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Cover image: Fisherman pushes his boat along the channels around Inhaca Island, Mozambique (© José Paula)

Microalgal distribution, diversity and photo-physiological performance across five tropical ecosystems around Mauritius Island

Shamimtaz B. Sadally[1], Nawsheen Taleb-Hossenkhan[1], Ranjeet Bhagooli[1,2,*]

[1] Department of Biosciences, Faculty of Science, University of Mauritius, Réduit 80837, Republic of Mauritius

[2] Department of Marine and Ocean Science, Fisheries and Mariculture, Faculty of Ocean Studies, University of Mauritius, Réduit 80837, Republic of Mauritius

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

Abstract

Microalgal density, diversity, photo-physiology and estimated productivity along with physico-chemical conditions across five tropical ecosystems, both at the water column and sediment levels, were assessed around Mauritius Island. The ecosystems studied were the coral reefs of Blue Bay (CRBB), the seagrass bed of Mahebourg (SEBM), the mangrove ecosystem at Pointe D'Esny (MAPD), the sandy beach of Blue Bay (SBBB) and the estuarine area of Le Goulet (ESTLG). Physico-chemical (nutrients, temperature, salinity and pH) and biological (chlorophyll *a* and microalgal density, diversity and distribution) parameters were measured and analysed. Photo-physiological status, (relative electron transport rate (*rETR*) and non-photochemical quenching (NPQ)), of microalgal cells was also determined and primary productivity was estimated using chlorophyll *a* and $rETR_{max}$ data. Microalgal density in the water column (micro-phytoplankton) was highest in the MAPD (2.55±0.22 x 10^6 cellsL^{-1}) and the CRBB areas (2.20±0.13 x 10^6 cellsL^{-1}), while for the sediment (micro-phytobenthos) the SBBB samples had the highest density (2.43±0.14 x 10^5 cellsL^{-1}). Diatoms were the most abundant microalgal group, followed by dinoflagellates and cyanobacteria. A total of 41 micro-phytoplankton genera and 33 micro-phytobenthos genera were recorded. Higher diversity of micro-phytoplankton and micro-phytobenthos occurred at SBBB. Although *Navicula* spp. was consistently present in high abundance in all the studied ecosystems, other species such as *Cylindrotheca*, *Stauroneis*, *Oscillatoria* and *Alexandrium* species occurred in high percentages in the water column at CRBB, SBBB and ESTLG areas. Chlorophyll *a* concentration was higher in the water column of the MAPD (1.49 ± 0.08 mgm^{-3}), and sediment of the CRBB (31.68 ± 6.59 mgm^{-2}) and the SBBB (28.10 ± 5.28 mgm^{-2}) areas. The relative electron transport rate ($rETR_{max}$) of micro-phytoplankton/micro-phytobenthos in the water column and sediment of CRBB, SBBB and MAPD area were similar while the $rETR_{max}$ value in the sediments was higher than that of the water column for the ESTLG. Micro-phytoplankon of MAPD, SEBM and ESTLG had higher non-photochemical quenching (NPQ) values compared to those found in sediment. Estimated productivity was about 10-40 fold higher in the micro-phytobenthos of the sediment compared to the micro-phytoplankton of the water column, though the latter had a higher diversity of microalgae.

Keywords: chlorophyll *a*, D-PAM, estimated productivity, microalgae, micro-phytoplankton, micro-phytobenthos, photo-physiology, tropical ecosystems.

Introduction

Microalgae are found both in the water column (micro-phytoplankton) and in sediment (micro-phytobenthos) and inhabit aquatic (including marine) ecosystems. Micro-phytoplankton are photosynthesising microorganisms that live in the euphotic zone of the ocean (Dongyan, 2008) and have limited locomotion ability. They are the primary producers of the sea and play an important role in biogeochemical cycles (Khenari *et al.*, 2010). Micro-phytobenthos communities, apart from being primary producers (Cahoon and Safi, 2002), are important in terms of coastal ecology and they play an important role in the production and cycling of organic matter, as well as in the stabilisation

of sediments (Suthers and Rissik, 2009). Microalgae are present in different habitats with a wide range of temperature and salinity regimes, such as creeks, rivers, lakes, estuaries and seas. Moreover, different microalgae have also been found to adapt to various substrates, such as aquatic plants, rocks, sand grains and unconsolidated sediments (Dongyan, 2008).

In shallow coastal ecosystems, the combined effect of mixing and inputs of nutrients as a result of wind, tides, discharges and benthic fluxes, have been found to affect microalgal community structure and primary production (Claquin *et al.*, 2010). Several factors have been found to affect microalgal distribution and abundance, including temperature, pH (Brock, 1973; Goldman and Shapiro, 1973; Hinga, 1992; Goldman *et al.*, 1982), dissolved oxygen, turbulence, nutrients (Sadally *et al.*, 2014a; b), competition, grazing, allelopathic interactions, and light. However, these factors showed significant temporal variation extending from short-term events to seasons (Pannard *et al.*, 2008; Sadally *et al.*, 2014b). Micro-tides on coral reefs have also been reported to affect microalgal diversity and distribution (Sadally *et al.*, 2016).

Light, together with the abundance and photosynthetic competence of microalgae, are determinant factors conditioning primary production of ecosystems (MacIntyre and Cullen, 1996). Light is an important factor that has a direct impact on microalgal photo-physiology which depends on light availability to manufacture food. However, high light intensities may hinder the proper functioning and may even cause permanent damage of photosystems, termed 'photoinhibition', possibly leading to the death of microalgae. This may in turn disturb the functioning of the ecosystem and threaten marine life (MacIntyre and Cullen, 1996).

The coastal areas of Mauritius comprise several ecosystems, which harbour a wide range of microalgal species. During recent years, the coastal areas have faced an increased level of threats due to the coastal activities and development linked to the expanding tourism industry (Ramessur, 2013; Turner *et al.*, 2000). These have impacted coastal ecosystems in various ways. Studies on pelagic micro-phytoplankton and micro-phytobenthos are very limited around Mauritius, probably because of the difficulties encountered in extracting, enumerating and identifying them. Photo-physiological investigations on marine microalgae are also almost non-existent. This study therefore aimed at investigating the photo-physiological performance of microalgae (both micro-phytoplankton and micro-phytobenthos) across five tropical ecosystems: an estuarine, coral reef, sandy beach, seagrass, and mangrove area around an oceanic island.

The study aimed at testing whether microalgal density, distribution, diversity, and photophysiology varied across the different tropical ecosystems at both the water column (micro-phytoplankton) and sediment (micro-phytobenthos) levels. The objectives of the study were: to measure physico-chemical parameters at all sampling sites; to collect and analyse water column and sediment samples for chlorophyll *a* and microalgal density, distribution and diversity; to assess the photo-physiological performance of microalgal cells in both the water column and sediments, in terms of relative electron transport rate and non-photochemical quenching across the studied ecosystems; and to determine the estimated productivity of microalgae in each studied ecosystem.

Sampling and methods

Study sites

Five sampling sites (Fig. 1) were selected to represent the five ecosystems (coral reefs, seagrass bed, mangroves, sandy beaches and estuaries). The sampling sites were Blue Bay sandy beach area (site 1: S 20° 26.512', E 57° 42.994'), Blue Bay coral reef area (site 2: S 20° 26.610', E 57° 42.708'), Mahebourg seagrass bed area (site 3: S 20° 24.335', E 57° 42.596'), Pointe D'Esny mangrove area (site 4: S 20° 25.506' , E 57° 48.392') and Le Goulet estuarine area (site 5: S 20° 06.407 / E 57° 31.031').

The sandy beach and the coral reef patch are situated in Blue Bay lagoon (Fig. 1), which is found on the South East Coast, and has been proclaimed a Marine Park by the Government since 1997. The sandy beach area is a public beach and has undergone much development due to the expanding tourism industry. The beach has not been affected by erosion and it does not harbour rich biodiversity. Fragments of dead corals are often found in this area as opposed to the reef area which contains rich biodiversity comprising of about 50 coral species and more than 50 fish species belonging to 25 families.

The seagrass bed is found at Mahebourg (Fig. 1-C) and the substrate consists of soft sediment. Seagrass occurs in the intertidal zone in shallow waters. This ecosystem serves as a nursery site for many species of fish and invertebrates.

The mangrove ecosystem is located at Pointe D'Esny. The site is a marine wetland consisting of pond-like depressions which are usually interconnected at low tide and submerged at high tide, and are dominated by the mangrove *Rhizophora mucronata*. During recent years, the coastal village of Pointe D'Esny has experienced much development due to the expanding tourism industry (Fig. 1D).

The estuarine area of Le Goulet (Fig. 1) is found around the mouth of the river Citron and extends into the river. The water is brackish and the bottom consists of soft sediments. This region has also undergone much development because of the tourism industry.

Seawater sampling

For characterization of both pelagic and benthic components of micro-phytoplankton, 10 L of seawater was filtered through a 5 µm plankton net and the residue inside the net was collected in an opaque 250 ml plastic bottle. Samples were collected between 6 and 8 am between high and low tides during the month of February 2012. Fifteen samples (five for each analysis) were collected at each site and these were brought to the laboratory for later analyses. For nutrient analysis, 500 ml clean and labelled plastic bottles were used to collect water at each sampling sites. Five water samples were collected at each site and all samples were kept in the dark and at low temperature in isotherm boxes. In the laboratory, samples for chlorophyll a analysis and micro-phytoplankton samples for density and diversity determination were processed, while seawater samples for nutrient analyses were kept at -20°C for later processing.

