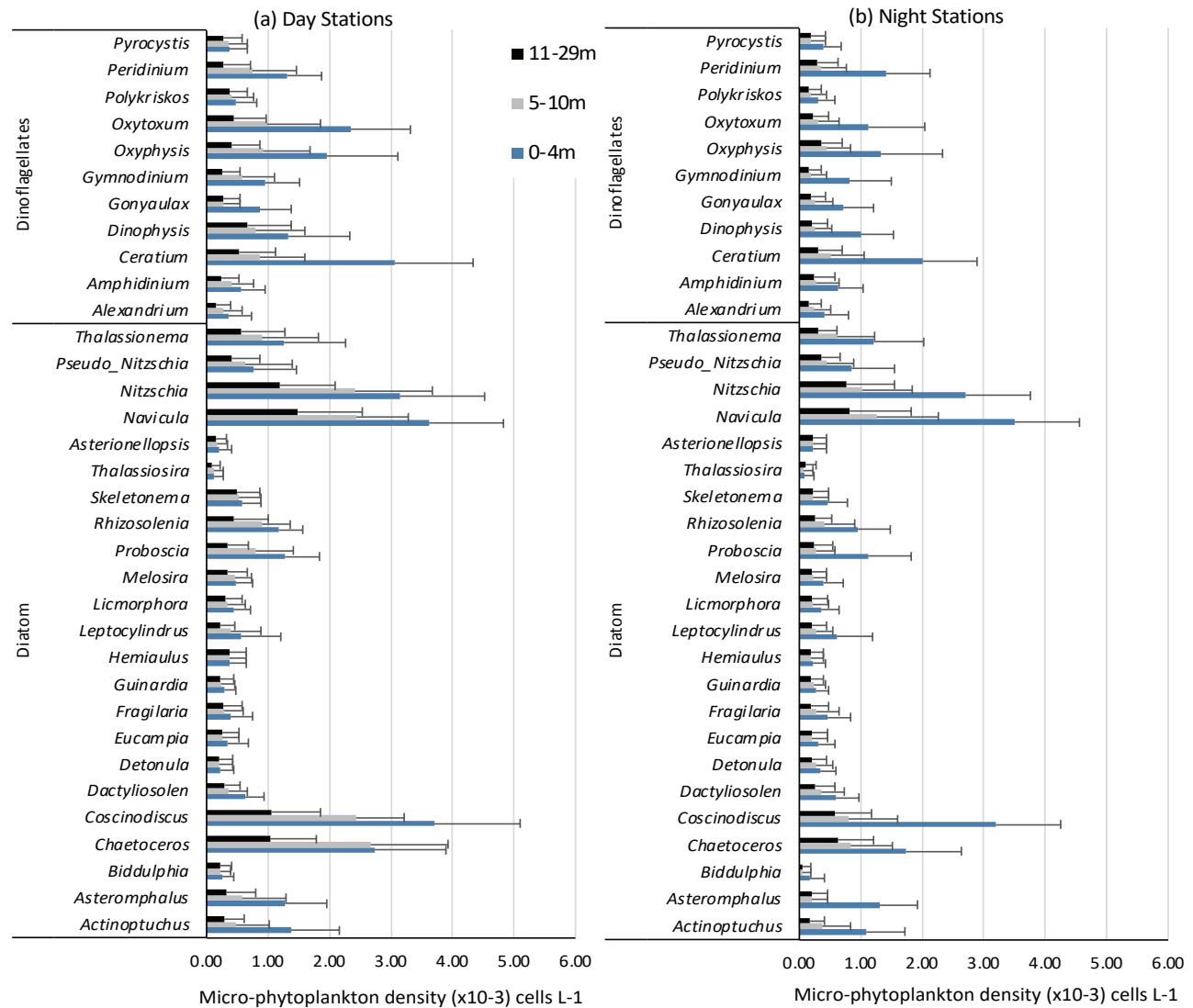
Figure 5. Average micro-phytoplankton abundance of different genera for samples collected during (a) day, and (b) night.

