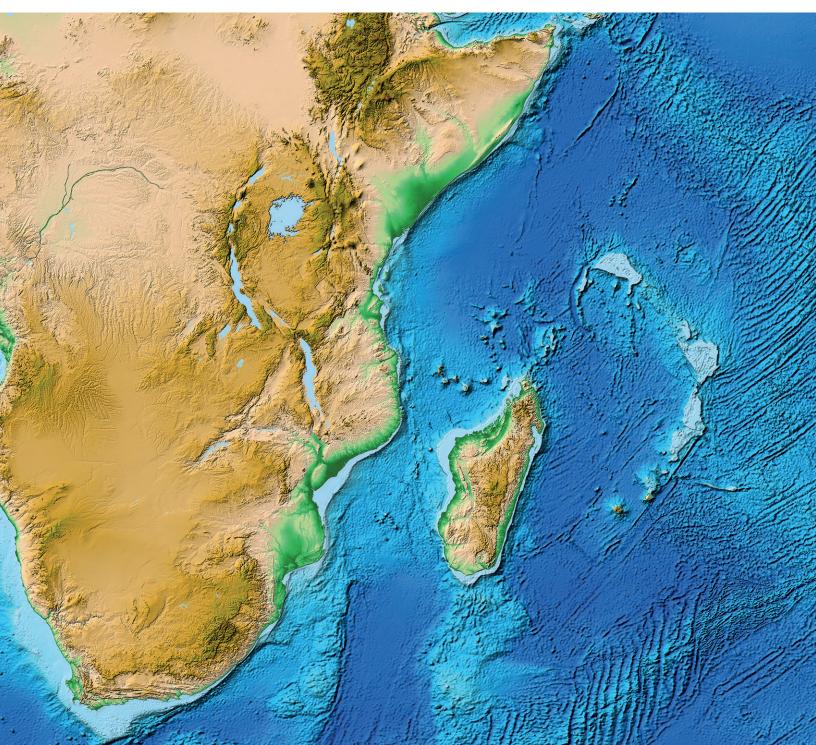
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### Micro-tidal dependent micro-phytoplankton C-biomass dynamics of two shallow tropical coral reefs

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### Abstract

This study investigates micro-tidally induced variations in micro-phytoplankton carbon biomass (C-biomass), concentrations of chlorophyll *a*, nitrate, phosphate and silicate, temperature, salinity and pH at three zones (near-coast, lagoon and reef) at two sites (Flic-en-Flac and Belle Mare) on two consecutive days covering two high and low tides in August (winter) and in November (summer) 2011. At Flic-en-Flac, 36 different genera of micro-phytoplankton were recorded, including 29 bacillariophyceae, *5* dinophyceae and 2 cyanophyceae. At Belle Mare, 34 different genera of micro-phytoplankton were recorded, including 31 bacillariophyceae, 3 dinophyceae and 2 cyanophyceae. At low tides the total micro-phytoplankton C-biomass (TMPB) and nutrient levels were significantly higher compared to those at high tides. At both sites, zonal variation in TMPB was evident with significantly higher C-biomass closer to the coast. Only bacillariophyceae and dinophyceae Was dominant, followed by cyanophyceae and dinophyceae, irrespective of micro-tidal changes, indicating their ability to tolerate a wide range of micro-phytoplankton dynamics and might have implications for carbon cycling over shallow tropical coral reefs and other inter-connected coastal ecosystems.

Keywords: C-biomass, chlorophyll a, environmental factors, micro-phytoplankton, micro-tides

### Introduction

Phytoplankton form the basis of marine food chains and food webs (Ersanli and Gönülol, 2003; Gameiro *et al.*, 2007; Zhou *et al.*, 2009) and they play an important role in the cycling of greenhouse gases since they participate in the biological pump of carbon dioxide (Tréguer and Pondaven, 2000), as well as in biogeochemical cycling (Khenari *et al.*, 2010). Pure physical forcing mechanisms mainly control the ratio between euphotic and mixing depth, which in turn determines net primary production (Falkowski and Raven, 1997). In coral reef-lagoons, the physical mechanisms that contribute to circulation can also influence the transport, dispersal, and retention of several organisms, including phytoplankton (Hench *et al.*, 2008). Environmental forcing by tidal cycle is one of the factors that has been found to govern variability in phytoplankton abundance, biomass and growth in coastal waters (Cloern, 1991; Torréton *et al.*, 2010; Blauw *et al.*, 2012). Tides have a crucial role to play in many coastal systems' functioning, by contributing to variations in both biotic and abiotic characteristics in these systems (Davies and Ugwumba, 2013). For example, tidal movements have been found to be partly responsible for variation in nutrient concentrations in coral reef areas (Torréton *et al.*, 2007), whilst tidal height and amplitude can influence light penetration, temperature, salinity and pH (Blauw *et al.*, 2012).

In shallow coastal waters, tide plays an important role in short-term variability in phytoplankton biomass (Cloern *et al.*, 1989; Cloern, 1991; Villate, 1997), such that vertical mixing intensity generated by wind action and tidal motion contribute to either settling or resuspension of coastal phytoplankton (Blauw *et al.*, 2012). Increase in phytoplankton biomass is usually a result of temporary phenomena, including variation in vertical mixing rate, brought about by the effect of tidal mixing, wind-driven mixing and thermal mixing/ stratification (Jin *et al.*, 2006). In addition, non-linear internal waves have also been found to considerably affect biogeochemical fluxes and distribution of phytoplankton in coastal areas (Cuypers *et al.*, 2011).

Carbon is the principal structural component of heterotrophic and phototrophic organisms; it can be used for comparing biomass and bioenergetics for community-wide and group-specific planktonic organisms. In fact, the carbon biomass of phytoplankton is considered to be an essential parameter in ecosystems models and biogeochemical carbon budgets (Menden-Deuer and Lessard, 2000). Few studies have focused on short-term variation of micro-phytoplankton and made use of C-biomass for the study of micro-phytoplankton. This process involves measuring the size of the different groups of micro-phytoplankton, converting these to cell volumes and finally to carbon biomass through existing formulae and equations. Knowledge on the carbon content of major planktonic organisms, including bacillariophytes, dinophytes and cyanophytes, can help in predicting and in quantifying the temporal and spatial variability in total and export primary production. However, to-date most of the studies carried out on phytoplankton comprise the enumeration and quantification of the density, and diversity, and limited C-biomass data sets for micro-phytoplankton are available, especially in tropical lagoons dominated by coral reefs.

Short-term temporal (hourly) and long-term (seasonal) variations are of great importance in assessing plankton processes (Torréton et al., 2010). However, studies have put more emphasis on the long-term (seasonal and weekly) variations in phytoplankton (Lucas and Cloern, 2002; Bresnan et al., 2009; Drake et al., 2010) despite the fact that short-term variations, such as those observed on an hourly basis, have been found to be equally significant. These short-term variations may be due to physical and biological forces, including internal current and wind-driven re-suspension of benthic microalgae (Cloern et al., 1989). To-date limited studies have reported the tidal influence on both nutrients and phytoplankton community, and this study therefore provides important information about the variation of phytoplankton C-biomass, chlorophyll a, distribution and diversity in response to micro-tidal changes.

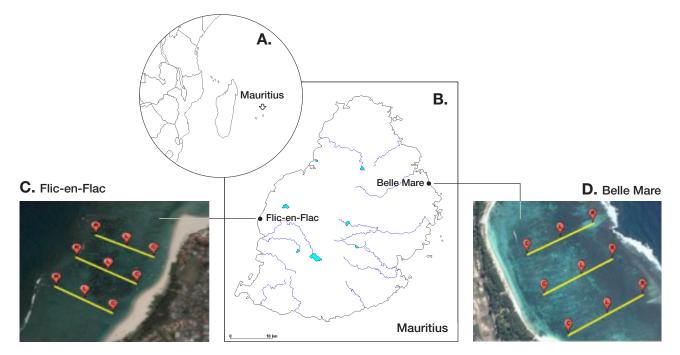


Figure 1. Maps showing the location of Mauritius in the Indian Ocean (A) (Source: https://sites.google.com/site/indianoceancommunityl/geo-politics) and the sampling sites in Mauritius (B) (Source: http://www.hmsmauritius.co.uk/pageone.htm), namely Flic-en-Flac (C) and Belle Mare (D) (Source: Google Earth).