Sediment sampling

Sediment sampling was carried out according to Montoya *et al.* (2006). Five samples for chlorophyll *a*, micro-phytobenthos and photo-physiological analysis were collected using a petri-dish (5 cm diameter and 1.3 cm height) at a depth not exceeding 1 m. This included inserting the petri-dish into the substrate and placing a spatula under the petri dish to trap the contents during the retrieval process. All samples were kept at low temperature in the dark prior to analyses in the laboratory. In the laboratory, the sediment samples were washed with 2 L filtered seawater and filtered twice, first with a coarse filter of mesh size of 600 µm, and then with the 5 µm plankton net. The residue was then collected in a 250 ml opaque plastic bottle.

Measurement of physico-chemical parameters

Temperature (Comark 314), salinity (Erma) and pH (Hanna H1 9024C) were measured *in situ*. Water

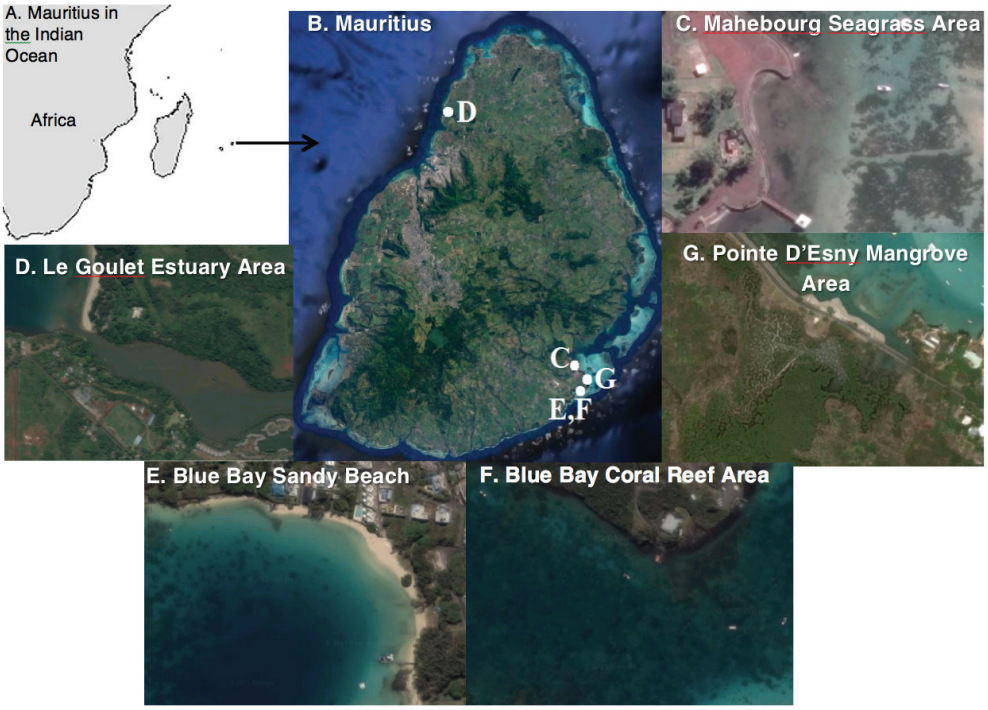

Figure 1. A. Location Mauritius in the Indian Ocean (Source: http://www.washburn.edu/cas/history/stucker/IndianOceanMap.html); B. Location of the sampling sites in Mauritius Island; C. Mahebourg Seagrass area; D. Le Goulet Estuary Area; E. Blue Bay Sandy Beach Area; and F. Blue Bay Coral Reef Area (Source: Google Earth)

samples collected for nutrient (nitrate, phosphate and silicate) analysis were tested according to Greenberg *et al.* (1992).

Chlorophyll *a*, micro-phytoplankton count and identification

Water samples collected from the water column and sediments for micro-phytoplankton/ micro-phytobenthos analysis were centrifuged (Häder, 1995) on the same day at a speed of 3000 rpm for 5 minutes (Khenari *et al.*, 2010). The supernatant was discarded and the pellet was dissolved in 6 ml filtered seawater for measurement of chlorophyll *a* fluorescence using a Diving-PAM (Underwater Fluorometer, HeinzWatz GmbH, 1998) and chlorophyll *a* analysis using the spectrometric method. One ml of sample was preserved in Lugol's iodine for later enumeration and identification.

For determination of chlorophyll *a* concentration, 90% acetone was used for extraction of chlorophyll *a* pigment at 4°C for 24hrs (Jeffrey and Humphrey, 1975). Concentration of chlorophyll *a* was determined by spectrophotometry (Spectronic® Genesys™ 8 spectrophotometer). Micro-phytoplankton/ micro-phytobenthos was identified according to Tomas (1997), Smith and Johnson (1996), and Verlencar and Desai (2004) and quantification was done using a Sedgewick Rafter Counting Chamber (Devassy and Goes, 1991) under a light microscope.

Fluorometric determination of photo-physiology and non-photochemical quenching of micro-phytoplankton

Light that stimulates photosynthesis is known as photosynthetically active radiation (PAR) and F_V/F_M is the maximum quantum yield (calculated as $(F_M'–F_0)/F_M'$), which determines the amount of solar energy that can be converted to fixed carbon.

PAM fluorometry was used to assess the photo-physiology of microalgal cells by measuring the fluorescence of chlorophyll *a*, thus determining the relative electron transport rate (*rETR*) and non-photochemical quenching (NPQ) when exposed to a series of rapidly (10s) changing light climates (RLC) (McMinn *et al.* 2012). Following the RLCs' recordings, samples were dark-adapted for 30 mins prior to F_v/F_m measurements. The *rETR* and NPQ were estimated, at each irradiance, using the RLC and the values were plotted as in Louis *et al.* (2016) and Bhagooli *et al.* (2008).

At each irradiance the respective relative electron transport rate (*rETR*) was calculated by the formula below (Underwood *et al.*, 2005):

$$rETR = 0.5 \times \phi_{PSII} \times PAR$$

where:
PAR is the photosynthetically active radiance;
ϕ_{PSII} is the effective quantum yield and is calculated as: $(F_M'— F)/F_M'$, where F_M' and F is the maximum and minimum fluorescence yield, respectively.
The 0.5 terms in the equation account for 50% of absorbed photons used by PSII.

Non-photochemical quenching (NPQ) is the process by which oxygenic photoautotrophs harmlessly dissipate excess light absorbed as heat and fluorescence (Roth, 2014; Szabò *et al.*, 2005). When light energy absorption exceeds the capacity for utilization, there is a need to dissipate the energy to protect the light harvesting structures from photo-oxidative damage. NPQ is derived from the formula:

$$NPQ = (F_m\text{-}F_m')/ F_m'$$

where:
F_m the maximal fluorescence of a dark-'adapted' sample and F_m' is the maximal fluorescence of a light-exposed alga under a given irradiance.

The double exponential decay function of Platt *et al.* (1980) was employed to fit curves to the RLCs and $rETR_{max}$, α (initial slope before the onset of saturation), I_k (minimum saturating irradiance) were determined (Louis *et al.*, 2016). Estimation of productivity for both water column and sediment samples from the five ecosystems was calculated using the following formula (McMinn *et al.*, 2005):

Estimated productivity = $rETR_{max}$ x [Chlorophyll *a*]

Statistical analyses

Computing and statistical analyses were used Statistica 10.0 software. One-Way analysis of variance (ANOVA) followed by the Posthoc Tukey Honest Significance Difference (HSD) analysis for comparison of means were carried out to test for differences in parameters at the five ecosystems, namely, coral reef patch, sandy beach, mangrove, seagrass and estuary. Microalgae density data was $\log_{10}$ transformed while temperature, salinity, pH, chlorophyll *a*, nitrate, phosphate and silicate data

were arcsin (square root) transformed prior to ANOVA analyses. Shannon's Diversity (H) and Similarity Index (SI) were also calculated for micro-phytoplankton in the water column and the micro-phytobenthos in the sediment at the five ecosystems sampled.

Results

Micro-phytoplankton distribution and biomass across the five ecosystems

One-Way ANOVA analyses revealed that all tested parameters, including total micro-phytoplankton/micro-phytobenthos, diatom, dinoflagellate, cyanobacteria density, chlorophyll *a* concentration and nutrient concentrations (nitrate, phosphate and silicate) were significantly different ($P < 0.001$) among the different sampling sites; that is, among the different ecosystems in both water column and sediment (Table 1).

Total micro-phytoplankton/micro-phytobenthos density and chlorophyll *a* concentration

Micro-phytoplankton density in the water column (Fig. 2A) was significantly higher in the mangrove area and the coral reef area compared to the other ecosystems. These were followed by the sandy beach, seagrass and estuary areas, respectively. In the sediment (Fig. 2B), highest density of micro-phytoplankton was recorded in the coral reef and the sandy beach area, while lowest density was recorded in the seagrass bed area (Table 2).