TMPA at all the studied depth ranges (Fig. 4b). For dinoflagellates, a similar trend was followed only for the depth 0-4 m. At 5-10 m, during daytime the highest dinoflagellates abundance was at CTD 394 and CTD 400 and lowest at CTD 401, and during night-time the highest was at CTD 412 and lowest at CTD 416. Moreover, at 11-29 m during daytime the highest dinoflagellates abundance was at CTD 397, and lowest abundances at CTD 394, CTD 401, CTD 404 and CTD 408, and during night-time the highest was at CTD 412 and lowest at CTD 396 and CTD 416. One-way ANOVA test revealed no significant differences among the different CTD stations ($P > 0.05$). Among the different depths, there were strong significant differences for diatoms, dinoflagellates and TMPA ($P < 0.001$). Significant difference was also revealed between daytime and night-time abundances of the different groups of micro-phytoplankton. When the

parameters of depth and time were combined, the difference was not significant ($P > 0.05$).

The TMPA had the highest percentage decrease (-61.15%) during night-time and it was between the depth ranges 0-4 m and 5-10 m. This trend was also observed for the diatom subgroup (-58.52%) and dinoflagellates (-66.18%). For depths between 5-10 m and 11-29 m, the highest decrease was noted during daytime for TMPA (-41.67%) and diatoms (-41.70%) followed by dinoflagellates (40.55%).

Micro-phytoplankton diversity

Thirty-four genera of micro-phytoplankton were identified out of which 23 were diatoms and 11 were dinoflagellates. Moreover, 5 genera revealed consistency in terms of percentage dominance at all the studied depths. These were *Chaetoceros* (range: 5.38-10.78%),

Coscinodiscus (range: 6.24-9.91%), *Navicula* (range: 8.85-10.82%), *Nitzschia* (range: 8.11-9.75%) and *Ceratium* (range: 3.42-7.91%). The lowest percentage dominance was exhibited by the genera *Biddulphia, Thalassiosira, Alexandrium,* and *Pyrocystis*.

The highest decrease in the abundance of genera was noted during the night-time at the depth change of 0-4 m to 5-10 m, where 27 out of the 34 genera revealed a decrease in abundance of over 40%. During the day-time, the highest decrease was between the depth changes of 5-10 m to 11-29 m where 15 of the 34 genera decreased by at least 40%. During daytime at a depth change of 0-4 m to 5-10 m, two genera (*Hemiaulus* and *Thalassiosira*) revealed no change in abundances, while from 5-10 to 11-29 m, five genera (*Biddulphia, Detonula, Eucampia, Hemiaulus,* and *Gonyaulax*) maintained their abundances (Fig. 5a). Moreover, during night-time at a depth change of 0-4 m to 5-10 m, one genus (*Asterionellopsis*) revealed no change in abundance, and at 5-10 to 11-29 m, seven genera revealed no change (*Asteromphalus, Biddulphia, Eucampia, Hemiaulus, Skeletonema, Asterionellopsis,* and *Pyrocystis*) (Fig. 5b). Among all the different depths and during day/night-time, *Hemiaulus* showed the lowest decrease of 16.67%.

The Shannon-Wiener (H') diversity index showed that the diatom subgroup had higher diversity values (H' > 2.5) compared to the dinoflagellates (H' < 2.5), irrespective of depth range and day/night-time (Fig. 6a). An increase in Equitability (E_H) values was noted when moving from 0-4 m to depth range of 11-29 m. For the dinoflagellates, there was an increase in E_H from 0-4 m

to 5-10 m, and a decrease from 5-10 m to 11-29 m (Fig. 6b). The Evenness (E_{var}) revealed highest values during night-time for all the depth ranges for both diatom and dinoflagellates, and overall, the dinoflagellates tended to have higher E_{var} than diatoms (Fig. 6c).

