

Temporal patterns of picoplankton abundance and metabolism on the western coast of the equatorial Atlantic Ocean

Maiara Menezes¹, Pedro C. Junger², Vinicius S. Kavagutti^{2†}, Bruno Wanderley¹, Anderson de Souza Cabral³, Rodolfo Paranhos⁴, Fernando Unrein⁵, André M. Amado^{1,6}, Hugo Sarmiento^{2,*}

¹ Departamento de Oceanografia e Limnologia, Universidade Federal do Rio Grande do Norte (UFRN), Natal - RN, Brazil

² Departamento de Hidrobiologia, Universidade Federal de São Carlos (UFSCar), São Carlos - SP, Brazil

³ Institute of Microbiology, Federal University of Rio de Janeiro (UFRJ), Rio de Janeiro - RJ, Brazil

⁴ Instituto de Biologia, Universidade Federal do Rio de Janeiro (UFRJ), Ilha do Fundão, Rio de Janeiro - RJ, Brazil

⁵ Instituto de Investigaciones Biotecnológicas-Instituto Tecnológico de Chascomús (IIB-INTECH), UNSAM-CONICET, Camino de Circunvalación Laguna Km 8.200, (7130) Chascomús, Buenos Aires, Argentina

⁶ Departamento de Biologia, Universidade Federal de Juiz de Fora (UFJF), Juiz de Fora-MG, Brazil

† Present address: Department of Aquatic Microbial Ecology, Institute of Hydrobiology, Biology Centre of the Academy of Sciences of the Czech Republic, Na Sádkách 7, 370 05, České Budějovice, Czech Republic

* Corresponding author: hsarmiento@ufscar.br

ABSTRACT

Picoplankton are central global carbon (C) cycling players and often dominate the ocean plankton communities, especially in low latitudes. Therefore, evaluating picoplankton temporal dynamics is critical to understanding microbial stocks and C fluxes in tropical oceans. However, the lack of studies on low-latitude picoplankton communities translates into a common conception that there is an absence of seasonality. Herein, we studied the temporal variation in abundance (measured by flow cytometry), and carbon flux (taking bacterial production and respiration as proxies) of the picoplanktonic community for the first time, as well as their environmental drivers in a low-latitude (05° 59' 20.7"S 035° 05' 14.6"W) Atlantic coastal station. We performed monthly samplings between February 2013 and August 2016 in a novel microbial observatory – hereafter called the Equatorial Atlantic Microbial Observatory – established on the northeastern Brazilian Atlantic coast. Our results revealed stability in temporal dynamics of picoplankton, despite a considerable inter-annual variation, with some related to the El Niño (ENSO) event in 2015. However, weak environmental relationships found were not enough to explain the variation in picoplankton's abundance, which suggests that other factors such as biological interactions may lead to picoplankton abundance variation over time. Heterotrophic bacteria dominated picoplankton during the entire study period and between photosynthetic counterparts, and *Synechococcus* showed greater relative importance than picoeukaryotes. These results bring a novel perspective that picoplankton may exhibit more pronounced fluctuations in the tropical region when considering inter-annual intervals, and is increasing prokaryotic contribution to carbon cycling towards the equator.

Descriptors: Flow cytometry, Bacterioplankton, Picoeukaryotes, Carbon cycling.

INTRODUCTION

The ocean is the largest and most important ecosystem for the earth's climate regulation and

plays an essential role in nutrient stocks and flows (Falkowski et al., 1998; Arrigo, 2005). The key players of global nutrient cycling are marine plankton organisms, which lead to organic carbon production in pelagic waters and form the base of the marine food web (Fenchel, 1988; Sherr and Sherr, 1988; Azam and Worden, 2004). The smallest size-class of plankton (cells < 3 µm, Sieburth et

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al., 1978; Vaulot et al., 2008) is picoplankton, which dominate microbial standing stocks in most oceans and is composed of heterotrophic bacteria (HB), archaea, and autotrophic phytoplankton, such as cyanobacteria (i.e. *Synechococcus* (Syn)) and picoeukaryotes (Peuk). Prokaryotes reach up to 10^9 cells L^{-1} (Kirchman, 2008), while picoeukaryotes have 10^6 cells L^{-1} – about three orders of magnitude less abundant in seawater. Although picoeukaryotes are less abundant than prokaryotes, they often contribute to a significant portion (60-80%) of microbial biomass due to their relatively larger cells, being on the picoplankton upper limit size fraction of 2-3 μm (Not et al., 2009; Marie et al., 2010; Massana, 2011; Massana and Logares, 2013).