Chlorophyll *a* concentration in the water column was highest and lowest in the mangrove and estuary area, respectively (Fig. 2C). Moreover, there was no significant difference in chlorophyll *a* concentration between coral reef and estuarine area samples. In the sediment samples, significantly higher chlorophyll *a* concentration was recorded in the coral reef and the sandy beach area compared to the other ecosystems, while the estuary area had the lowest chlorophyll *a* concentration (Fig. 2D). No significant difference was observed in chlorophyll *a* concentration in the sediment of the mangrove and seagrass area.

Diatoms dominated the micro-phytoplankton population in both the water column and sediment samples collected at the different ecosystems (Fig. 2E; F). Higher density was recorded in the water column in the mangrove area, followed by the coral reef, sandy beach, seagrass, and estuary area (Fig. 2E). In the sediment, significantly higher density of diatoms was recorded for the sandy beach and the coral reef while estuarine and seagrass bed sediment had lower density (Fig. 2F). No significant difference was observed between coral reef and mangrove area sediment samples.

Higher densities of dinoflagellates were recorded in the water column of the coral reef, sandy beach and estuary area (Table 2). The water column in the mangrove and the seagrass bed area had a significantly lower density of dinoflagellates compared to the other ecosystems (Fig. 2E). Dinoflagellates were more abundant in the sediment of the estuarine area compared to the other ecosystems (Fig. 2F; Table 2).

Cyanobacteria were the least abundant micro-phytoplankton. Significantly higher density was obtained in the water column of the seagrass and estuary area compared to the other ecosystems (Fig. 2E; Table 2).

Table 1. One-Way ANOVA comparing different parameters at the five ecosystems (coral reef, sandy beach, mangrove, seagrass and estuary). Asterisks indicate significant differences at 5% level. (* = $P< 0.05$; ** = $P< 0.01$; *** = $P< 0.001$).

	Water column					Sediment			
Parameters	**DF**	**SS**	**MS**	**F**	***P*-Value**	**SS**	**MS**	**F**	***P*-Value**
TPD	4	2.607	0.652	511.5	***	0.859	0.215	21.49	***
Diatom density	4	4.181	1.045	952.4	***	1.334	0.334	27.14	***
Dinoflagellate density	4	4.685	1.171	26.45	***	1.052	0.263	9.03	***
Cyanobacteria density	4	3.876	0.970	49.21	***	1.265	0.316	14.11	***
Chlorophyll *a*	4	0.150	0.038	477.2	***	0.353	0.088	27.30	***
Nitrate	4	0.993	0.248	45.503	***	-	-	-	-
Phosphate	4	0.461	0.115	18.57	***	-	-	-	-
Silicate	4	0.042	0.010	50.24	***	-	-	-	-

Table 2. Tukey HSD Posthoc Tests for comparing means of studied parameters at the five ecosystems. Asterisks indicate significant differences at *5%* level. (* = *P*< 0.05; ** = *P*< 0.01; *** = *P*< 0.001; NS = not significant). CRBB: coral reef area; SBBB: sandy beach area; MAPD: mangrove area; SEBM: seagrass bed area; ESTLG: Estuary area

			Water column					Sediment				
	Parameters		**CRBB**	**SBBB**	**MAPD**	**SEBM**	**ESTLG**	**CRBB**	**SBBB**	**MAPD**	**SEBM**	**ESLG**
Biological parameters	**Total micro-phytoplankton/ micro-phytobenthos Density**	CRA	-	**	NS	***	***	-	NS	NS	***	***
		SBA	**	-	***	***	***	NS	-	*	***	***
		MA	NS	***	-	***	***	NS	*	-	**	**
		SA	***	***	***	-	***	***	***	**	-	NS
		EA	***	***	***	***	-	***	***	**	NS	-
	Diatom Density	CRA	-	*	***	***	***	-	NS	NS	***	***
		SBA	*	-	***	***	***	NS	-	*	***	***
		MA	***	***	-	***	***	NS	*	-	***	***
		SA	***	***	***	-	***	***	***	***	-	NS
		EA	***	***	***	***	-	***	***	***	NS	-
	Dinoflagellate Density	CRA	-	NS	***	***	NS	-	NS	NS	NS	***
		SBA	NS	-	*	***	NS	NS	-	NS	NS	**
		MA	***	*	-	*	*	NS	NS	-	NS	**
		SA	***	***	*	-	***	NS	NS	NS	-	*
		EA	NS	NS	*	***	-	***	**	**	*	-
	Cyanobacteria Density	CRA	-	NS	NS	***	***	-	NS	NS	NS	**
		SBA	NS	-	NS	***	***	NS	-	*	***	***
		MA	NS	NS	-	***	***	NS	*	-	NS	*
		SA	***	***	***	-	NS	NS	***	NS	-	NS
		EA	***	***	***	NS	-	**	***	*	NS	-
	Chlorophyll *a*	CRA	-	**	***	***	NS	-	NS	**	***	***
		SBA	**	-	***	***	***	NS	-	***	***	***
		MA	***	***	-	***	***	**	***	-	NS	*
		SA	***	***	***	-	***	***	***	NS	-	NS
		EA	NS	***	***	***	-	***	***	*	NS	-
Physico-chemical parameters	**Nitrate**	CRA	-	**	***	***	NS	-	-	-	-	-
		SBA	**	-	NS	***	***	-	-	-	-	-
		MA	***	NS	-	**	***	-	-	-	-	-
		SA	***	***	**	-	***	-	-	-	-	-
		EA	NS	***	***	***	-	-	-	-	-	-
	Phosphate	CRA	-	***	NS	NS	NS	-	-	-	-	-
		SBA	***	-	***	***	***	-	-	-	-	-
		MA	NS	***	-	NS	NS	-	-	-	-	-
		SA	NS	***	NS	-	NS	-	-	-	-	-
		EA	NS	***	NS	NS	-	-	-	-	-	-
	Silicate	CRA	-	***	NS	***	NS	-	-	-	-	-
		SBA	***	-	***	*	***	-	-	-	-	-
		MA	NS	***	-	***	NS	-	-	-	-	-
		SA	***	*	***	-	***	-	-	-	-	-
		EA	NS	***	NS	***	-	-	-	-	-	-

Likewise, density of cyanobacteria was higher in the sediment from the seagrass and estuary area. However, no significant difference was obtained when comparing seagrass data to samples from the coral reef and mangrove area (Fig. 2F; Table 2).

Diversity of micro-phytoplankton/ micro-phytobenthos in the different ecosystems

A total of 42 genera were sampled during this study at the five ecosystems (Table 3). Higher Shannon's Diversity Index (H) was recorded in the water column of the seagrass bed area (H= 2.848), followed by the coral reef (H= 2.815), sandy beach (H= 2.703), mangrove (H= 2.547) and estuary area (2.540). In the sediment samples, the sandy beach area had the highest H value (H= 2.588), followed by the mangrove area (H= 2.44), the coral reef area (H= 2.389), the seagrass bed area (H= 2.214) and the estuary area (H=2.010).

The water column samples comprised a total of 41 micro-phytoplankton genera, while 33 genera of micro-phytobenthos were recorded in the sediment. All the 33 genera recorded in the sediment were also present in the water column, except the genera *Gomphonema*. The genera *Leptocylindricus*, *Synedra*, *Meuniera*, *Thalassiothrix*, *Stauroneis*, *Chaetoceros*, *Rhizosolenia*, *Diatoma* and *Phormidium* were only recorded in the water column samples. *Navicula* spp. was consistently present in high abundance in all the different ecosystems but a higher percentage of *Cylindrotheca*, *Stauroneis*, *Oscillatoria* and *Alexandrium* were recorded in the water column of the coral reef, sandy beach and estuarine area, respectively (Table 3). *Cocconeis* was also found to be dominant in the sediment of the estuarine area.