### Study sites

Mauritius is situated in the South West Indian Ocean and the tidal cycle comprises two high and two low tides in each lunar cycle (Turner *et al.*, 2000). Tidal characteristics around Mauritius include micro-tides (Magori, 2009) of 0.3-0.8 m changes (Baird and Associates, 2003).

Micro-phytoplankton sampling was carried out at Flic-en-Flac (FEF) and Belle Mare (BM), which are situated on the western and eastern coasts of Mauritius Island respectively (Fig. 1a, b). Micro-phytoplankton samples were collected in three zones; namely shore, lagoon, and reef, at both FEF and BM (Fig. 1c, d).

The two sites were chosen because they differ in terms of percentage coral cover, coral diversity, topography, lagoonal area, level of coastal development and anthropogenic input, and wind intensity. The percentage of live coral cover was higher at BM (45%) than at FEF and this is evenly distributed throughout the lagoon compared to FEF, where live corals are mostly concentrated near the coral reef area, which is around 500 m from the shore. BM has a larger lagoonal area compared to FEF, with a distance of 850 m from the shore to the reef (MoE, 2004). Water depth is also greater at BM than at FEF. FEF is among the Mauritian beaches with extensive coastal development, and where the coastline has been artificially modified to accommodate new developments. Meethoo (2010) recorded higher building density, including hotels, near the coast of FEF compared to BM. However, although BM is less developed than FEF, anthropogenic inputs in the form of fertilisers and sewage discharge are a major problem, especially during periods of heavy rainfall, when these pollutants are washed into the nearby lagoon. These run-off events in turn promote growth of algae and may even lead to algal blooms. BM, being situated on the eastern coast of the island, is more exposed to the South East Trade Winds and wind intensity is higher there than at FEF.

### Micro-phytoplankton and seawater sampling

Micro-phytoplankton sampling was carried out twice a day over a period of 24 hours covering two low tides and two high tides in the months of August and November 2011. For micro-phytoplankton and chlorophyll *a* samples, 10 L of seawater was collected at a depth not exceeding 1 m. The seawater was filtered and concentrated (Chowdhury *et al.*, 2007) using a 5 µm plankton net (Rigosha and Co. Ltd, Japan) and the concentrate was collected in 250 ml opaque plastic bottles. Triplicate water samples for nitrate, phosphate, silicate and chlorophyll *a* analysis were collected in 500 ml plastic bottles at a depth not exceeding 1 m.

All sampling bottles were kept in the dark and at low temperature in isotherm boxes during transportation to the laboratory. Samples for chlorophyll *a* and micro-phytoplankton were processed on the day of collection while samples collected for nutrient analysis were kept at -20°C for later analyses.

#### Measurement of physico-chemical parameters

*In-situ* temperature (Comark 314 thermometer), salinity (Erma) and pH (Hanna H1 9024C) were measured. Nitrate, phosphate and silicate concentrations were estimated using the cadmium reduction method, ascorbic acid method, and the molybdenum blue method, respectively (Greenberg *et al.*, 1992).

### Measurement of biological parameters: Chlorophyll a, micro-phytoplankton identification and C-biomass

Chlorophyll *a* samples were filtered through a Glassfibre filter (0.45 µm pore size) (Whatman Paper Limited) and chlorophyll *a* pigment was extracted using 90% acetone for 24 hrs at 4°C. Concentration of chlorophyll *a* was determined using a spectrophotometer (Spectronic<sup>®</sup> Genesys<sup>TM</sup> 8 spectrophotometer) (Jeffrey and Humphrey, 1975).

Prior to identification and counting, the collected samples were centrifuged (Häder, 1995) at 3000 rpm for 5 minutes (Khenari *et al.*, 2010) and the concentrate was fixed with Lugol's solution (Meesukko *et al.*, 2007) and kept in the dark at 4°C. One millilitre of sample was placed in a Sedgewick-Rafter Counting chamber (Sidik *et al.*, 2008) and micro-phytoplankton was identified and counted using a light microscope at magnifications X100, X200 and X400 (Smith and Johnson, 1996; Tomas, 1997; Dhargalkar and Ingole, 2004). Micro-phytoplankton were grouped into Bacillariophyceae, Dinophyceae and Cyanophyceae. Biovolumes of the different micro-phytoplankton classes were calculated and these were in turn converted to C-biomass according to Jun and Dongyan (2003).

### Statistical analyses

Statistica 10.0 software was used for computing data and statistical analyses. Two-way analysis of variance (ANOVA) was carried out to test the tidal differences within measured parameters and different stations at

the study sites, followed by Tukey's Post hoc analysis for comparison of means. C-biomass data was log<sub>10</sub> transformed while temperature, salinity, pH, chlorophyll a, nitrate, phosphate and silicate data were arcsin (square root) transformed prior to ANOVA analyses. Correlations between physico-chemical and biological parameters, namely pH, temperature, salinity, dissolved oxygen, chlorophyll *a* concentrations, nitrate, phosphate and silicate concentrations, with the total C-biomass of micro-phytoplankton at the different study sites were tested using Pearson correlation with SPSS software (version 14). Shannon's diversity Index at the sampling sites (BM and FEF), seasons (summer and winter) and tides (both high and low) were calculated using Primer software (version 6). Further Simpson's diversity was used to test for correlation among the different tested parameters.

### Results

### Physico-chemical parameters

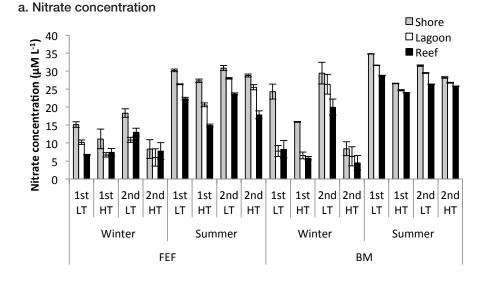
Table 1 summarises the variations in temperature, pH and salinity recorded at FEF and BM at high and low tides during both summer and winter. Temperature and pH were slightly higher during summer compared to winter but these were not significantly different. Variations in pH at the different zones at both sampling sites were not significant. Furthermore, salinity did not show significant variability between low and high tide, and during summer and winter seasons.

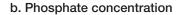
Nitrate and phosphate concentrations exhibited spatial variation in term of sites, with higher concentration recorded at BM, while no significant differences were observed among the different zones (Two-way ANOVA) (Fig. 2a, b). Silicate concentrations showed spatial variation both in terms of sites (higher concentrations at FEF) and zones (higher near the shore and lagoon of FEF) (Fig. 2c). Only nitrate and silicate concentrations exhibited seasonal variations with higher concentrations in summer. No clear tidal effect was recorded for nitrate and silicate at the study sites, but higher concentrations were obtained at several occasions at low tide. Phosphate at FEF was not influenced by tidal changes, but at BM, phosphate concentration was higher at high tides during winter, while the contrary was observed during summer (Fig. 2b).

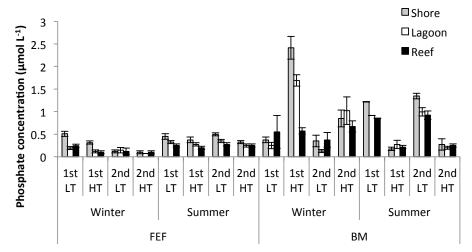
No significant seasonal variation in chlorophyll *a* concentration was recorded at both FEF and BM. Chlorophyll *a* concentration exhibited spatial variation, in terms of sites, with higher values recorded at BM. Significant spatial variation within the different zones at each site was also observed. Significantly higher concentrations were recorded near the shore and in the lagoon

Table 1. *In-situ* measurement of temperature (°C), pH and salinity (ppt). Data represent mean ± SD (n = 3). LT: low tide; HT: High tide; Temp:: Temperature; S: Shore; L: lagoon; and R: reef.