Photo-physiology of micro-phytoplankton

The effective quantum yield (Φ_{PSII}) varied mostly below 0.4 with not much difference with respect to depth changes. At the depth range 0-4 m and 11-29 m, Φ_{PSII} revealed a decrease with time-scale reaching 15:00 pm with R^2 of 0.034 and 0.721, respectively. At the depth range of 5-10 m, an increase with $R^2 = 0.597$ was apparent. The highest mean Φ_{PSII} was recorded at 11-29 m (0.32 ± 0.11) and the lowest at 5-10 m (0.21 ± 0.06) (Fig. 7a). As for $rETR_{max}$, an increasing trend was noted at both the depth ranges 0-4 m and 5-10 m, whereas a decreasing trend was revealed at 11-29 m through the time scale 5:00 am to 15:00 pm. Highest mean $rETR_{max}$ was recorded at 0-4 m (6.27 ± 2.97) and lowest at 5-10 m (4.57 ± 2.33) (Fig. 7b). The value of α (Fig. 7c) showed a decreasing trend throughout all the different depth ranges with high R^2 values of 0.686, 0.426 and 0.562, and on the contrary, the values of β (Fig. 7d) showed increasing trends with lower R^2 values (0.390, 0.262 and 0.077). Moreover, α had slightly higher values at depth 11-29 m. The NPQ_{max} depicted an increasing trend at the depth range of 0-4 m and decreasing trends in the other depth ranges with low R^2 values. In terms of means, the higher NPQ_{max} was at a depth range 0-4 m (3.38 ± 1.85) and lowest at 11-29 m (2.04 ± 2.23) (Fig. 7d). Finally, E_k revealed decreasing trends at all the different depth ranges with highest
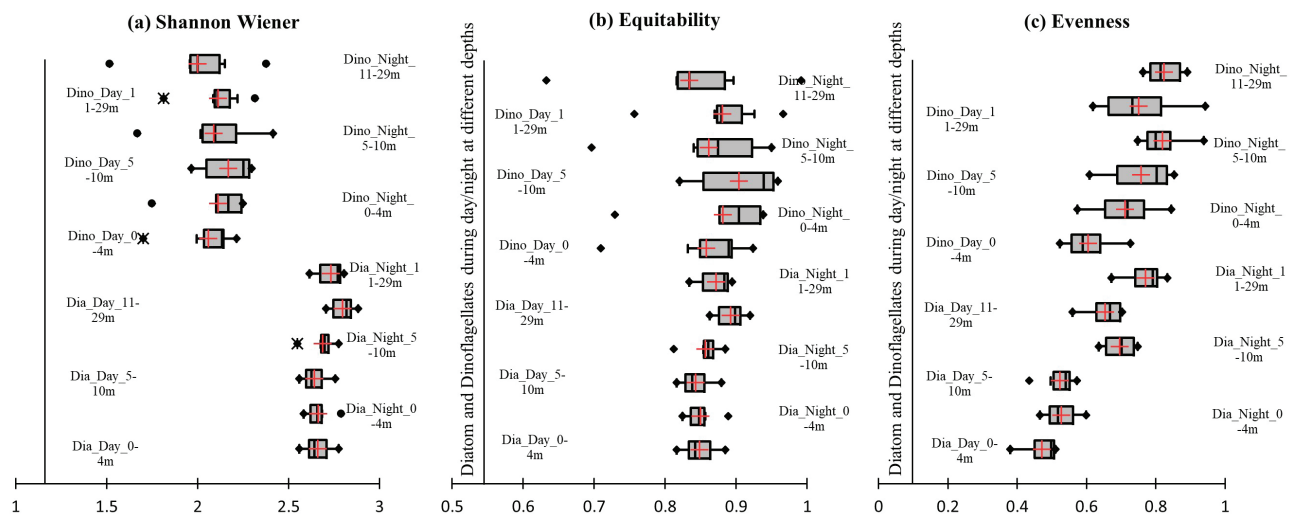

Figure 6. The diversity indices (a) Shannon Wiener (H'), (b) Equitability (E_H) and (c) Evenness (E_{var}) for the diatom and dinoflagellates at different depth ranges and time (day/night).

mean at 0-4 m (240.67 ± 322.89 μmol photons $m^{-2} s^{-1}$) and lowest at 11-29 m (101.73 ± 106.83 μmol photons $m^{-2} s^{-1}$) (Fig. 7e). For all the different photo-physiological parameters, there was no significant differences with depth, where P > 0.05.