The Similarity Index (SI) for the water column samples from the sandy beach, mangrove, coral reef and

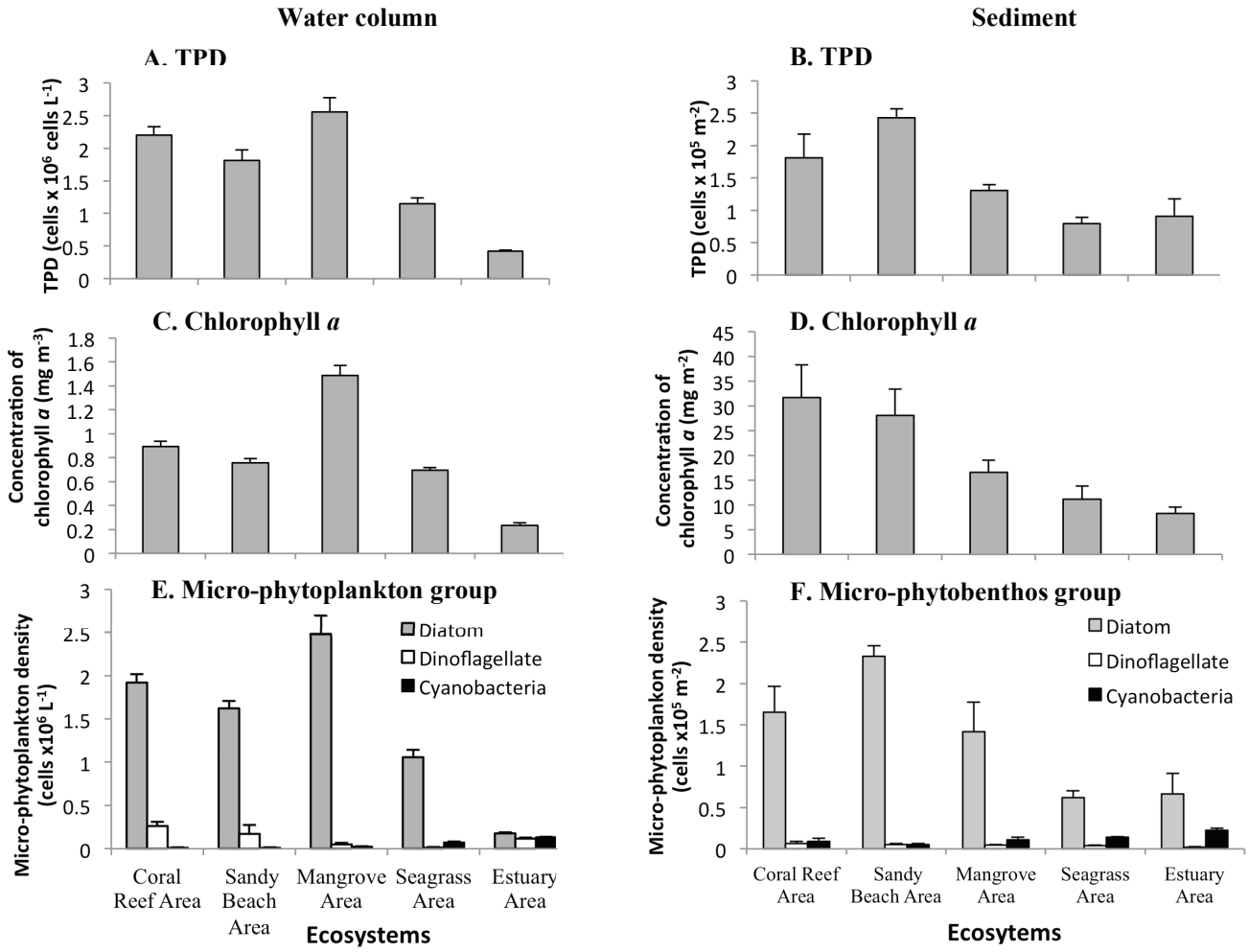

Figure 2. Total micro-phytoplankton/micro-phytobenthos density (TPD) in the water column (A) and sediment (B), chlorophyll *a* concentration in water column(C) and sediment (D) in the different ecosystems and micro-phytoplankton group (diatom, dinoflagellate and cyanobacteria) density in the water column (E) and sediment (F) in the five ecosystems studied. Data represent mean ± sd (n = 5).

Table 3. Percentage and Shannon's Diversity Index (DI) of micro-phytoplankton/micro-phytobenthos genera recorded in the water column and sediment of the five ecosystems (coral reef, sandy beach, mangrove, estuary and seagrass bed ecosystems).

Ecosystems	Coral reef		Sandy beach		Mangrove		Estuary		Seagrass bed	
Micro-phytoplankton// micro-phytobenthos genera	Water column	Sediment	Water column	Sediment	Water column	Sediment	Water column	Sediment	Water column	Sediment
Cylindrotheca sp.	24.2	1.3	3.1	1.9	0.5	2.1	3.1	0.0	1.5	3.6
Navicula sp.	11.9	19.5	11.6	30.8	15.3	31.9	7.6	15.4	18.8	25.0
Pseudonitzschia sp.	3.6	1.3	2.3	0.0	0.5	3.2	0.8	2.6	1.5	0.0
Thalassiosira sp.	0.5	0.0	1.6	0.0	1.0	1.1	0.8	1.3	0.8	0.0
Pleurosigma	1.5	0.0	0.0	0.0	6.6	8.5	0.8	0.0	9.8	3.6
Cymatopleura sp.	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.8	0.0
Melosira sp.	1.5	0.0	0.8	1.9	3.6	3.2	0.8	2.6	1.5	0.0
Cocconeis sp.	5.2	19.5	0.8	7.7	0.5	13.8	11.5	44.9	9.0	0.0
Mastogloia sp.	0.0	0.0	0.8	0.0	0.5	5.3	0.0	0.0	1.5	0.0
Fragilaria sp.	4.1	16.9	1.6	11.5	5.1	8.5	0.0	0.0	3.0	10.7
Achnanthes sp.	1.5	3.9	2.3	3.8	1.5	3.2	0.0	1.3	1.5	3.6
Gomphosphaeria sp.	0.5	0.0	2.3	1.9	14.3	4.3	3.8	2.6	0.0	14.3
Lyngbya sp.	0.5	1.3	0.0	1.9	0.5	2.1	12.2	5.1	3.8	10.7
Coscinodiscus sp.	1.5	0.0	1.6	1.9	1.5	1.1	0.0	0.0	11.3	3.6
Asterionellopsis sp.	3.1	5.2	0.8	0.0	1.0	1.1	0.8	0.0	2.3	0.0
Lioloma sp.	1.5	1.3	1.6	5.8	2.0	1.1	0.0	0.0	0.8	3.6
Manguinea sp.	1.0	0.0	0.8	1.9	0.5	0.0	0.0	0.0	0.0	0.0
Diploneis sp.	3.6	7.8	0.8	3.8	4.1	0.0	1.5	2.6	2.3	0.0
Nitzschia sp.	8.8	0.0	10.1	1.9	0.5	0.0	0.0	0.0	1.5	3.6
Cavinula sp.	0.5	5.2	2.3	3.8	1.0	1.1	0.8	2.6	11.3	14.3
Leptocylindricus sp.	0.0	0.0	0.0	0.0	0.5	0.0	0.8	0.0	0.8	0.0
Biddulphia sp.	2.1	0.0	0.0	0.0	3.6	0.0	0.0	1.3	0.8	0.0

Ecosystems	Coral reef		Sandy beach		Mangrove		Estuary		Seagrass bed	
Micro-phytoplankton// micro-phytobenthos genera	**Water column**	**Sediment**	**Water column**	**Sediment**	**Water column**	**Sediment**	**Water column**	**Sediment**	**Water column**	**Sediment**
Prorocentrum sp.	2.6	2.6	3.9	1.9	0.5	1.1	3.1	1.3	0.0	0.0
Protoperidinium sp.	4.6	1.3	6.2	1.9	0.5	1.1	11.5	1.3	1.5	3.6
Licmophora sp.	4.1	0.0	0.8	3.8	0.0	0.0	0.0	0.0	2.3	0.0
Striatella sp.	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	2.3	0.0
Thalassionema sp.	0.5	0.0	0.8	1.9	0.0	0.0	0.8	1.3	1.5	0.0
Synedra sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0
Meuniera sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0
Thalassiothrix sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lyrella sp.	1.5	1.3	0.8	1.9	0.0	2.1	0.0	1.3	0.8	0.0
Oscillatoria sp.	0.0	1.3	0.8	0.0	1.0	2.1	15.3	5.1	3.0	0.0
Climacosphenia sp.	0.0	2.6	0.0	1.9	0.0	0.0	3.8	7.7	0.0	0.0
Gomphonema sp.	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Pinnularia sp.	1.0	6.5	14.7	0.0	15.3	0.0	3.1	0.0	0.0	0.0
Stauroneis sp.	1.0	0.0	18.6	0.0	17.3	0.0	0.0	0.0	0.8	0.0
Chaetoceros sp.	0.0	0.0	0.8	0.0	0.0	0.0	2.3	0.0	0.0	0.0
Alexandrium sp.	5.2	0.0	7.8	0.0	0.5	1.1	15.3	0.0	0.8	0.0
Craticula sp.	0.5	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhizosolenia sp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diatoma sp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phormidium sp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
No. of genera	31	18	27	22	27	22	22	17	30	12
Shannon DI	2.815	2.389	2.703	2.588	2.547	2.440	2.540	2.010	2.848	2.214

Table 4. Similarity index (SI) for every combination in both the water column and sediment of the five ecosystems sampled for micro-phytoplankton/micro-phytobenthos genera. WC: water column; SED: sediment.

		Coral Reef		Sandy Beach		Mangrove		Estuary		Seagrass	
		WC	SED	WC	SED	WC	SED	WC	SED	WC	SED
	WC	-									
Coral Reef	SED	0.653	-								
	WC	0.828	0.667	-							
Sandy Beach	SED	0.717	0.650	0.735	-						
	WC	0.793	0.667	0.852	0.653	-					
Mangrove	SED	0.679	0.700	0.776	0.636	0.816	-				
	WC	0.642	0.600	0.694	0.545	0.735	0.682	-			
Estuary	SED	0.625	0.629	0.636	0.667	0.636	0.667	0.718	-		
	WC	0.754	0.583	0.772	0.615	0.807	0.769	0.615	0.596	-	
Seagrass	SED	0.558	0.533	0.462	0.647	0.615	0.647	0.412	0.414	0.524	-

estuary areas did not show great variation, except for the estuary area, which had lower similarity values compared to the other ecosystems (Table 4). In the sediment samples, seagrass and estuary areas were dissimilar compared to the other ecosystems (SI = 0.414). Comparison between the water column and sediment samples showed that the mangrove sediment and water column were more similar (SI = 0.816), while the water column and sediment at the seagrass area was more dissimilar (SI = 0.524).