0	Tists	Obsting	Flic	-en-Flac (FE	EF)	Ве	lle Mare (BN	/)
Season	Ilde	Station ·	Temp (°C)	рН	Salinity (ppt)	Temp (°C)	рН	Salinity (ppt)
Winter	LT	S	$25.62 \pm 0.21$	8.23±0.02	$35.42 \pm 0.45$	25.18±1.34	7.88±0.33	35.33±0.24
		L	$25.08 \pm 0.34$	$8.42 \pm 0.24$	35.50±0.41	$24.05 \pm 0.44$	7.92±0.15	35.33±0.37
		R	$25.00 \pm 0.50$	$8.34 \pm 0.20$	$35.42 \pm 0.61$	$23.58 \pm 0.12$	7.94±0.08	$35.25 \pm 0.25$
·	HT	S	25.92±0.30	8.27±0.02	$35.42 \pm 0.34$	23.63±0.37	8.00±0.08	35.50±0.41
		L	$24.32 \pm 1.51$	$8.26 \pm 0.05$	$35.50 \pm 0.41$	$23.92 \pm 0.43$	7.95±0.12	35.75±0.69
		R	$24.22 \pm 1.27$	$8.29 \pm 0.01$	$35.08 \pm 0.45$	$24.22 \pm 0.17$	7.92±0.19	$35.83 \pm 0.62$
Summer	LT	S	$26.93 \pm 0.24$	$8.44 \pm 0.10$	34.33±1.11	27.73±0.94	8.54±0.10	$34.92 \pm 0.34$
		L	$26.95 \pm 0.45$	$8.45 \pm 0.10$	$35.00 \pm 0.58$	27.22±0.58	8.51±0.14	$35.42 \pm 0.45$
		R	26.87±0.27	$8.47 {\pm} 0.02$	$35.00 \pm 0.29$	27.00±0.84	8.51±0.06	$35.00 \pm 0.29$
	HT	S	27.23±0.35	8.38±0.14	34.50±0.76	27.57±0.76	$8.55 \pm 0.05$	35.25±0.38
		L	27.45±0.55	$8.44 \pm 0.13$	$35.00 \pm 0.58$	27.10±0.45	8.51±0.15	$35.25 \pm 0.38$
		R	$26.97 \pm 0.62$	8.51±0.06	35.33±0.47	26.87±0.36	8.50±0.04	$35.25 \pm 0.25$







c. Silicate concentration

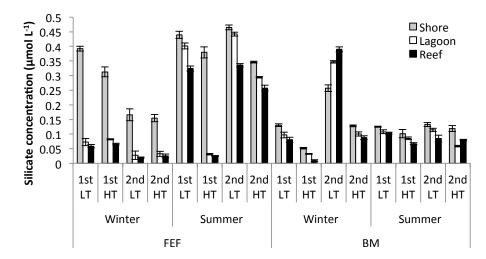
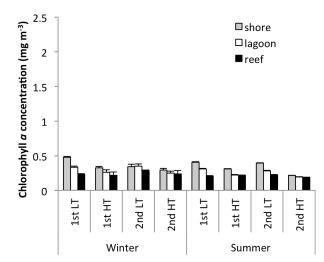


Figure 2. Nitrate (a), Phosphate (b) and silicate (c) concentrations at Flic-en-Flac (FEF) and Belle Mare (BM).

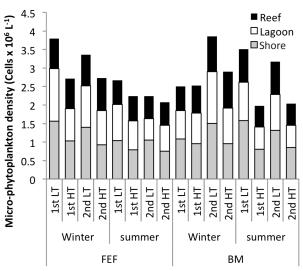
of FEF (Fig. 3A). At BM, chlorophyll *a* concentrations increased from the shore to the reef area (Fig. 3b).

The overall effect of tides on chlorophyll *a*, irrespective of sampling sites, was significantly different during the sampling period. However, analysis of the effect of tides at each study site, showed no significant effect on chlorophyll *a* at FEF (Two-way ANOVA), while higher concentrations were recorded during low tides at BM. As the water level increased during periods of high tide, the concentration of chlorophyll *a* was found to decrease, and this corresponded to episodes of increase in total micro-phytoplankton C-biomass.

#### a. Chlorophyll a concentration at FEF





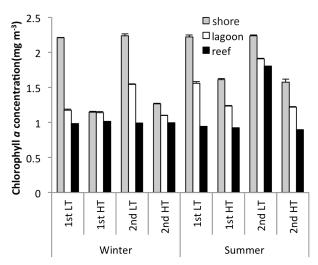


### Micro-phytoplankton density, C-biomass and diversity

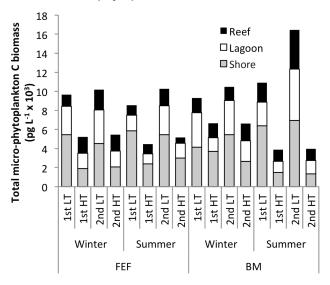
Tides and zones had significant effects on the overall total C-biomass of total micro-phytoplankton and bacillariophytes, and concentrations of chlorophyll *a*, nitrate, phosphate and silicate (Table 2).

There was no significant difference in C-biomass of micro-phytoplankton between the two sites. C-biomass of total micro-phytoplankton, bacillariophytes and dinophytes, nitrate, silicate and chlorophyll a exhibited significant spatial variations in terms of zones (shore, lagoon and reef) within each site. Tides had no effect on C-biomass of dinophytes and

#### b. Chlorophyll a concentration at BM



#### d. Total micro-phytoplankton C-biomass



**Figure 3.** Total micro-phytoplankton density and carbon biomass (pg L<sup>-1</sup>) at Flic-en-Flac (FEF) and Belle Mare (BM) at low tide (LT) and high tide (HT) during summer and winter. Data represent mean (n=9 at each zone for micro-phytoplankton C-biomass and density; n=3 at each zone for chlorophyll a) at both sites.

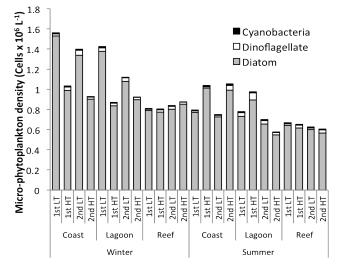
**Table 2.** Two-Way ANOVA comparison of the tidal cycles, in terms of C-biomass (pg L<sup>-1</sup>) of total micro-phytoplankton, micro-phytoplankton groups (bacillariophyceae, dinophyceae and cyanophyceae) and physico-chemical parameters at the different stations within and across the two sites (FEF and BM). Asterisks indicate significant differences at 5% level. (\* = P < 0.05; \*\* = P < 0.01; \*\*\* = P < 0.001; NS = not significant).

Parameters		DF	MS	F	р
	Site	1	0.04	3.73	NS
	Season	1	0.04	3.08	NS
Total micro-phytoplankton	Tide	2	0.53	44.3	***
C-biomass (pg L <sup>-1</sup> )	Zone	1	0.98	82.1	***
	Site*Tide	1	0.02	1.60	NS
	Site*Season*Tide	1	0.07	5.97	*
	Site	1	0.05	3.70	NS
C-biomass of	Season	1	0.06	4.55	*
Bacillariophyceae	Tide	2	0.65	51.6	***
(pg L-1)	Zone	1	1.04	82.5	***
(19 - )	Site*Tide	1	0.04	3.39	NS
	Site*Season*Tide	1	0.07	5.65	*
	Site	1	0.01	0.02	NS
	Season	1	1.18	5.05	*
C-biomass of Dinophyceae	Tide	2	0.06	0.24	NS
(pg L-1)	Zone	1	1.36	5.81	*
	Site*Tide	1	0.44	1.87	NS
	Site*Season*Tide	1	0.01	0.023	NS
	Site	1	0.55	1087	***
	Season	1	0.00	1.5	NS
Chlorophyll a	Tide	2	0.02	39.7	***
$(mg m^{-3})$	Zone	1	0.02	45.0	***
	Site*Tide	1	0.01	11.0	**
	Site*Season*Tide	1	0.00	0.32	NS
	Site	1	0.02	7.21	*
	Season	1	0.47	163	***
Nitrate	Tide	2	0.04	12.8	***
(Um L-1)	Zone	1	0.09	29.9	***
	Site*Tide	1	0.01	2.05	NS
	Site*Season*Tide	2	0.01	1.78	NS
	Site	1	0.12	62.8	***
	Season	1	0.00	1.23	NS
Phosphate	Tide	2	0.01	4.75	*
(Um L <sup>-1</sup> )	Zone	1	0.00	1.82	NS
(,	Site*Tide	1	0.00	0.72	NS
	Site*Season*Tide	1	0.09	49.6	***
	Site	1	0.20	8.54	**
			0.20	8.11	**
Ciliante	Season Tide	1 2	0.19 0.16	6.65	**
Silicate (Um L-1)	Zone	2	0.18	0.05 11.4	**
(OIII L )	Site*Tide	1	0.27	0.02	NS
	Site*Season*Tide		0.00		NS *
	Sile"Season" Hide	1	0.17	7.25	4-

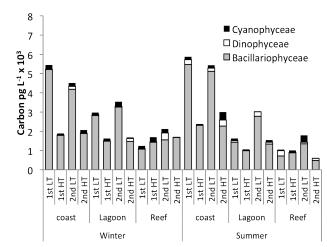
cyanophytes. Nutrient (nitrate, phosphate and silicate) levels were significantly different in terms of sites and season and among the three zones.