It is noteworthy that the photo-physiological parameters of the micro-phytoplankton at the three studied water depths varied differentially with the time of the day. Φ_{PSII} at 0-4, 5-10 and 11-29 m exhibited no clear trend, slight linear decline and a clear gradual
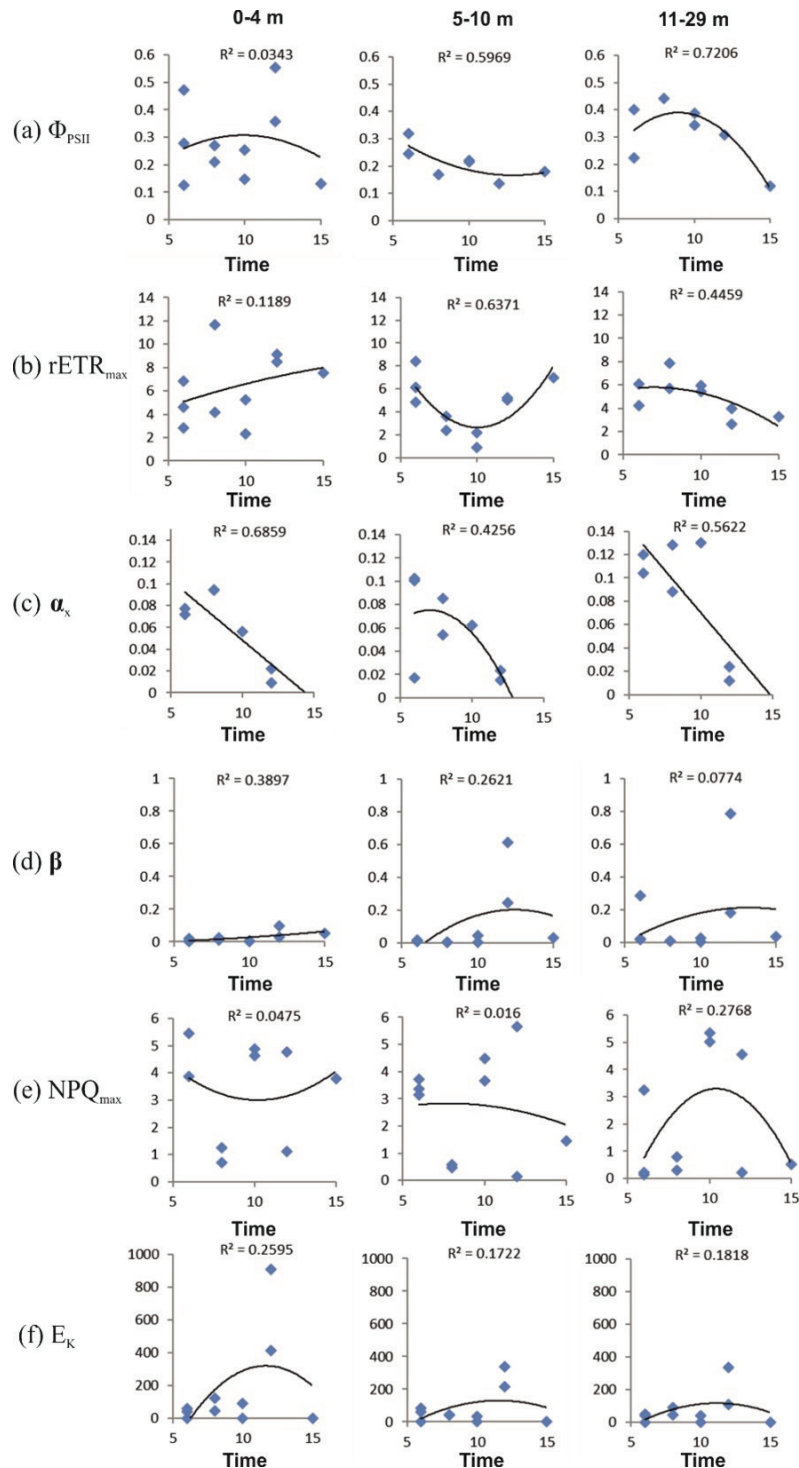

Figure 7. Physiological parameters (y-axis) (a) Effective quantum yield (Φ_{PSII}), (b) rETR$_{max}$, (c) α, (d) β, (e) NPQ$_{max}$ and (f) E$_k$ at three depth ranges of 0-4 m, 5-10 m and 11-29 m where the x-axis represents the time scale from 5:00 am to 15:00 pm, and the y-axis is the scale for the different parameters.
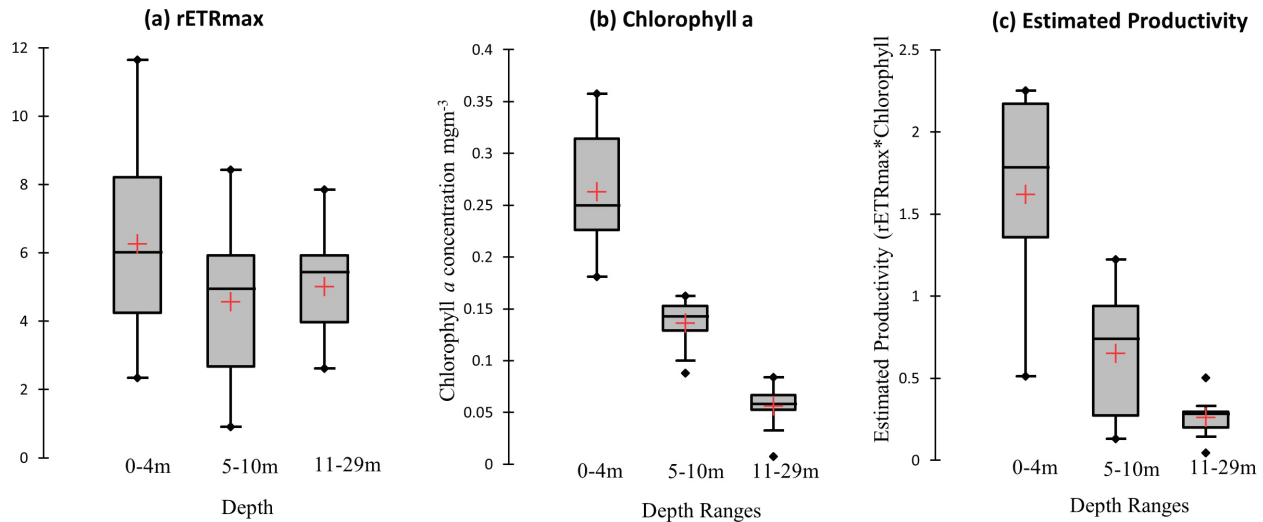
Figure 8. rETR$_{max}$ (a), Chl$a$ concentration (b) and Estimated productivity (c) at depth ranges of 0-4 m, 5-10 m and 11-29 m at Saya de Mlaha Bank