Photo-physiological status of micro-phytoplankton/ micro-phytobenthos

The physiological status ($rETR_{max}$, NPQ_{max} and estimated relative productivity) of micro-phytoplankton/ micro-benthos were significantly different in both the water column and the sediment at the five different ecosystems, with the exception of the effective quantum yield (ϕ_{PSII}) (Table 5).

Photochemical efficiency

The mean photochemical efficiency of $\phi_{PSII,}$ of micro-phytoplankton/micro-phytobenthos sampled in the water column and sediments measured from Diving PAM was computed for each site (Fig. 3). The photo-physiology of micro-phytoplankton from the water column and sediments were relatively similar for the different ecosystems.

Relative electron transport rate (rETR) and non-photochemical quenching

The $rETR_{max}$ values for the water column and sediments at the coral reef, sandy beach, and mangrove area were found to be comparatively the same, indicating little variation in photo-physiology (Fig. 4A-C). However, at the seagrass bed area (Fig. 4D), the $rETR_{max}$ values for the water column was found to be much higher compared to that of sediments, while the contrary was observed for the estuarine area (Fig. 4E). Thus microalgae in the water column had a much higher photosynthetic activity than those present in the sediments.

The NPQ_{max} values for the water columns and sediments at the coral reef and sandy beach area were found to be relatively the same, indicating equal capacity for the dissipation of excess light energy (Fig. 4F; G). However, at the mangrove (Fig. 4H), seagrass bed (Fig. 4I), and the estuarine area (Fig. 4J), the NPQ_{max} value for the water column was found to be moderately higher compared to that of sediments at the mangrove area. Thus, the micro-phytoplankton in the water column had a higher capacity for energy dissipation as compared to those from the sediments.

Mean $rETR_{max}$ values, and I_k for each ecosystem

The mean $rETR_{max}$ value was highest in estuarine sediment followed by sandy beach, with the lowest value was obtained in the seagrass bed and mangrove area, based on samples from the water column (Fig. 5). Moreover, the mean $rETR_{max}$ was lower in the sediment of the seagrass bed ecosystem compared to the water column in that ecosystem.

The I_k values for the water column for the coral reef, sandy beach, mangrove, seagrass bed, and estuarine

Table 5. One-way ANOVA to test the photo-physiological status (ϕ_{PSII}, $rETR_{max}$, NPQ_{max} and estimated relative productivity) of micro-phytoplankton at the five ecosystems (coral reef, sandy beach, mangrove, seagrass and estuary). Asterisks indicate significant differences at 5% level. (* = P< 0.05; ** = P< 0.01; *** = P< 0.001).

	Dependent variables	Source of variation	df	MS	F	P-value
Water column	ϕ_{PSII}	0.004	4	0.001	0.577	NS
	$rETR_{max}$	3712	4	928.1	4.807	**
	NPQ_{max}	0.020	4	0.005	3.791	*
	Estimated Productivity	4812	4	1203	39.82	***
Sediment	ϕ_{PSII}	0.005	4	0.001	0.707	NS
	$rETR_{max}$	11067	4	2767	22.69	***
	NPQ_{max}	0.2481	4	0.062	61.12	***
	Estimated Productivity	1265	4	316.3	17.54	***

areas were 212.39±58.18, 159.66±43.02, 94.75±7.90, 163.45±41.07, 167.44±35.56, respectively. While for the sediment samples, the I_k values were 157.21±42.53, 272.16±74.41, 232.99±87.86, 39.15±9.91, 343.29±100.59 in these ecosystems, respectively.

Estimated Productivity

The water column of the sandy beach and the coral reef area had the highest estimated productivity while the seagrass bed area had the lowest (Fig. 6A). Productivity estimates were highest in the sediment of the coral reef and sandy beach area, and lowest in the estuarine area (Fig. 6B).

Physical parameters

The tidal pool of the mangrove swamp at Pointe D'Esny had the highest temperature (33±0.41°C), whereas temperature was lowest in the coral reef area of Blue Bay (27.7±0.24°C). Highest salinity was obtained in the mangrove area (40.7±0.47 ppt), with the lowest value recorded in the estuarine area (28.7±0.47 ppt) (Fig. 7A). The pH was highest in the estuarine area of Le Goulet (pH = 8.5±0.30), and lowest in the mangrove area (pH = 7.4±0.14) (Fig. 7B).

Nutrient concentrations differed among the different ecosystems (Table 1). Significantly higher nitrate

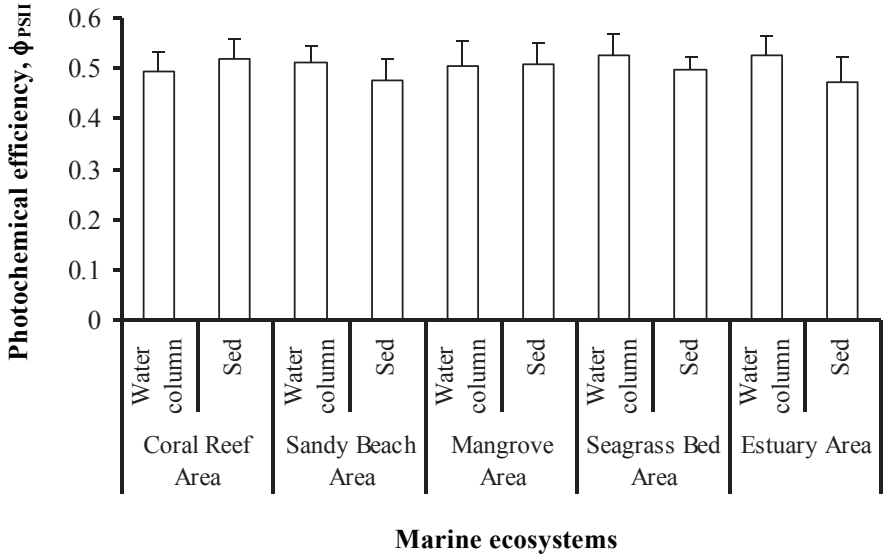

Figure 3. Photochemical efficiency, ϕ_{PSII}, of micro-phytoplankton/micro-phytobenthos sampled from the water column and sediment (Sed) in different marine ecosystems. Data represent mean ± sd (n=5).

(0.86±0.06 mg L^{-1}) and silicate (1.46±0.05 mg L^{-1}) concentrations were obtained in water samples collected in the estuary area (Fig. 7C). Although there was no significant difference in nitrate concentration between the seagrass and mangrove area, and between the coral reef and sandy beach area, nitrate was higher in the coral reef area (0.44±0.08 mg L^{-1}) than in the seagrass bed area (0.35±0.03 mg L^{-1}). However, phosphate concentration was significantly lower in the sandy beach area (0.13±0.06 µg L^{-1}), while no significant difference was obtained for the other ecosystems. Silicate concentration was higher in the estuarine (1.46±0.05 mg L^{-1}) and the sandy beach area (1.25±0.06 mg L^{-1}) (Table 2) while no significance difference was obtained between the coral reef (0.85±0.07 mg L^{-1}), mangrove (0.83±0.09 mg L^{-1}), and seagrass area (0.88±0.10 mg L^{-1}).

Discussion

Micro-phytoplankton in the water column

The higher total micro-phytoplankton density (TPD) and chlorophyll *a* concentration in the mangrove ecosystem indicates that this ecosystem is highly