During winter, at both FEF and BM, there was no significant difference in total micro-phytoplankton density (TPD) near the shore and the lagoon, but lower TPD was recorded near the reef area. During summer, FEF had higher TPD near the shore, with no difference between lagoon and reef, while at BM, TPD was higher near the shore followed by the lagoon and the reef area. The C-biomass of total micro-phytoplankton exhibited short-term variations in response to tidal changes throughout the sampling periods, with higher biomass during low tides (Fig. 3). TPD C-biomass varied over the tidal cycle, and also showed spatial variations, with significantly higher biomass being recorded near the shore at both sites (Fig. 3).

#### a. Density of micro-phytoplankton groups at FEF



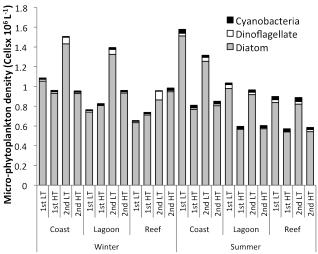
c. C-biomass of micro-phytoplankton groups at FEF

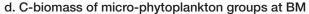


At both sites, bacillariophytes, in terms of densities and C-biomass (Fig. 4a-d), were the dominant micro-phytoplankton group as compared to dinophytes and cyanophytes. Although the correlation coefficients were generally very low, there was a positive correlation between bacillariophytes and nutrient concentrations (Table 3). Bacillariphytes C-biomass showed seasonal and spatial (in terms of zones) variation at both sites. Higher C-biomass was recorded near the shore, followed by lagoon and reef. Although no distinct tidal-related variations were observed during summer, higher micro-phytoplankton C-biomass was recorded mostly at low tides (Fig. 4c). However, diatom C-biomass at BM showed a clear trend and exhibited short episodes of rapid increase during low tides (Fig. 4d).

At BM, the distinct tidal-associated difference in diatom C-biomass is a result of changes in silicate

### b. Density of micro-phytoplankton groups at BM





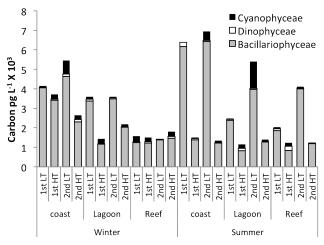


Figure 4. Density (cells  $L^{-1}$ ) and carbon biomass (pg  $L^{-1}$ ) of micro-phytoplankton groups at FEF (a and c) and BM (b and d). Data represent mean  $\pm$  SD (n=9 at each zone for micro-phytoplankton C-biomass) at both sites.

		FEF	BM
	Site	3.007	3.093
Saaaaa	Winter	2.841	3.052
Season	Summer	3.013	3.073
<b>T: 1</b> -	Low tide	2.979	3.086
Tide	High tide	2.959	3.060

Table 3. Shannon's Diversity Indices (H') for micro-phytoplankton genera at Flic-en-Flac (FEF) and Belle Mare (BM).

concentrations since it was significantly correlated with diatom C-biomass (Table 3). It must be noted that marked tidal-induced differences in micro-phytoplankton was more apparent near the shore and in the lagoon, compared to the reef area (Fig. 4c, d).

Dinophytes and cyanophytes were the least observed during the study. Dinophytes showed seasonal variation with higher C-biomass in the summer season and spatial variation in terms of zones. No spatial variation between the two sites was observed. At FEF, dinophytes C-biomass was generally higher near the shore and the lagoon, while lower C-biomass was recorded near the reef. There was no spatial variation among the three zones at BM.

Cyanophytes exhibited no seasonal and spatial (both in terms of sites and zones) variation at both sites. However, C-biomass of cyanobacteria was higher than that of dinophytes. Moreover, higher C-biomass of cyanobacteria was recorded on several occasions and this corresponded to periods of low tides and was mostly near the shore and lagoon (Figs. 4C, D).

A total of 36 micro-phytoplankton genera were identified at FEF while 34 genera were sampled at BM. Among the 36 micro-phytoplankton genera sampled at FEF, 29 bacillariophytes genera, 5 dinophytes and 2 cyanophytes genera were identified (Appendix A). At BM, 31 bacillariophytes genera, 3 dinophytes and 2 cyanophytes genera were recorded (Appendix B). Shannon's diversity at BM was slightly higher than at FEF, during summer and at low tide (Table 3).

### Correlation of biological parameters (micro-phytoplankton and chlorophyll a) with nutrient variability

Positive Pearson's correlation was obtained between parameters tested (C-biomass of total micro-phytoplankton, bacillariophytes, dinophytes and concentration of chlorophyll *a*) and nutrient concentrations, but these were not always significant. At FEF, total

Table 4. Pearson's correlation coefficient, *r* value, tested at Flic-en-Flac (FEF) and Belle Mare (BM). TMP= Total Micro-Phytoplankton. Asterisks indicate significant correlation at 5% level. (\* = P< 0.05; \*\* = P< 0.01; \*\*\*= P< 0.001).

Site	Parameters	Nitrate	Phosphate	Silicate	Temperature	рН	Salinity
	TMP C-biomass	0.359	0.542**	0.456*	0.031	-0.264	-0.084
	Bacillariophyceae C-biomass	0.328	0.544**	0.441*	0.022	-0.254	-0.096
FEF	Dinophyceae C-biomass	0.484*	0.155	0.317	0.318	-0.213	0.192
	Cyanophyceae C-biomass	0.107	0.062	0.085	-0.198	-0.051	-0.079
	Chlorophyll a	0.127	0.509*	0.361	-0.070	-0.111	-0.135
	TMP C-biomass	0.415*	0.361	0.221	0.223	-0.285	0.044
	Bacillariophyceae C-biomass	0.425*	0.355	0.240	0.221	-0.309	0.042
BM	Dinophyceae C-biomass	0.194	0.041	0.033	0.141	-0.208	0.165
	Cyanophyceae C-biomass	0.078	0.195	0.009	0.078	-0.062	0.001
	Chlorophyll a	0.605**	0.086	0.240	0.458*	-0.349	0.200

micro-phytoplankton and bacillariophytes C-biomass were significantly (positively) correlated with phosphate and silicate concentrations, while at BM, total micro-phytoplankton and bacillariophytes were significantly (positively) correlated with nitrate (Table 3). Similarly, significant positive correlation was obtained between chlorophyll *a* concentration and phosphate at FEF while at BM chlorophyll *a* was positively correlated with nitrate only. Although positive correlations were found between physical parameters and micro-phytoplankton C-biomass, these were not significant.