The relative importance of picoplankton in aquatic ecosystems follows a general trend where smaller organisms have higher contributions to carbon stocks and fluxes with increasing oligotrophy (Pomeroy, 1974; Waterbury, 1979; Gasol and Duarte, 2000). Low nutrient supply ensures a competitive advantage to picoplankton due to higher surface: volume ratios that result in more efficient use of nutrients when compared to larger cells (Taylor et al., 2015; Lewis, 1986; Agawin and Agustí, 2005). As the tropical ocean is usually oligotrophic, even in some coastal areas, microbial processes related to carbon cycling (microbial food web and microbial loop) may set the main trophic pathways (see Azam et al., 1983). Although new evidence has challenged this concept of competitive advantage of small cells over large ones (Behrenfeld et al., 2022), greater relative contribution of small cells in the tropics has been well accepted for marine (Herbland et al., 1985; Marañon et al., 2000; Pérez et al., 2005) and freshwater environments (Sarmiento, 2012), while classical food chains dominate in high latitudes, maintained by large organisms such as diatoms (Legendre & Rassoulzadegan, 1995).

Latitudinal gradients influence nutrient (i.e. N and P) availability and stoichiometry in the ocean, which in turn may affect picoplankton abundance and metabolism (Martiny et al., 2013). For example, bacteria use algal-based carbon more efficiently for biomass production in more productive environments, such as temperate,

polar, and coastal waters where water conditions may supply nutrients (Gasol and Duarte, 2000). In contrast, high respiration rates in oligotrophic tropical waters reduce bacterial growth efficiency (BGE) (White et al., 1991; del Giorgio and Duarte, 2002; Amado et al., 2013). The nutrient depletion in superficial waters of low latitudes possibly reflects the difference in light intensity affecting the sestonic C:nutrient ratio (Sterner et al., 1998) and stratification processes. Solar radiation and light attenuation in the water column is another critical factor influencing picoplankton composition, distribution, and dominance patterns across spatial scales, from latitudes (Schattenhofer et al., 2009), coastal versus open-ocean waters (Partensky et al., 1996), and in vertical profiles in the water column (Moore et al., 1995). Considering the relatively time-stable high temperatures and nutrient depletion in most tropical regions (except river discharges and upwelling areas), it is not surprising that bacteria commonly dominate microbial abundance and carbon production near the Equator (Fuhrman et al., 1989; Hoppe et al., 2002; Bergo et al., 2017).

Equatorial oceans have relatively stable environmental conditions throughout the year, although time-series observations which may confirm picoplankton dominance in this region are lacking. Most studies in this area use lagrangian (spatial) sampling strategies (Zubkov et al., 1998; Marañon et al., 2000; Hoppe et al., 2002; Moreno-Ostos et al., 2011), while time-series studies of microbial observatories (Eulerian sampling) have predominantly been carried out in temperate (i.e. WCO-Western English Channel; BBMO-Blanes Bay) or subtropical regions (i.e. SPOT-San Pedro California; BATS-Sargasso Sea) of the Northern Hemisphere. Considering studies performed in the equatorial Pacific, it was revealed that there are minor seasonal influences but clear inter-annual patterns in picoplankton, mainly influenced by El Niño Southern Oscillation/ENSO events (Dandonneau et al., 2004), with a significant reduction of larger phytoplankton groups (Bidigare and Ondrusek, 1996). Picoplankton time-series studies in the equatorial Atlantic are scarce, especially near the Brazilian coast (Frazão et al., 2021). So far, time-series approaches have only

been conducted in the south-southeast region with contrasting seasonal dynamics, including intrusions and high productivity events (Andrade et al., 2004; Moser et al., 2016; Bergo et al., 2017). Moreover, the persistent oligotrophic nature of Brazilian waters near the Equator is influenced by warm and nutrient-poor waters coming from the north and northeast of the Brazilian coast (Longhurst and Pauly, 1987).