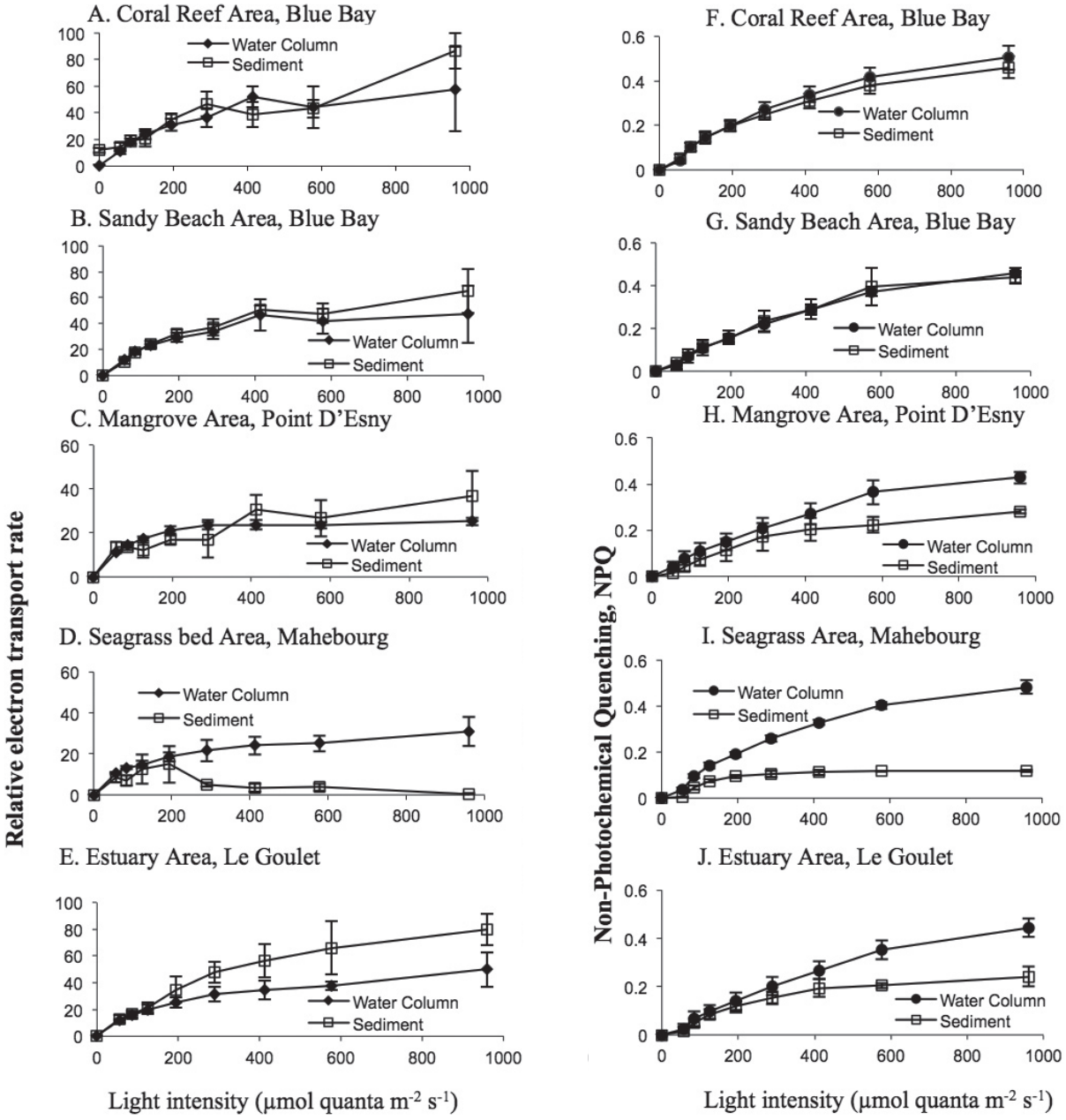

Figure 4. Relative electron transport rates (A-E) and non-photochemical quenching (F-J) of micro-phytoplankton/micro-phytobenthos collected from the water column (●) and sediment (□) from five near shore marine ecosystems (coral reef, sandy beach, mangrove, seagrass bed, and estuary).

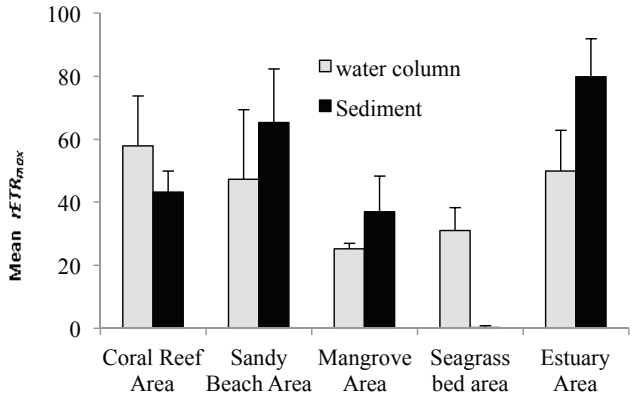

Figure 5. $rETR_{max}$ for each marine ecosystem. Data represent mean ± sd (n = 5).

productive compared to the other studied ecosystems. Indeed, the nutrient enrichment in the mangroves ecosystem is due to the presence of highly efficient nutrient retention mechanisms, characteristics of mangrove swamps (Alongi, 2002). Availability of nutrients in these ecosystems appeared to be a determinant of micro-phytoplankton (Teissier *et al.*, 2011) with higher TPD recorded at higher nutrient concentration, except in the coral reef and estuarine area. In the coral reef area, nutrients seemed to be a limiting factor, and their lower concentration may be attributed to their uptake by micro-phytoplankton.

However, the contrary was observed in the estuarine area where low density of TPD was recorded despite the high level of nutrients prevailing there. Although estuaries have high productivity, this does not necessarily extend to the water column, and phytoplankton production may be lower compared to other marine environments (Cloern, 1987). Considering the high level of nutrients recorded in the estuarine area at Le Goulet, micro-phytoplankton density and estimated productivity were expected to be higher, but the contrary was observed. This might be attributed to high level of turbidity observed at the time of sampling, which may have been due to river inputs, suspended particulate matter and/or suspension of bottom sediments (Cloern, 1987). Light availability greatly affects primary production (Diehl *et al.*, 2002), and the high turbidity limits light penetration, which in turn reduces algal production. This explains the low density of micro-phytoplankton and low productivity estimates at the estuarine area.

The degree of turbulence at the different ecosystems may contribute to the difference in micro-phytoplankton densities observed during the study, since primary production has often been correlated to turbulence and mixing (Jouenne *et al.*, 2007). Higher turbulence at the coral reef and sandy beach area may contribute to the higher TPD prevailing there compared to the seagrass bed, estuarine and mangrove ecosystems. In conditions of high turbulence, phytoplankton displacement is higher compared to their maximum sinking rate (Cullen and MacIntyre, 1998). The interaction between turbulence, coupled with solar radiation and depth regulation behavior,

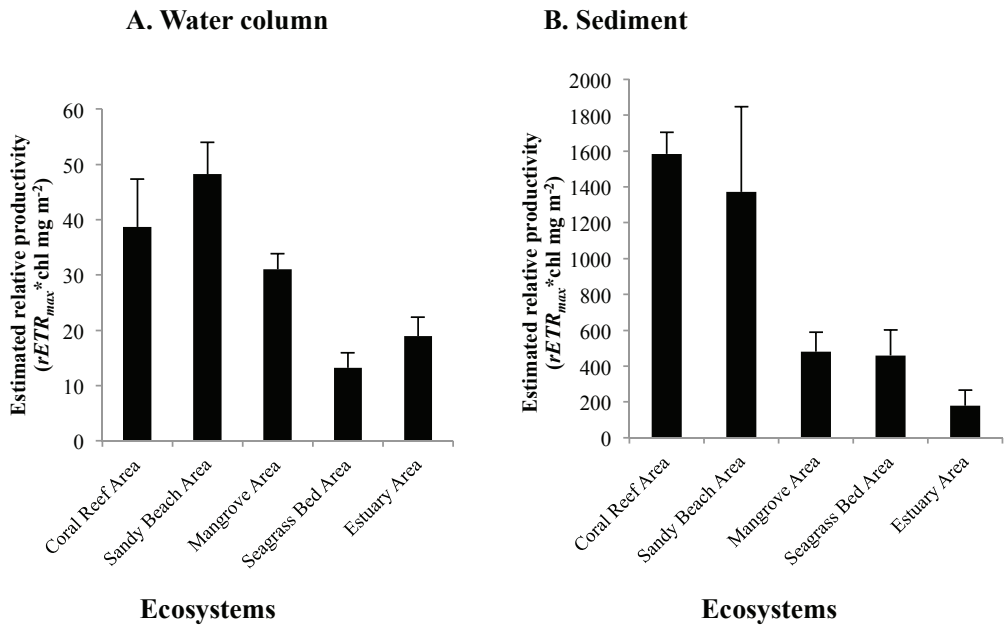

Figure 6. Variation in estimated relative productivity (expressed as the product of $rETR_{max}$ and chl mg m^{-2}) in the water column (A) and sediment (B) in different ecosystems. Data represent mean ± sd (n=5).