### Discussion

Short-term variations of micro-phytoplankton biomass can be as significant as long-term ones, governed either by high frequency physical forcing (such as vertical displacement of chlorophyll gradients caused by internal waves, re-suspension of benthic microalgae by wind-driven waves, and re-distribution of phytoplankton biomass by wind-driven surface currents) or biological processes (such as diel vertical migrations of dinoflagellates, diel periodicity of grazing by zooplankton, high frequency periodicity of chlorophyll a, among others) (Cloern et al., 1989). However, although studies on short- and long-term variation of micro-phytoplankton diversity, biomass and distribution pattern, as well as factors and processes influencing them, are of great importance, they have received little consideration, with almost no data available on how these physico-chemical and biological factors interact at temporal scales in the Mauritian lagoons. In this study, we investigated the variations of micro-phytoplankton C-biomass, including different micro-phytoplankton groups (Bacillariophyceae, Dinophyceae and Cyanophyceae), chlorophyll a and nutrient (nitrate, phosphate and silicate) concentrations at short (in response to tide) and long (seasonal) time frames. Therefore, this study attempts to generate novel information by investigating the effect of tide in governing short-term variations in micro-phytoplankton density, distribution, diversity and carbon biomass (C-biomass) in two coral reef lagoons in Mauritius, in an effort to better understand the mechanisms and strategies adopted by micro-phytoplankton, including behavioural and physiological responses, and migration in the water column, during their response to micro-tidal changes.

### Micro-phytoplankton composition and nutrients

Tides had no clear effect on nutrient status at both BM and FEF, but higher concentrations of nitrate and phosphate were recorded on several occasions at BM during periods of low tides; probably as a result of internal waves leading to upwelling of nutrients. This may suggest that mineralisation is taking place in the sediment, releasing nitrite and phosphate as first by-products to the overlying water, which has been found to affect the water column mainly at low tides (Morales-Zamorano *et al.*, 1991).

Nutrients, mainly nitrate and phosphate, showed spatial variation with higher concentration being recorded at BM. The effect of the South East Trade Winds are more significant at BM due to its geographical location and according to Lowe et al. (2005) this particular wind stress forcing can stay stable for extended periods in exposed reef regions. Given that wind and tide-induced currents play an important role in enhancing vertical circulation (Arfi et al., 1993), their coupling effect might have contributed to the enhanced sediment re-suspension and release of trapped nutrients at this site, leading to nutrient loading in the lagoon of BM. The intrusion of sub-marine ground water inputs at FEF may also contribute to inputs of nutrients in the coastal water as reported by Ramessur et al. (2011), which could also explain the low salinity recorded at both sites during summer, as well as explain the higher silicate concentration at FEF. In addition, BM also appears to experience runoff events due to the presence of nearby agricultural fields (Bhagooli and Taleb-Hossenkhan, 2012), which likely added to the nutrient regime in its coastal water.

Further comparison within the two sites showed that variation in nitrate and phosphate concentrations were not significant among the different zones at BM and FEF, however, variation could be seen at the seasonal level, with higher nitrate and phosphate concentrations during summer. Although this is a snapshot study and does not provide sufficient data to extrapolate on variations in nutrient concentrations at the seasonal and spatial levels, the long-term seasonal and spatial variations in the study of Sadally *et al.* (2014) showed that nutrient concentrations, with higher concentration being recorded at BM and near the shore and lagoon compared to the reef area.

A lower N:P ratio as compared with the normal Redfield ratio was also recorded during this study, implying that nitrate was limiting at both study sites. This result is usual for coral reef waters and is in agreement with the study of Jacquet *et al.* (2006) in the New Caledonian's SW lagoon. Moreover, the lower Si:N ratio observed during this study showed that silicate concentration was below the normal range, suggesting its rapid uptake by the dominant diatoms (bacillariophytes) at both sites.

Micro-phytoplankton composition changes with nutrient fluxes since individual taxa have different requirements (Davies and Ugwumba, 2013). In the present study the possible correlation between micro-phytoplankton groups and nutrient concentration (Spearman's Correlation) was also tested. It was found that the community composition of micro-phytoplankton at both sites respond differently to varying levels of nutrients since correlation between the latter and C-biomass of micro-phytoplankton showed the differential response of micro-phytoplankton groups (Bacillariophyceae, Dinophyceae and Cyanophyceae) to nutrient inputs at each study site, thus conforming with the result of Jacquet *et al.* (2006).

### Micro-phytoplankton density, C-biomass and distribution in response to micro-tidal changes

Tropical ecosystems can experience rapid changes in physical and meteorological variables, which can in turn induce short-term variations in biological processes (Torréton et al., 2010). The present study indeed showed that tidal forcing contributes to short-term variability in micro-phytoplankton density, C-biomass and chlorophyll a concentration in the lagoons of Mauritius. The semi-diurnal tidal system in Mauritius accounts for the short-term fluctuation of micro-phytoplankton over a 6-hour periodicity through alternating sinking and re-suspension brought about by tidal mixing, tidal current and the effect of wind (Blauw et al., 2012). These semi-diurnal tidal-generated internal waves could have contributed to enhancing phytoplankton productivity and dynamics at the study sites by moving nutrients to shallower depths, whereby solar irradiance is higher at the surface, corresponding to the results of Neveux et al. (2010).

The higher density and C-biomass of micro-phytoplankton during low tides corroborates the results of Melo and Huszar (2000) and could have been a result of wind-induced vertical mixing of the water column leading to sediment re-suspension, or advection (Torréton *et al.*, 2010). The higher C-biomass and density of micro-phytoplankton with the receding tide could be a result of increased photosynthetic rate and rapid phytoplankton growth occurring during periods of low tidal energy as reported by Davies and Ugwumba (2013) and Winter *et al.* (1975). The lower C-biomass of micro-phytoplankton during high tide could be due to the effect of water currents derived from semi-diurnal tide and wind-induced advection, coupled with the South East Trade Winds inducing rapid renewal of lagoon water by oceanic water. Thus the incoming tide may entrain oceanic waters, causing a diluting effect in the lagoon.

The higher micro-phytoplankton biomass and density at low tide may further be explained by the stability of the water column, inhibiting vertical mixing such that the rate of micro-phytoplankton biomass production in the euphotic zone is faster than the rate at which it is being transported to the lower aphotic zone, or to benthic grazers (Cloern, 1991). Indeed, a study by Lucas and Cloern (2002) showed that net phytoplankton growth decreases with increasing tidal range in a shallow, clear water column with strong benthic grazing, which might have contributed to the observed result at both sites.

In-phase dynamics of chlorophyll *a* can partly be explained in terms of the alternating sinking and vertical mixing of phytoplankton driven by the tidal cycle (Blauw *et al.*, 2012). Despite the fact that there was no significant difference in terms of total micro-phytoplankton biomass between the two sites, a significantly higher chlorophyll *a* concentration was recorded at BM compared to FEF, which might be due to the presence of other photosynthetic microorganisms such as nano- and pico-plankton, that were not taken into account in this study. However, it is also probable that the more nutrient-rich water at BM, coupled with its more significant exposure to the effect of the South East Trade Winds, contributed to a higher chlorophyll *a* concentration (Neveux *et al.*, 2010).

### Micro-phytoplankton diversity and tidal change

Tide had varied effects on the nutrient status and phytoplankton community (in terms of genera composition, diversity, abundance, and distribution). Bacillariophytes were the dominant micro-phytoplankton group and contributed more towards total micro-phytoplankton C-biomass during the study period, which is in accordance with the study of Chakraborty *et al.* (2015). Furthermore, it is common that re-suspended benthic diatoms contribute temporarily to enhancing phytoplankton populations (Lucas, 2003). Indeed, the higher C-biomass contribution and dominance over the other micro-phytoplankton groups at both low and high tide during the study, might be due to the re-suspension of several benthic and attached (epilithic, epiphytic) bacillariophytes such as *Navicula, Licmophora, Biddulphia*, among others (Appendix A and B). Moreover, their capacity for rapid cell division (Davies and Ugwumba, 2013) with higher growth rate (Cermeño *et al.*, 2005; Wilkerson *et al.*, 2006), their ability to thrive in conditions of high mixing (Pikaitytė and Razinkovas, 2007), as well as their resilience to high turbidity at high tide (Davies and Ugwumba, 2013), might have contributed to the observed result.