In view of the above, herein we provide the first study evaluating the temporal dynamic of picoplankton in the Western equatorial Atlantic on the Northeastern Brazilian coast. Our goal was to address and discuss the following questions: (1) Are the picoplankton following any seasonal pattern in the tropics? (2) Which environmental factors may regulate picoplankton abundance and metabolism in this coastal region? and (3) What is the contribution of the bacterial heterotrophic metabolism to the carbon cycle in this central region of the western Atlantic? We hypothesized that seasonality has no influence on the picoplankton dynamics in the western equatorial Atlantic, since the seasonal signal is low compared to more dynamic and predictable coastal areas of higher latitude oceans. Thus, we expect low fluctuation in the abundance of picoplankton populations throughout the year, and with other non-seasonal factors driving these fluctuations (i.e. oceanographic or biological interactions). Considering metabolic rates, we hypothesize that bacterial carbon production will not surpass respiration losses, resulting in low BGE, as expected for low latitude oceans.

METHODS

STUDY SITE AND ENVIRONMENTAL MEASURES

We performed monthly samplings from February 2013 to August 2016 in the Equatorial Atlantic Microbial Observatory (EAMO) located in Rio Grande do Norte State, Northeast Brazil -05°59'20.7"S 035°05'14.6"W, 3 km from the coastline (Figure. 1A). The sampling station is located within the narrow continental shelf (15-30 km), specifically at the interface between the internal and external shelves, with depths up to

20 m where longshore currents flow from south to north (Vital et al., 2010). High atmospheric temperatures (26-28°C) prevail throughout the year, and seasonality is marked by the displacement of the Inter-Tropical Convergence Zone (ITCZ) and trade wind forces (Silva et al., 2009; Castellanos et al., 2015). The historically short rainy period of approximately 3 months occurs between April and June, while a longer dry period occurs between September and December (NIMER, 1979). We used the historical climatic data for the last 50 years (data from the National Institute of Meteorology (*Instituto Nacional de Meteorologia – INMET*)) to classify the rainy (March to July) and dry (August to February) seasons.

We carried out vertical profiles of temperature profiles, salinity, and total dissolved solids (TDS) using a multiparameter probe (Horiba U-50 Series). We estimated the euphotic zone by associating Secchi disk measurements (Zeu, depth at which light is 1% of subsurface light) and the vertical light attenuation coefficient for coastal waters (sensu Luhtala and Tolvanen, 2013). We collected seawater samples (20 L) in the subsurface (~1 m depth) and immediately passed the samples through a 120 µm mesh to remove large planktonic organisms. Samples were then stored in a dark bottle, kept refrigerated and brought to the laboratory for further analysis (maximum 2 hours after sampling).

We collected cumulative monthly rainfall data from the National Institute of Meteorology (*INMET*) database. Chlorophyll-*a* concentration was collected in the Plymouth Marine Institute database. The concentration of particulate organic carbon (POC) was obtained in the MODIS aqua database. All online data was provided by the Weather Prevision and Climate Studies Center (*Centro de Previsão de Tempo e Estudos Climáticos - CPTEC/INPE*). The South Oscillation Index data collected online is available at: <https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>.