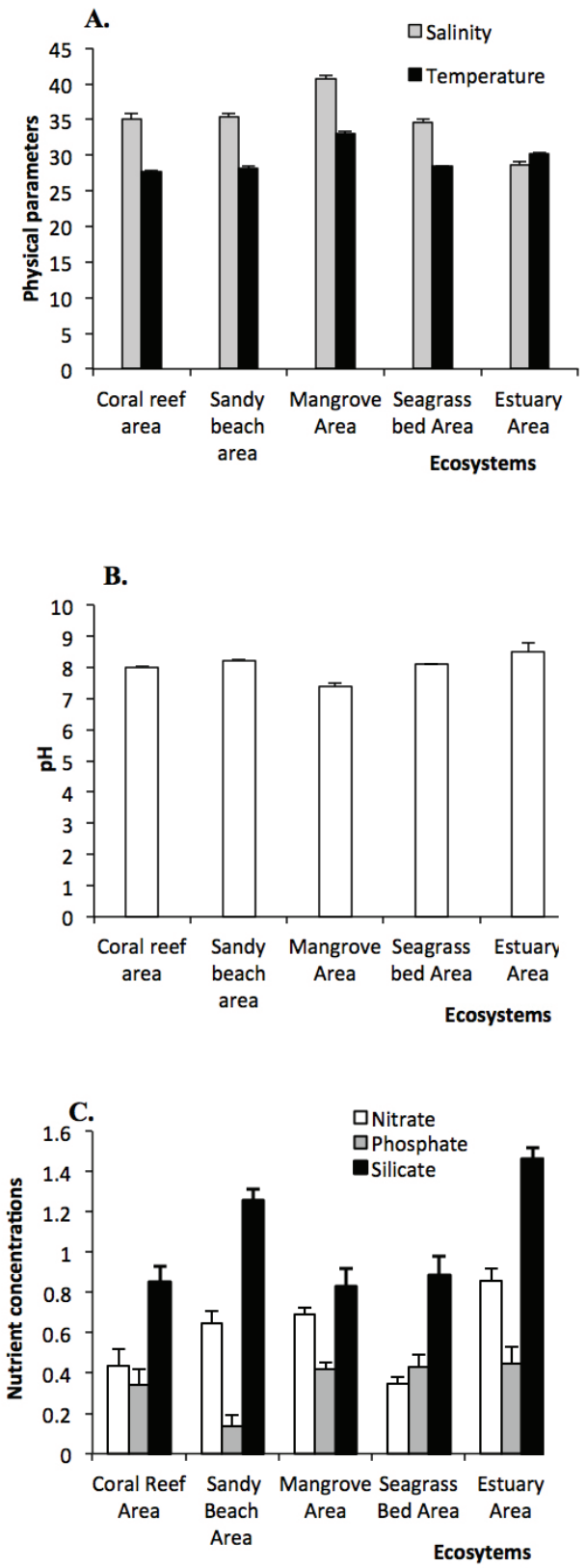

Figure 7. Physical parameters (pH, salinity (ppt) and temperature (°C)) measured in the water column and/or sediments in the five ecosystems (a); pH (b); Nitrate, phosphate and silicate concentrations, measured as mg L^{-1} (for nitrate and silicate) and µg L^{-1} (for phosphate) (c), in the water column from five near shore ecosystems. Data represent mean ± sd (n=5).

plays an important role in determining the irradiance experienced by phytoplankton. These phytoplankton, in turn, respond to variations in irradiance through a series of adjustments known as photoacclimation (Cullen and MacIntyre,1998). The turbulent environment may favour large species which may have higher resistance to physical disturbance, but it also contributes to the resuspension of small benthic species (Jouenne *et al.*, 2007).

Other factors, including wind, waves and tidal currents, also contribute to the deep mixing of the water column, transporting phytoplankton cells to the bottom. However, this deposition in shallow waters is counteracted by the effect of the velocity and turbulence of bottom currents, which may exceed the settling velocity of organic material (Huettel and Rusch, 2000). The low wave characteristics of the mangrove area, together with high nutrient concentrations, may have accounted for the high density of micro-phytoplankton found here. Micro-phytoplankton respond quickly to increasing nutrient by increasing their growth rate and standing crop (Alongi, 2002).

Micro-phytobenthos in the sediment

Substrate type is usually one of the main factors governing phytoplankton assemblages (Potapova and Charles, 2005) and is considered as an important variable influencing the biomass and composition of benthic microalgae (Cahoon and Safi, 2002). For example, Cahoon *et al.* (1999) reported higher phytoplankton biomass in sandier substrates while others contradict this finding and reported higher phytoplankton biomass associated with finer sediments (Underwood and Kromkamp, 1999). This study is in accordance with the study of Cahoon *et al.* (1999), where higher TPD and chlorophyll *a* was recorded in the sandy sediment in the coral reef and sandy beach ecosystems while lowest density was recorded in the estuarine and seagrass bed area. The lower density in the seagrass ecosystem is because the sediment is coarse and loose, and micro-phytobenthos in the sediment are easily exported from the sediment to the water column.

The transportation of phytoplankton into and within the sediment is limited to the open pore size of the substrate, as well as the phytoplankton cell characteristics. The depth at which these phytoplankton penetrate the sediment is determined by the size, shape, density, surface characteristics of the algae, and the movement of living cells (Huettel and Rusch, 2000). Permeable shelf sands have been proposed to efficiently

filter particulate organic matters, at the same time acting as a catalyst, increasing the rate of mineralization of organic carbon and nutrient recycling. This explains the higher micro-phytobenthos density in the sandy sediments of the sandy beach and coral reef area. However, sediment sizes at the different ecosystems were not investigated during this study.

Benthic phytoplankton plays an important role in nutrient uptake from pore water, as well as in the water column (Brito *et al.*, 2009). Nutrient enrichment in the mangrove ecosystem might have contributed to increased benthic macro-invertebrate density, which may directly feed on phytoplankton (Blumenshine *et al.,* 1997), reducing their density. Moreover, the fact that mangroves serve as a nursery ground for a wide range of aquatic organisms that feed directly or indirectly on phytoplankton, coupled with filter feeders, could account for the lower TPD in the mangrove sediment. Although micro-phytoplankton density in the water column of the mangrove area was comparatively high, their lower densities in the sediment compared to the other ecosystem might also be due to reduced light penetration which would limit the growth of autotrophic microalgae attached to the micro-phytoplankton (Blumenshine *et al.*, 1997).

Well-illuminated shallow bottoms and moderate to high nutrient loadings in estuarine ecosystems offer an optimum environment for the growth of benthic microalgae, contributing to total primary production in these ecosystem (Cahoon and Safi, 2002). However, this was not the case for the estuarine area at Le Goulet where lower TPD and diversity were recorded. Land disturbing activities (construction of hotels in this case) are known to contribute to increased sediment loading, especially fine-grained materials, to receiving waters, leading to the accumulation of fine sediments in estuaries (Wanielista and Yousef, 1993). This anthropogenic sedimentation may thus lower the total biomass of micro-phytoplankton, and may also alter the composition of phytoplankton communities in estuarine ecosystem (Cahoon and Safi, 2002). According to these authors, this might be attributed to several factors such as reduced interstitial space volumes, level of nutrients, and light penetration in the muddy sediments, all contributing to lower biomass of micro-phytoplankton. Another explanation might be that muddy substrates harbour a taxonomically different assemblage of benthic microalgae as compared to sandier substrates, and these differ in their growth rates, standing crop, or differences in their dislodgment or grazing susceptibilities (Cahoon and Safi, 2002). However, this study showed that micro-phytoplankton assemblages in the sediment did not differ from those in the water column with the 33 genera recorded in the sediment also present in water column, with the exception of the genera *Gomphonema.* Therefore, micro-phytobenthos differences in the sediments at the different ecosystems in this case might be attributed to light regime, biovolume and nutrient fluxes.

Micro-phytoplankton/micro-phytobenthos diversity

Different micro-phytoplankton taxa may exhibit vertically heterogeneous distributions. Usually these are due to the ability of species to regulate their position in the water column by actively swimming (flagellates) or by controlling their buoyancy (cyanobacteria) (Klausmeier and Lichman, 2001). Moreover, under optimum resource conditions such as high irradiance and nutrient concentrations, diatoms have a greater growth rate compared to flagellates of the same size (Cermeno *et al.*, 2005), accounting for their dominance in both the water column and sediment samples in the 5 studied ecosystems. Cyanobacteria density was higher compared to dinoflagellates in the sediment samples in the different ecosystems, probably because these are benthic organisms.

Although diversity indices showed no great variation in micro-phytoplankton in the water column among the different ecosystems, the species composition was different. This difference in species composition appears to be dependent on the resources available that might favour the growth of particular species. In highly productive ecosystems, large-size phytoplankton form the bulk of phytoplankton biomass, while smaller ones are dominant in unproductive regions (Cermeno *et al.*, 2005). Similar observations were made in the present study where the dominance of the larger-sized *Staureneis* sp. in the sandy beach and mangrove area, and *Cylindrotheca* sp. in the coral reef area, was recorded. Dominance of smaller micro-phytoplankton such as *Oscillatoria* sp, *Cocconeis* sp. and *Navicula* sp. were recorded in the estuarine and seagrass bed ecosystems.

A total of 33 micro-phytobenthos genera were recorded in the sediment in the different ecosystems studies. Diatoms were the most dominant micro-phytobenthos group, compared to dinoflagellates and cyanobacteria, and this corroborates with previous studies

(Vant and Budd, 1993; Vant and Safi, 1996). Micro-phytobenthos diversity was slightly higher in the sandy beach area (H = 2.588), followed by the mangrove (H = 2.44), coral reef (H = 2.389), seagrass bed (H = 2.214), and the estuary area (H = 2.010). Microscopic analysis of sediment samples from the different ecosystems showed the dominance of the pennate diatom, *Navicula* spp. in the sediment of the sandy beach, coral reef, mangrove, and seagrass bed areas, and *Cocconeis* in the estuarine area. Similar results were also obtained from studies carried out in other estuaries, where pennate diatoms were dominant, along with centric diatoms (Cahoon and Safi, 2002). Vant and Budd (1993) also reported diatom genera, which were large centric or pennate forms. This is because these species can easily be suspended by the effect of tides and waves, compared to more firmly attached benthic phytoplankton. This may explain the dominance of *Navicula* spp. in both the water column and sediment in almost all the studied ecosystems.