The various micro-phytoplankton groups also appeared to be differentially influenced by tidal effects, such that only bacillariophytes showed significant variations in response to tides at both sites, with higher biomass during periods of low tides. Temporal variation in the micro-phytoplankton community may result from temporal variation in turbulent mixing (Blauw et al., 2012). Many species migrate vertically in sediments and these migrational periodicities have been found to be strongly correlated with tidal and diurnal cycles (Admiraal et al., 1982). Moreover, several epilithic diatoms migrate in an upward direction during low tide and downwards with the incoming tide (Pinkney and Zingmark, 1991) and certain of these epilithic diatoms were encountered in the current study. This upward and downward migration in response to tide, as well as the re-suspension of benthic micro-phytoplankton, could explain the higher biomass of bacillariophytes at low tides. Therefore, the fact that they contributed to the higher C-biomass at the sampling sites implies that they are the main contributor to primary productivity and thus play an important role in increasing the C-biomass of micro-phytoplankton in these tropical lagoons as reported by Jacquet et al. (2006).

Little contribution of dinophytes and cyanophytes to the total micro-phytoplankton C-biomass in both lagoons in Mauritius was recorded during this study, which could be attributed to their behavioural and physiological response. The fact that dinophytes have a lower growth rate compared to bacillariophytes (Camacho et al., 2007; Davies and Ugwumba, 2013) and can regulate their position in the water column in response to environmental parameters (Hackett et al., 2004), could have contributed to their lower densities and C-biomass during the study period. Similarly the low irradiance preference of cyanophytes (Jones and Gowen, 1990) and their comparatively lower growth rate as compared to many other algal species (WHO, 1999), also accounted for their low biomass.

In fact, planktonic unicellular cyanobacteria, such as Synechococcus and Prochlorococcus, have also been found to dominate oligotrophic waters surrounding coral reef ecosystems and lagoons (Charpy et al., 2012) with abundances ranging from  $10 \times 10^3$  to  $500 \times 10^3$  cells mL<sup>-1</sup> and  $10 \times 10^3$  to  $400 \times 10^3$  cells mL<sup>-1</sup>, respectively. The role of cyanobacteria as an important source of dissolved organic carbon (DOC) in reef ecosystems was also not investigated during this study. Indeed, any change in their abundance may alter the quantity and chemical composition of organic materials being provided to the reef environment, as well as long-term impacts on reef communities (Brocke et al., 2015). Moreover, given that several species of cyanobacteria are less than 5µm, including both Synechococcus (size 0.8 µm) and Prochlorococcus (size 0.6 µm), this important contributor to primary production (Ribes et al., 2003; Patten et al., 2011) and to DOC were not taken into account since a size range corresponding to micro-phytoplankton only was focused on, and thus requires future attention. Therefore, C-biomass production in Mauritian coral reef lagoons seems primarily supported by bacillariophytes primary production.

Shannon's Diversity Indices (H') for micro-phytoplankton genera at FEF and BM were not significantly different in this study. The presence of almost the same micro-phytoplankton genera at both high and low tides was recorded, indicating that these genera were true species (permanent residents) at these sites. According to Blauw *et al.* (2012), a periodicity of 6 hours results in rapid environmental fluctuations that will be faster than the generation time of most phytoplankton species, leading mainly to a vertical re-distribution of existing populations. Indeed, the present study showed that the semi-diurnal system comprising of 6 hour periodicities in Mauritius, is not sufficient to cause a shift in micro-phytoplankton diversity but rather caused a re-distribution of the same species.

### Spatial (sites and zones) and seasonal variation of micro-phytoplankton C-biomass

Although in this study seasonal trends were weak using August and November 2014 data, probably as a result of limited sampling, the long-term study of Sadally *et al.* (2014) clearly showed how nutrients, chlorophyll *a*, as well as the different micro-phytoplankton groups and genera, exhibited temporal and spatial variations over a three-year period. In the current study, only bacillariophytes exhibited spatial and seasonal variations at both sites, which may be attributed to their sensitivity to a wide range of limnological and environmental conditions (Verma *et al.*, 2011), and the rapid response of their community structure to variations in physical, chemical, and biological conditions in the immediate environment (Davies and Ugwumba, 2013). However, their higher C-biomass in summer is due to the combination of higher solar radiation and increased frequency of heavy rainfall, which causes run-off events and nutrient loading in the coastal waters.

The high C-biomass of bacillariophyes in summer was due to the high concentration of silicate during this season because bacillariophytes showed rapid development with increasing silicate concentrations (Lasternas *et al.*, 2008). Bacillariophytes were positively correlated with silicate and their higher biomass in summer corresponded to higher silicate concentrations. Higher C-biomass of dinophytes was also recorded in summer and could be due to the higher nutrient levels and because their preference to warmer waters (Lasternas *et al.*, 2008).

No site-specific variation in total micro-phytoplankton C-biomass was recorded between the two sites but significant spatial differences among the different zones were observed, with higher biomass near the shore, compared to the lagoon and the reef areas. This spatial variation in terms of zones is in accordance with previous studies (Sadally *et al.*, 2011; Sadally *et al.*, 2014) and might be attributed to several factors, including nutrient availability. Nutrient concentration near the shore was higher at both sites and this may account for the higher micro-phytoplankton C-biomass near the shore by increasing their growth rate, as reported by Fu *et al.* (2009).

### Conclusion

This study showed that micro-phytoplankton biomass exhibited short-term variability in response to microtidal effects, with higher biomass recorded during periods of low tides. This tidal oscillation of micro-phytoplankton biomass with higher and lower C-biomass at low and high tides, respectively, may be a result of micro-tidally-induced water movement and water stability during low tides and increased micro-phytoplankton growth rate and high grazing pressure at high tide. No seasonal variation was apparent in total micro-phytoplankton C-biomass, chlorophyll *a* and cyanophytes. However, the bacillariophytes and dinophytes showed seasonal variation with higher C-biomass in summer and this was mainly attributed to seasonal changes in nutrients. Spatial variation of C-biomass of micro-phytoplankton was significant in terms of zones within the sites but was not significant across the sites. Higher biomass of micro-phytoplankton was recorded near the shore, possibly as a result of higher nutrient concentrations there. Therefore, micro-tide has varied effects on the nutrient status and phytoplankton community (in terms of micro-phytoplankton groups) and this study also demonstrated the importance of episodic micro-tidal forcing in determining the primary productivity in coral reef lagoon systems. This study provides baseline information on the short-term variability of micro-phytoplankton biomass in response to micro-tidal changes. Continuous monitoring is warranted in predicting long-term response of coastal micro-phytoplankton C-biomass, and thus primary productivity, to changing environmental conditions in coral reef ecosystems.