decline (Fig. 7a), respectively, with the time of the day. The lowest ΦPSII occurred at around noon and 15:00 for 0-4 and 11-29 m, respectively. As for rETR$_{max}$, a very weak linear increase for 0-4 m, a U-shaped curve for 5-10 m and a gradual linear decrease for 11-29 m were recorded (Fig. 7b). For α and β, clear opposite trends were observed where α linearly decreased (Fig. 7c) and β linearly increased (Fig. 7d) with the time of the day. For NPQ$_{max}$ and E$_k$, a bell-shaped trend was observed for depths 11-29 m (Fig. 7e) and 0-4 m (Fig. 7f), respectively.

rETRmax, Chla concentration and estimated productivity

Mean highest rETR$_{max}$ was recorded at the surface from 0-4 m and decreased at depth range 5-10 m and then increased slightly in the deeper water of 11-29 m (Fig. 8a). Both the Chl$a$ concentration and estimated productivity were inversely proportional to the depth range of the water column. The Chl$a$ concentration varied from the lowest at depth 11-29 m (0.05 ± 0.02 mgm^{-3}) to the highest of 0.26 ± 0.06 mgm^{-3} at 0-4 m (Fig. 8b). This trend was followed by estimated productivity where the lowest (0.23 ± 0.15 mgm^{-2}) was at the deeper depth range and the highest (1.62 ± 0.67 mgm^{-2}) at 0-4 m (Fig. 8c). Both the Chl$a$ concentration and estimated productivity differed significantly among the depth ranges studied.

Principle Component Analysis

The Principle Component Analysis (PCA) showed the separation of the photo-physiological parameters from the biological parameters such as micro-phytoplankton densities, but not with Chl$a$. PCA explained 66.13% of the total data variance whereby F1 had more influence with 40.89% compared to F2 at 25.25%. It was clear that the station with highest density of micro-phytoplankton was at CTD 397 at the depth 0-4 m. Moreover, Chl$a$ at depth 5-10 m showed the highest positive correlation with the TMPA and also with the subgroups of diatoms and dinoflagellates. The highest Φ$_{PSII}$ (Yield) was at station CTD 404 in the near-surface layer of 0-4 m. In terms of stations, there were two cluster groupings; firstly CTD 401, 404 and 408 which had stronger correlation with the photo-physiology parameters, and a second cluster comprising of CTD 391, CTD 397 and 400 which correlated strongly with micro-phytoplankton abundance (Fig. 9).

Discussion

In oceanic waters, the abundance and growth performance of phytoplankton in the water column is partially dependent on vertical mixing as this process brings nutrients to the upper photic zone and thus boosts primary productivity (Diehl, 2002; Huisman *et al.*, 2004). Moreover, as highlighted by Bode *et al.* (1996), light plays an important role in the biomass of phytoplankton such that, if there are high nutrient levels, the absence of sufficient light will hinder phytoplankton growth.