Although micro-phytoplankton from the water column were more diverse with a total of 41 genera compared to the 33 genera from the sediment samples, they did not show great variation in terms of taxonomic composition as 32 genera from the sediment samples were also present in the water column. The genus *Gomphonema* was only present in the sediment while the genera *Leptocylindricus*, *Synedra*, *Meuneira*, *Thalassiothrix*, *Stauroneis*, *Chaetoceros*, *Rhizosolenia*, *Diatoma* and *Phormidium* were only recorded in the water column samples. This similarity could be due to mixing of micro-phytoplankton through sinking, or from the re-suspension of those in the benthos.

Photo-physiology of micro-phytoplankton/ micro-phytobenthos

The growth of phytoplankton is limited by light (De Swart *et al.*, 2009) and its availability greatly affects primary production and may influence the positioning and density of the phytoplankton layer (Klausmeier and Lichman, 2001). However, it has been shown that high light intensity may result in photoinhibition and the relative strength of the process is dependent on the exposure time at high irradiance. Prior to photoinhibition, phytoplankton maintain high photosynthesis during the first few minutes following exposure to saturating or inhibiting light (Macedo and Duarte, 2006). To adapt and respond to light regimes in their environment, phytoplankton have developed a series of mechanisms known as photoacclimation (Cullen and MacIntyre, 1998).

The $rETR_{max}$ of micro-phytoplankton/micro-phytobenthos in the water column and sediments for the coral reef, sandy beach, and mangrove area were similar, while the $rETR_{max}$ value in the water column was higher than that of sediments for the seagrass bed area. However, micro-phytobenthos in the sediment of the estuarine area had a higher electron transport rate compared to those in the water column. This implies that the micro-phytoplankton/micro-phytobenthos in the water column and sediment of the coral reef, sandy beach and mangrove area are ecophysiologically close and they are acclimated to similar environmental factors, including light regime. The higher $rETR_{max}$ recorded for micro-phytobenthos species living in the sediment of the estuarine area might be due to the vertical migration of micro-phytoplankton to escape high light intensities during the day. Similar observations were also made by Perkins *et al.* (2002), where it was noted that high light levels may drive the downward movement of microalgal cells, probably as a mechanism to prevent excessive exposure to disturbances, including predation or physical disturbances (Saburova and Polikarpov, 2003). Similarly, epipelic diatoms have been found to migrate downward in the sediment when exposed to high irradiance to avoid photoinhibition and increase photosynthetic performance (Cartaxana *et al.*, 2016). For the species in the seagrass bed sediments, they were probably more protected from light by the seagrasses and sediments, as they only reached their $rETR_{max}$ at a light intensity of 200 µmol quanta $m^{-2}s^{-1}$.

Micro-phytoplankton in the water column and sediment of the different studied ecosystems are exposed to distinct light regimes towards which they have developed adaptations enabling them to thrive in such conditions. Therefore, their response varies according to their level of tolerance to high light intensity. When exposed to increasing light intensities, there was no difference in $rETR_{max}$ and NPQ in micro-phytoplankton/micro-phytobenthos samples from both the sediment and water column in the coral reef and sandy beach area, probably because these are exposed to similar light regimes given that the coastal water in both these areas is clear.

The difference in $rETR_{max}$ of micro-phyoplankton/ micro-phytobenthos between the water column and sediment of the seagrass and estuarine area, and NPQ between the water column and sediment of the mangrove, seagrass and estuarine area indicates the differential physiological state and responses of these

organisms. This implies that at higher light intensity, $rETR_{max}$ and NPQ of micro-phytobenthos in sediment are greatly reduced which could be attributed to photoinhibition and damage to photosystem II (PSII). This could be due to their photosynthetic acclimation characteristics in response to their natural environment, and the characteristics of the ecosystem may help to explain the observed results. The shading effect provided by seagrass blades in the seagrass bed area and the mangrove roots in the mangrove area might result in the micro-phytoplankton/micro-phytobenthos being exposed to low light intensity in their natural habitat. This may have a strong effect in reducing the exposure time of phytoplankton cells to inhibiting light intensity and may explain the decrease in $rETR_{max}$ and NPQ_{max} when exposed to high light intensities. Therefore, these organisms appear to have developed adaptations which may result from interaction of structural, behavioural, physiological and biochemical factors, which enable them to survive and grow in conditions of low light intensity (Richardson *et al.*, 1983).

According to Barlow *et al.* (2010), phytoplankton readily adapt to variations in light intensity and quality and they have developed specific sets of pigments enabling them to respond to fluctuating light regimes in different ecosystems. At low irradiance, photosynthesis is limited by the rate at which light harvesting complexes absorbed protons (Cermenõ *et al.*, 2005). In this study, it appears that micro-phytoplanktkon/micro-phytobenthos in the water column and sediment at the different ecosystems had different adaptation strategies which could be due to their photoacclimation and photoadaptation to the irradiance regime at these ecosystems.

The different responses of micro-phytoplankton/micro-phytobenthos in the water column and sediment of the seagrass bed, mangrove and estuarine area is not only dependent on the ecosystem characteristics (Macedo and Duarte, 2006) but on the species composition as well (Jouenne *et al.*, 2007). Different phytoplankton taxa have varying ability to adapt (Cullen and MacIntyre, 1998) with some species being able to exert some control over their light environment by regulating their position in the water column (Richardson *et al.,* 1983). For example, diatoms (e.g. *Thalassiosira pseudonana*) that are adapted to low light intensity have been shown to strongly inhibit short-term photosynthesis, adapt and survive when exposed to high light intensity, while the cyanobacteria *Oscillatoria agardhii*, showed inhibition of photosynthesis and could not survive when exposed to short-term exposure to much higher than saturating irradiance (Cullen and MacIntyre, 1998). According to Cermeno *et al.* (2005), there has been previous evidence of taxon-related differences in F_v/F_m. This probably explains the lower F_v/F_m of micro-phytoplankton samples in the estuarine area, where the dominance of the cyanobacteria *Oscillatoria* spp. was recorded.

The presence of a higher percentage of the cyanobacteria *Gomphosphaeria* sp., coupled with the dominance of benthic microalgae, including *Pinnularia* sp., *Stauroneis* sp., *Navicula* sp., and *Cocconeis* sp., in the water and sediment samples of the mangrove area might have contributed to the lower $rETR_{max}$ at this sampling site, since cyanobacteria have very low F_v/F_m (Koblizek *et al.*, 2001), and benthic microalgae have a low ability to adapt to increasing light intensity. This could explain the lower estimated productivity (which is the product of $rETR_{max}$ and chlorophyll *a* concentration), although higher microalgal densities and chlorophyll *a* concentration was recorded in the mangrove area.

There are several new ways of measuring primary productivity, including Fast Repetition Rate fluorometry (FRRf), as described by Oxborough *et al.* (2012), that enable the direct calculation of the absorption cross section of PSII photochemistry, but this study focused mainly on relative values, for example through the use of chlorophyll data. It is suggested that future studies should focus on the use of different techniques in measuring photophysiology of micro-phytoplankon/micro-phytobenthos. It is imperative to better understand the photo-physiological responses of micro-phytoplankton/micro-phytobenthos to varying environmental conditions, especially because climate change-driven disturbances are increasingly exerting pressures on coastal ecosystems. Future attention is also needed to better understand the functioning of these different ecosystems to contribute to the improved management of coastal areas.

Conclusion

This study has shown that although the different ecosystems varied in terms of total micro-phytoplankton/micro-phytobenthos density, they had almost similar micro-phytoplankton composition, with diatoms being the dominant group, followed by dinoflagellates and cyanobacteria. This might due to the fact that diatoms have a high growth rate. The lower density of dinoflagellates is possibly because they can actively swim and regulate their position in the water column

avoiding collection, while cyanobacteria were least sampled because these are benthic. This study also showed that even if estuarine areas are known to be highly productive, anthropogenic sedimentation may alter their functioning and productivity. The ecosystems' characteristics and physico-chemical parameters influenced density patterns, and higher densities were recorded in nutrient-rich waters. Light is the factor that has been found to greatly influence the density of micro-phytobenthos. Lower densities were recorded in turbid water or in waters with higher micro-phytoplankton densities, which limit light penetration to bottom micro-phytobenthos. A total of 41 micro-phytoplankton genera were recorded in the water column at the different ecosystems, while a total of 33 genera were obtained in the sediment samples. However, with the exception of *Gomphonema*, all micro-phytobenthos genera present in the sediment samples were also recorded in the water column. Both the water column and sediment samples had very similar micro-phytoplankton/micro-phytobenthos assemblages, which can either result from mixing from micro-phytoplankton sinking, or re-suspension of benthic micro-phytoplankton. The same photo-physiological responses towards increasing light intensities were observed for micro-phytoplankton/micro-phytobenthos from both the water column and sediment in the sandy beach and coral reef ecosystems. In the other ecosystems, a decrease in $rETR_{max}$ and NPQ_{max} with increasing light intensities in sediment samples was observed. This implies that these organisms are adapted to live in conditions of low light intensity and they are susceptible to increasing light intensities, exposure to which can result in death, hindering the proper functioning of these ecosystems. The need to study the photo-physiological status of micro-phytoplankon/micro-phytobenthos in different ecosystems is crucial if we are to better manage coastal ecosystems, which are under increasing threat from climate change.

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