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st	udy 						reef		80	7	4	0	0	4	0	0	0	1	0	0	7	80	0	0	0	0	4	0	0	4	4	~
		IN HT	æ	0.0	2.7	8.1	2.7	2.7	10.8	2.7	2.7	0.0	0.0	2.7	0.0	0.0	0.0	8.1	0.0	0.0	2.7	10.8	0.0	0.0	0.0	0.0	2.7	0.0	0.0	2.7	5.4	0.0
		2nd		0.0	28.9	0.0	4.4	4.4	11.1	2.2	2.2	2.2	0.0	2.2	0.0	0.0	0.0	2.2	2.2	2.2	8.9	11.1	0.0	0.0	0.0	0.0	6.7	0.0	0.0	2.2	2.2	0.0
			S	0.0	0.0	5.4	8.1	0.0	8.1	2.7	2.7	5.4	0.0	2.7	0.0	0.0	2.7	5.4	5.4	0.0	0.0	10.8	0.0	0.0	16.2	0.0	8.1	0.0	2.7	2.7	2.7	0.0
	11)	2nd LT	Я	0.0	2.5	0.0	2.5	0.0	25.0	2.5	2.5	0.0	0.0	2.5	0.0	0.0	0.0	5.0	10.0	0.0	10.0	7.5	0.0	0.0	2.5	0.0	10.0	0.0	2.5	2.5	5.0	0.0
	er 20	2n	_	0.0	0.0	0.0	6.8	3.4	10.2	3.4	3.4	0.0	0.0	3.4	0.0	0.0	0.0	6.8	0.0	0.0	3.4	23.7	0.0	0.0	0.0	0.0	10.2	0.0	6.8	6.8	3.4	0.0
ľ	emp		S	0.0	0.0	11.3	7.3	1.7	5.1	1.7	0.0	1.7	0.0	3.4	0.0	0.0	1.7	3.4	5.1	0.0	5.1	20.9	0.0	5.6	5.1	0.0	1.7	0.0	0.0	1.7	1.7	0.0
	Summer (November 2011)	노	æ	0.0	1.5	1.5	9.1	0.0	13.6	3.0	3.0	3.0	0.0	1.5	0.0	0.0	0.0	1.5	7.6	4.5	6.1	21.2	3.0	0.0	3.0	3.0	4.5	0.0	3.0	1.5	1.5	0.0
	mer	1st		0.0	1.5	0.0	10.6	0.0	16.7	1.5	3.0	1.5	0.0	3.0	0.0	1.5	1.5	0.0	6.1	3.0	6.1	22.7	1.5	0.0	4.5	1.5	3.0	0.0	1.5	3.0	1.5	0.0
	Sun		S	0.0	11.3	1.4	2.8	1.4	7.0	5.6	5.6	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	1.4	8.5	18.3	0.0	15.5	2.8	0.0	4.2	0.0	2.8	1.4	0.0	0.0
		5	Ж	0.0	6.1	0.0	12.2	0.0	8.2	2.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	14.3	0.0	0.0	0.0	0.0	2.0	0.0	2.0	4.1	2.0	0.0
		1st		0.0	15.7	0.0	2.9	2.9	7.1	1.4	2.9	0.0	0.0	1.4	0.0	0.0	0.0	1.4	1.4	1.4	12.9	8.6	0.0	0.0	0.0	0.0	2.9	0.0	1.4	2.9	1.4	0.0
			S	0.0	0.0	6.5	3.3	1.6	9.8	0.0	3.3	3.3	0.0	1.6	0.0	8.1	0.0	4.9	1.6	1.6	3.3	29.3	1.6	0.0	4.9	0.0	4.9	1.6	0.0	1.6	0.0	0.0
		H	ж	0.0	0.0	2.9	1.9	1.0	17.1	3.8	4.8	0.0	0.0	1.0	0.0	0.0	1.0	0.0	1.9	0.0	12.4	42.9 2	0.0	0.0	0.0	0.0	3.8	0.0	1.0	2.9	0.0	0.0
		2nd	_	0.0	0.0	0.0	4.3	5.7	7.1	1.4	2.9	1.4	0.0	7.1	0.0	1.4	1.4	1.4	5.7	0.0	15.7	12.9 4	1.4	0.0	0.0	1.4	4.3	0.0	1.4	4.3	10.0	1.4
			S	0.0	0.0	0.0	3.5	3.5	8.8	0.9	0.0	1.8	0.0	14.2	0.0	0.9	2.7	1.8	8.0	3.5	4.4	18.6 1	0.9	8.8	0.0	0.9	7.1	0.0	0.9	2.7	2.7 1	0.0
		님	В	0.0	0.0	0.0	0.9	3.5	6.1	0.9	1.8	1.8	0.0	13.2 1	0.0	2.6	0.9	0.9	7.9	0.0	4.4	34.2 1	0.0	2.6	0.0	0.0	4.4	0.0	0.9	8.8	1.8	0.0
	11)	2nd	_	0.0	6.1 (	4.0 (	8.1	3.0	10.1	1.0	0.0	3.0	0.0	6.1 1	0.0	2.0	2.0	4.0 (	7.1	6.1 (	2.0	15.2 3	2.0 (	0.0	0.0	2.0 (	5.1	0.0	2.0	4.0	1.0	1.0
	Winter (August 2011)		S	1.9	2.5	1.3 4	8.8	0.6	30.6 1	1.9	1.9 (	8.1 8	0.0	2.5	0.0	1.3	1.9 2	0.6 4	0.6	0.0	0.0	20.6 1/	0.0	0.0	0.0	0.6	2.5	0.0	1.3 2	0.6 4	0.6	0.0
	Augu	E	В	0.0	8.1	0.0	8.1	1.8 (	2.5 3(	5.4	0.7	0.0	0.0	5 1.7	0.0	0.0	8.1	0.0	.8.1	0.0	0.7 (	0.	0.0	0.0	0.0	.8	5.4	0.0	0.0	3.9 (	0.0	0.0
	nter (	1st H	_	0.0	0.0	0.0 0	2.6	0.0	6.6 12	1.3	0.0 10	2.6 C	0.0 0	7.9	0.0	0.0	3.9	3.9 C	22.4	1.3 0	13.2 10	13.2 25	1.3 0	0.0 C	0.0	1.3	6.6	0.0	1.3 C	6.6 8	0.0	0.0
	Ň		S	0.0 0	1.9 0	0.0 0	5.7 2	1.9 0	13.2 6	3.8 1	3.8 0	3.8	0.0 0	7.5 7	0.0 0	1.9 0	1.9 3	1.9 3	3.8 22	0.0 1	0.0 13		0.0 1	0.0 0	0.0 0	1.9 1	5.7 6	0.0 0	0.0 1	7.5 6	0.0 0	0.0
		н	В	0.0 0	0.0 1	0.0 0	1.5 5	0.0 1		3.0 3	3.0 3	1.5 3	0.0 0		0.0 0	4.5 1	3.0 1	0.0 1	4.5 3	0.0 0	6.1 0	.8 28.3	0.0 0	0.0 0	0.0 0	1.5 1	6.1 5	0.0 0	1.5 0	9.1 7	0.0 0	0.0
		1st LT		4.4 0					2 12.1				1.1 0.	4.4 10.6			4.4 3.			6.7 0.	1.1 6	3 28.8					7.8 6			1.1 9	3.3 0.	1.1 0.
			S		3 2.2	4 3.3	7 5.6	4 3.3	8 12.2	0 2.2	0.0 0.0	4 3.3			0 0.0	7 2.2		0 3.3	7 3.3			5 13.3	3 2.2	0.0 0.0	0 0.0	3 2.2		4 0.0	7 0.0			
				0.0	1.3	3.4	4.7	5.4	14.8	0.0	4.0	3.4	0.0	6.0	0.0	2.7	0.0	0.0	6.7	2.0	0.0	23.5	1.3	0.0	0.0	1.3	a 6.7	3.4	2.7	1.3	0.0	1.3
			Genera	Achnanthes	Asterionellopsis	Biddulphia	Cavinula	Climacodium	Cocconeis	Coscinodiscus	Cyclotella	Cylindrotheca	Diatoma	Diploneis	e Ditylum	ce Fragilaria	op Haslea	Licmophora	Ba Lyrella	Manguinea	U Melosira	Navicula	Nitzschia	Odontella	Pinnularia	Pleurosigma	Pseudo-nitzschia	Stauroneis	Striatella	Thalassionema	Thalassiosira	Thalassiothrix
															91		140	~°[[]	A	000												

Appendix A. Micro-phytoplankton diversity at FEF. Data represents percentage of the different micro-phytoplankton genera sampled during the study. S: Shore, L: lagoon, R: reef.

					5	Winter	r (Aug	r (August 2011)	2011)								Sum	Summer (November 2011)	Nove	edme	r 201	1)			
			1s	1st LT		1st	HT		2nd	2nd LT		2nd HT	Ħ		1st LT	5		1st HT	H		2nd LT	5		2nd HT	Ħ
	Genera	S	_	Ж	s	_	æ	s	_	Ж	s	_	æ	s	_	ж	s	_	æ	s	_	щ	s	┙	٣
ərə	Ceratium	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
элүс	Gymnodinium	1.3	2.2	1.5	0.0	1.3	1.8	1.9	2.0	1.8	2.7	4.3	0.0	1.6	1.4	2.0	1.4	3.0	3.0	3.4	3.4	2.5	2.7	2.2	2.7
Ioui	Prorocentrum	2.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	1.0	1.6	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
U 221	Protoperidinium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	36.7	0.0	0.0	0.0	11.3	3.4	2.5	2.7	0.0	2.7
CJ	Symbiodinium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.3
s Суапорћусеае	Oscillatoria	0.7	2.2	1.5	03 03	2.6	1.8	1.3	1.0	0.9	0.9	1.4	1.0	1.0 8	30.0	2.0	1.4	1.5	0.0	1:1	1.7	2.5	2.7	2.2	2.7
Class	Phormidium	0.0	0.0 0.0 0.0 0.0	0.0		0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix B. Micro-phytoplankton diversity at BM. Data represents percentage of the different micro-phytoplankton genera sampled during
the study. S: Shore, L: lagoon, R: reef.