In the present study, the highest abundance of micro-phytoplankton was recorded in the near-surface layer of the water column. The study was conducted during the winter season and thus, the high abundance may possibly be explained by upwelling where cold deeper nutrient rich water tends to mix with photic layers which eventually results in an increased abundance
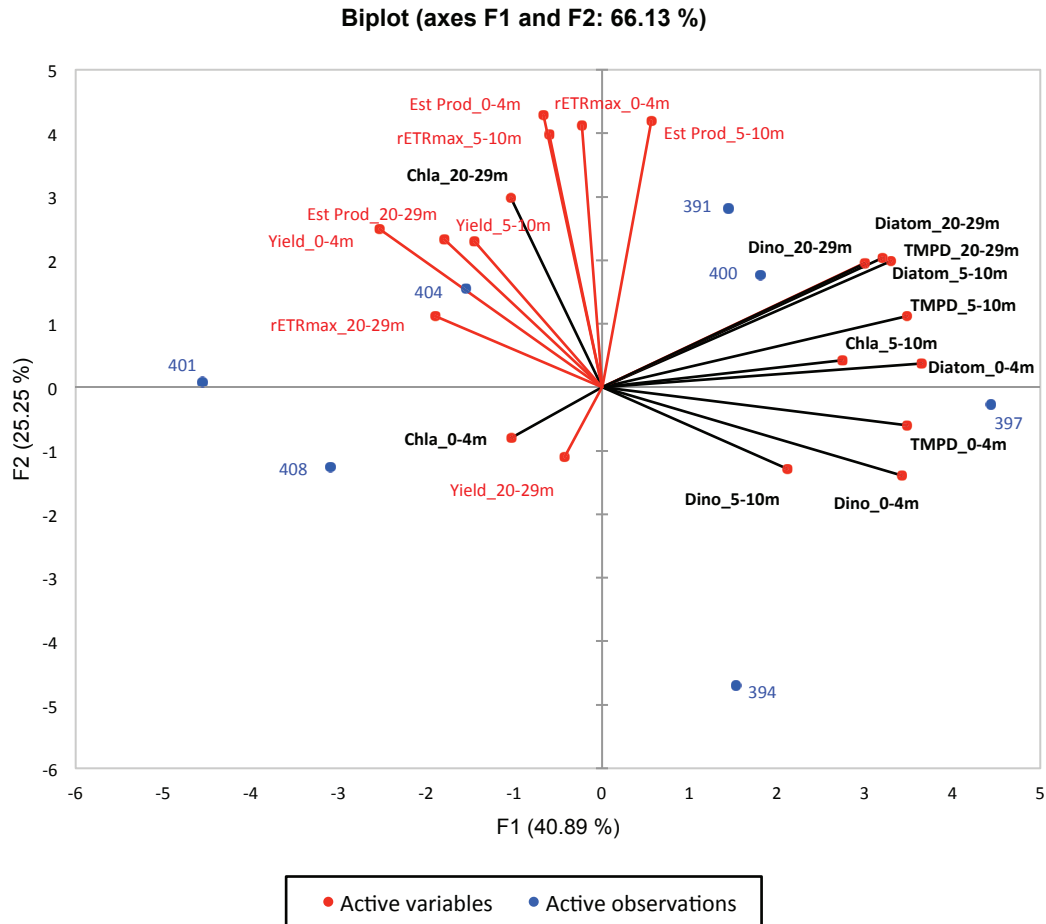
Biplot (axes F1 and F2: 66.13 %)

Figure 9. The Principal Component Analysis (PCA) representing correlation coefficient analysis for the different CTD stations with the photophysiology parameters, namley, Φ_{PSII} (Yield), $rETR_{max}$, Estimated productivity (Est Prod), and biological parameters such as Chl*a* concentration, and the abundances of Diatom, Dino (Dinoflagellates) and Total Micro-phytoplankton (TMP) at the studied depth ranges of 0-4 m, 5-10 m and 11-29 m.

of phytoplankton (Pitcher *et al.*, 2011; Yoder *et al.*, 1983). Water depth and abundance of phytoplankton displayed inverse proportionality. The highest difference in the abundance of micro-phytoplankton occurred between the near-surface layer of 0-4 m and the depth of 5-10 m at night. This may be partially attributed to the migration of zooplankton to the upper water layers in search of food while at the same time escaping predators at deeper depths. Goldyn and Kowalczewska-Madura (2007) demonstrated that a high abundance of zooplankton tends to cause a significant decrease in the phytoplankton abundance. The growth of phytoplankton decreases at night due to the absence of light, and coupled with the grazing activity by zooplankton, results in lower abundance of phytoplankton (Roman *et al.*, 1988; Shaw and Robinson, 1998).

Moreover, throughout the study period, diatoms were more dominant compared to dinoflagellates, irrespective of depth ranges, time of sampling and stations (Bazin *et al.,* 2014; Bernardi Aubry *et al.*, 2006). This may be explained by their ability to thrive under varying environmental conditions such as temperature or even light availability (Kokfelt *et al.*, 2009). Margalef (1978) found that strong vertical mixing favors the dominance of diatoms and that dinoflagellates more likely preferred stratified water columns where they are able to compete advantageously over other groups of phytoplankton due to their ability of locomotion which helps greatly in reaching light and nutrient rich water zones (Glibert, 2016; Smayda and Reynolds, 2003). It is also noteworthy that dinoflagellates are ecologically diverse with different species specifically adapted to different levels of nutrients, mixing and euphotic zone depth (Smayda and Reynolds, 2003). Other studies have confirmed the higher abundance of diatoms over dinoflagellates in intensely turbulent mixed waters (Irigoien, 2000; Jones and Gowen, 1990) aligning with the findings from Saya de Malha. The study conducted by Barlow *et al.* (2004) indicated that in oligotrophic waters, there was dominance of pico-plankton over micro and nano-plankton. Further

studies on pico- and nano-plankton are therefore warranted to obtain a thorough understanding of the variations in and dominance of different groups of phytoplankton at the Saya de Malha bank.

The genera that were recorded as having the highest percentage contribution in the current study were *Chaetoceros* (range: 5.38%-10.78%), *Coscinodiscus* (range: 6.24%-9.91%), *Navicula* (range: 8.85%-10.82%), *Nitzschia* (range: 8.11%-9.75%) and *Ceratium* (range: 3.42%-7.91%). These results are in accordance with the findings of Savidge and Lennon (1987) where the authors showed the numerical dominance of *Chaetoceros* in the planktonic community in oceanic Scottish waters. Similarly, Yang *et al.* (2014) reported a dominance of *Chaetoceros* from 1959 to 2009 in the Changjiang River Estuary and pointed out that the seasonal succession of *Chaetoceros* by *Coscinodiscus* could be attributed to the seasonal variation of nutrient level and water stability. Recently, Park *et al.* (2020) conducted a study around the Korean islands and reported the abundance of *Navicula*, among other genera. Muñiz *et al.* (2019) reported a high number of *Ceratium* in the Bay of Biscay. Kopczynska *et al.* (1986) documented the dominance of *Nitzschia* in the Antarctic Ocean. Thus, ample studies have in fact confirmed the common prevalence of the genera *Chaetoceros*, *Coscinodiscus*, *Navicula, Nitzschia* and *Ceratium* throughout oceanic waters, ranging from temperate to cold regions. Globally, the species diversity of phytoplankton is driven by temperature in the tropical regions coupled with different environmental conditions (Righetti *et al.*, 2019).

Furthermore, photo-physiological studies by Li *et al.* (2016) and McMinn and Hegseth (2004) indicated higher Φ_{PSII} at deeper depths, which corroborates with the findings in the present study where high Φ_{PSII} tended to occur at a depth of 11-29 m. A plausible explanation for this may be that high nutrient availability at such depths may have boosted the photosynthetic rate. In the upper layer of water, even if the water is nutrient rich, lower Φ_{PSII} could indicate photo-inhibition and photo-protection (Barlow *et al.*, 2017; Oliver *et al.*, 2003). The Φ_{PSII} increased with depth in concurrence with the findings of Yuan *et al.* (2019). In addition, Silsbe *et al.* (2015) showed that light had a greater influence on the Φ_{PSII} compared to different nutrient regimes. In the near-surface layer of 0-4 m, the micro-phytoplankton faced high light intensity and responded by making optimal use of this light and eventually dissipating the excess. Higher $rETR_{max}$ values indicated that the micro-phytoplankton has higher acclimatization

potential and thus a higher light saturation point (Ralph and Gademann, 2005; Wagner *et al.*, 2006).