					Winter		(August 2011)	2011								Sun	nmer	NoV	Summer (November 2011)	er 201	Ē			
			1st LT		-	1st HT		21	2nd LT		2nc	2nd HT		1st	1st LT		1st	보		2nc	2nd LT		2nd HT	Ŧ
Genera	S		L R	S		R	S	-	В	S	-	В	S	_	Я	S	-	Ж	S	_	В	S	-	щ
Achnanthes	0.0	0.0	0 0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asterionellopsis	3.6	0.0	0 3.2	0.0	2.0	0.0	7.8	1.2	3.8	0.0	3.9	5.5	4.1	6.3	3.0	6.2	6.8	2.4	1.5	2.8	2.8	2.4	2.1	2.6
Biddulphia	0.0	0.0	0 0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cavinula	4.6	4.9	9 0.0	5.2	2.0	7.5	3.4	4.7	3.8	11.5	11.7	16.5	5.3	4.2	3.0	3.1	6.8	4.7	21.9	8.3	12.3	7.3	16.7	7.9
Climacodium	1.5	2.5	5 6.5	0.0	0.0	0.0	4.5	2.4	0.0	5.8	0.0	2.8	1.8	2.1	0.0	3.1	3.4	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Cocconeis	4.6	7.4	4 16.1	l 12.9	26.5	5 17.5	24.0	12.9	15.0	5.8	3.9	8.3	5.3	4.2	11.9	6.2	6.8	25.9	4.4	8.3	2.8	7.3	6.3	7.9
Coscinodiscus	3.0	2.5	5 3.2	5.2	2.0	5.0	1.7	2.4	0.0	0.0	7.8	2.8	3.6	2.1	3.0	3.1	3.4	2.4	8.8	8.3	2.8	0.0	0.0	0.0
Cyclotella	0.0	0.0	0 0.0	) 5.2	4.1	1 2.5	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	3.0	0.0	0.0	2.4	1.5	0.0	5.7	0.0	0.0	0.0
Cylindrotheca	4.6	4.9	9 3.2	0.0	0.0	0.0	5.0	2.4	0.0	0.0	0.0	0.0	5.3	6.3	3.0	3.1	3.4	2.4	7.3	11.0	5.7	9.8	10.4	7.9
Diatoma	0.0	0.0	0 0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diploneis	3.0	2.5	5 $3.2$	5.2	4.1	1 5.0	5.0	2.4	0.0	2.9	3.9	0.0	3.6	2.1	3.0	3.1	6.8	4.7	1.5	2.8	0.0	2.4	2.1	5.3
Ditylum	0.0	2.5	5 0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.0	0.0
Fragilaria	1.5	0.0	0 3.2	2.6	2.0	0.0	6.7	0.0	0.0	2.9	0.0	0.0	1.8	10.5	0.0	15.4	0.0	0.0	1.5	2.8	0.0	0.0	0.0	0.0
Haslea	1.5	2.5	5 0.0	) 2.6	0.0	0.0	0.0	1.2	3.8	0.0	0.0	4.6	1.8	4.2	0.0	3.1	3.4	0.0	1.5	2.8	0.0	2.4	2.1	2.6
Licmophora	11.7	7.4	4 9.7	7 2.6	2.0	10.0	1.7	3.5	16.3	5.8	7.8	2.8	13.6	6.3	11.9	6.2	10.2	11.8	4.4	8.3	5.7	9.8	8.3	10.5
Lyrella	0.0	2.5	5 0.0	) 2.6	0.0	2.5	0.0	0.0	0.0	2.9	3.9	0.0	0.0	0.0	9.0	0.0	0.0	4.7	2.9	0.0	5.7	2.4	2.1	2.6
Manguinea	0.0	0.0	0 6.5	5 2.6	0.0	) 2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	4.7	0.0	2.8	0.0	2.4	2.1	2.6
Melosira	0.0	0.0	0 0.0	7.8	14.3	3 0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	5.7	0.0	0.0	0.0
Navicula	11.7	19.8	8 19.4	ļ 10.3	16.3	3 10.0	16.8	23.5	15.0	19.2	11.7	8.3	13.6	8.4	26.9	9.2	13.6	18.8	7.3	13.8	16.0	9.8	10.4	7.9
Nitzschia	3.0	4.9	9 9.7	7 2.6	0.0	2.5	3.4	2.4	3.8	5.8	3.9	5.5	3.6	4.2	0.0	0.0	3.4	0.0	8.8	2.8	0.0	0.0	0.0	0.0
Odontella	13.7	9.6	9 0.0	) 11.2	0.0	12.5	0.0	17.6	0.0	0.0	19.5	9.2	16.0	0.0	0.0	0.0	0.0	0.0	4.4	0.0	4.7	24.4	22.9	21.1
Pinnularia	6.1	2.5	5 3.2	0.0	2.0	0.0	0.0	3.5	3.8	2.9	3.9	2.8	7.1	0.0	0.0	0.0	6.8	0.0	0.0	0.0	2.8	0.0	0.0	0.0
Pleurosigma	0.0	4.9	9 0.0	0.0	0.0	2.5	0.0	3.5	0.0	0.0	0.0	2.8	0.0	4.2	0.0	6.2	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Podocystis	0.0	2.5	5 0.0	) 2.6	0.0	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudo-nitzschia	ia 1.5	4.9	9 0.0	) 5.2	4.1	1.5	8.4	3.5	3.8	4.8	3.9	8.3	1.8	6.3	3.0	6.2	3.4	0.0	7.3	2.8	2.8	4.9	4.2	7.9

								•	ſ																
			1s	1st LT		1st H	t HT		2n(	2nd LT		2no	2nd HT		1s	1st LT		1st	HT		2nc	2nd LT		2nc	2nd HT
	Genera	S	-	۳	S	-	۳	S	-	۳	S	-	۳	S	┙	۳	S	-	۳	S	┙	۳	S	-	œ
ອຮອວ	Stauroneis	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0	0.0	1.8	2.1	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
л́цdo	Striatella	0.0	2.5	0.0	5.2	4.1	0.0	3.4	3.5	3.8	5.8	0.0	2.8	0.0	4.2	0.0	3.1	0.0	0.0	4.4	0.0	2.8	0.0	0.0	0.0
cillari	Thalassionema	1.5	4.9	3.2	5.2	6.1	2.5	3.4	2.4	3.8	2.9	0.0	5.5	1.8	14.7	6.0	12.3	3.4	4.7	1.5	2.8	5.7	2.4	2.1	2.6
ea Ba	Thalassiosira	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	2.9	3.9	0.0	1.8	0.0	3.0	0.0	3.4	2.4	0.0	5.5	2.8	2.4	2.1	2.6
CJa	Thalassiothrix	0.0	0.0	3.2	0.0	2.0	0.0	0.0	0.0	3.8	0.0	3.9	2.8	0.0	2.1	0.0	3.1	0.0	0.0	1.5	0.0	0.0	2.4	2.1	2.6
<b>ອ</b> ຮອວ.	Ceratium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
λųdot	Gymnodinium	1.5	2.5	0.0	2.6	2.0	2.5	1.7	1.2	3.8	2.9	0.0	2.8	1.8	0.0	3.0	0.0	3.4	2.4	1.5	0.0	2.8	2.4	2.1	2.6
riU se	Prorocentrum	1.5	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	4.2	0.0	6.2	3.4	0.0	1.5	2.8	0.0	0.0	0.0	0.0
Cla	Protoperidinium	1.5	0.0	0.0	0.0	2.0	2.5	1.7	0.0	3.8	2.9	3.9	2.8	1.8	0.0	0.0	0.0	3.4	2.4	1.5	5.5	0.0	2.4	0.0	0.0
усеяе	Gomphosphaeria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	2.8	0.0	0.0	0.0
qdou	Lyngbya	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
eyD sa	Oscillatoria	15.2	1.2	3.2	0.9	2.0	2.5	1.1	1.2	2.5	1.9	2.6	0.9	1.2	1.1	1.5	1.5	1.7	1.2	0.7	3.7	1.9	2.4	2.1	2.6
Clas	Phormidium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0