Micro-phytoplankton in the near-surface layer of 0-4 m had lower α compared to the depth range of 11-29 m. This showed that the micro-phytoplankton in the near-surface layer had higher acclimatization potency to high irradiance and explained the lower light usage efficiency (α). In contrast, the micro-phytoplankton at the depth of 11-29 m revealed higher light utilization efficiency maintaining a high photosynthetic rate even when there is lower light level. These results corroborate those of Yuan *et al.* (2019) and are indicative of the photo-adaptive strategies of the micro-phytoplankton in this under-explored region of the Saya de Malha. Higher dissipation of excess light at PSII (NPQ_{max}) was observed in the near-surface layer of 0-4 m compared to the depth range of 11-29 m; in line with the findings of Kashino *et al.* (2002) who reported an increase in NPQ_{max} of phytoplankton when exposed to high light regimes. Such responses in dissipating excess light is natural in micro-phytoplankton exposed to high light as a high level of NPQ may act as a safety valve to photo-protect its PSII, which is indicated by lower Φ_{PSII}. The minimum saturating irradiance, E_k, tended to be highest in the near-surface layer of 0-4 m and this was also the case in the study conducted by Yuan *et al.* (2019).

It is noteworthy that the trend in photochemical efficiency in terms of Φ_{PSII}, $rETR_{max}$ and NPQ_{max} with the time of the day was not clear in the micro-phytoplankton at any of the studied depths, as compared to dinoflagellates harbored by sedentary cnidarians, which show clear depressions in Φ_{PSII}, and increases in $rETR_{max}$ and NPQ_{max} around mid-day (Brown *et al.*, 1999; Hoegh-Guldberg and Jones, 1999). The fact that micro-phytoplankton are in the water column, and not fixed to the seafloor and exposed to high light environments like the shallow sedentary corals, may likely explain the absence of a clear similar diurnal trend in photochemical efficiency. In laboratory-based experiments differential photochemical efficiency responses to variable light climates among diatoms (Lavaud and Lepetit, 2013) and dinoflagellates (Islabão *et al.*, 2016) have been reported. The light-induced photochemical efficiency trends in micro-phytoplankton, when measured in communities, may mask the responses among the species present and thus, lead to poor detection of a clear trend in the overall response. Additional investigations using microscopy-PAM to look at the photo-physiology of individual cells from the different micro-phytoplankton species may help

to better understand their respective photo-physiological contributions and adjustments to diurnal variations in light regimes. On the other hand, the light usage efficiency (α) and photo-inhibition (β, the slope of the light curve beyond the onset of photo-inhibition) of the micro-phytoplankton at all studied depths exhibited clear decreasing and increasing trends, respectively, with the time of the day. This may be indicative of the micro-phytoplankton in the water column being collectively more sensitive in terms of α and β, as dynamic diurnal responses to photo-acclimate with the changes in light during the day.

Both the Chl*a* concentration and the estimated productivity decreased with depth. The fairly oligotrophic waters could be the reason behind the low level of Chl*a* in the waters surrounding Saya de Malha Bank (Jena *et al.*, 2013). Bergstad *et al.* (2019) reported that surface salinity varied from 34.1 PSU to 34.6 PSU and the oligotrophic waters were characterized by phosphate levels of less than 0.5 µM, silicate levels of less than 0.05 µM, and ammonia levels below detectable range (< 0.01 µM) at the Saya de Malha Bank. Even though the rETR$_{max}$ might have shown a declining trend with the decrease in light, the low Chl*a* concentration contributed to the decrease in the estimated productivity (Bot, 1996). It should, however, be highlighted that estimated productivity deduced from Chl*a* biomass and the photo-physiological parameter, rETR$_{max}$, are rapid, relative measures and are only indicative of the changes with depth. Further studies using conventional methods of determining absolute productivity would be necessary to thoroughly understand productivity changes with depth.

Conclusion

This study presents additional data on spatial variation in micro-phytoplankton abundance and diversity, and the first photo-physiological assessment of micro-phytoplankton with depth and time of the day at the Saya de Malha Bank. Micro-phytoplankton abundance varied among the studied stations and decreased with depth. The most dominant micro-phytoplankton group was the diatoms at the Saya de Malha Bank. The photo-physiological assessments revealed that the Φ_{PSII}, rETR$_{max}$, NPQ$_{max}$ did vary with the time of the day without clear general trends with respect to depth, while α and β exhibited clear opposite trends with the time of the day at all studied depths. The significant decline in estimated productivity with depth was mainly due to a significant decrease in Chl*a* as the rETR$_{max}$ only tended to diminish with depth. Further studies on other classes of phytoplankton like picoflagellate prokaryotes (*Prochlorococcus* and *Synechococcus*) and nanoflagellates (Haptophytes, Pelagophytes, Prasinophytes), and photochemical efficiency of important and dominant genera of micro-phytoplankton are necessary to thoroughly understand their contributions and their potentially depth-dependent photosynthetic functioning in relation to oceanic primary production in the Mascarene Plateau.

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