ANALYTICAL PROCEDURES

Samples (1.6 mL) were preserved with 1% paraformaldehyde + 0.05% glutaraldehyde (final conc.) and frozen at -80°C until the analysis to estimate picoplankton abundance (Marie et

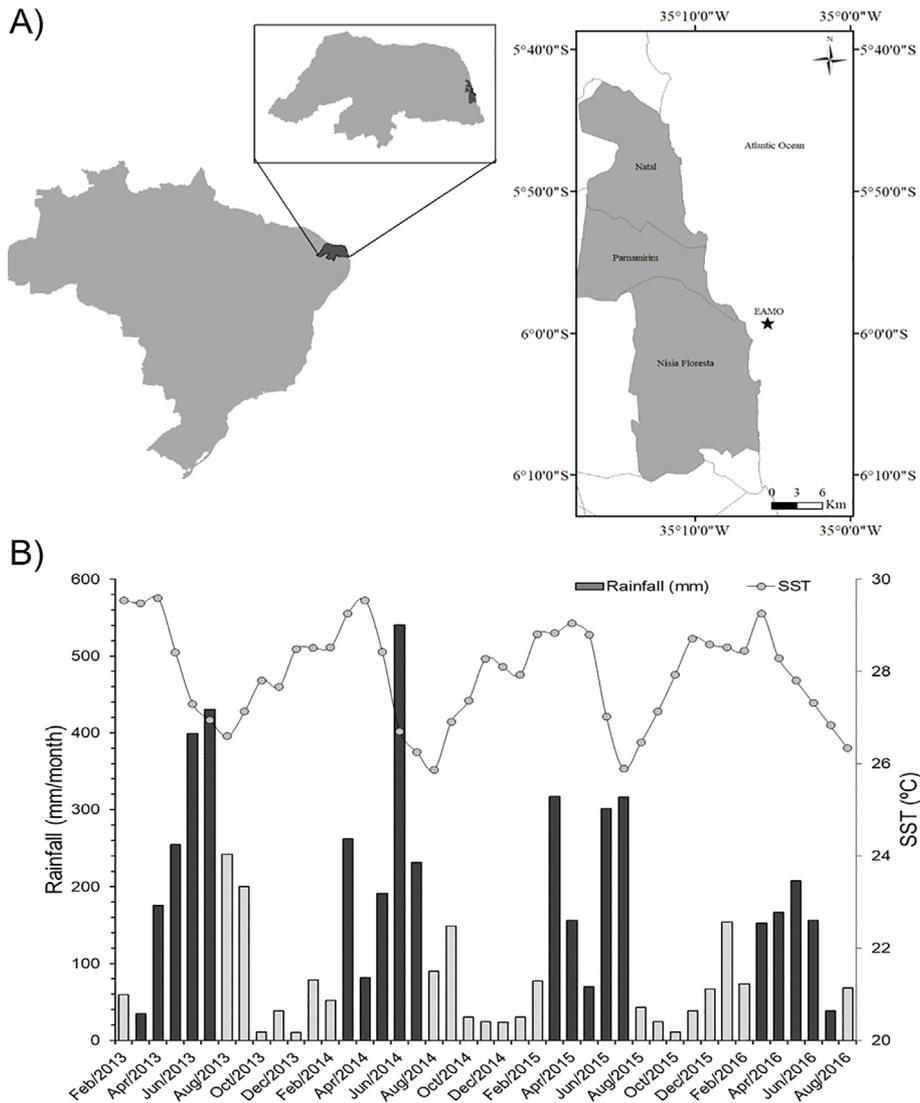


Figure 1. A) Map of the Northeast Brazil coast showing the location of the Equatorial Atlantic Microbial Observatory - EAMO. B) Rainfall seasonality, showing dry (light gray bars) and rainy (dark gray bars) seasons, and sea-surface temperatures (gray circles) in the Northeast Brazilian coast between 2013 and 2016.

al., 1997). Cell abundance was determined by flow cytometry (BD FACScalibur) equipped with a blue laser (emission at 488 nm) as described in (Marie et al., 1997). For HB, 300 μl samples were stained with 3 μl SYBRGreen - Molecular probes (Marie et al., 1997), left for 10 min in the dark before running at low speed (ca. 9.18 $\mu\text{l min}^{-1}$). HB cells were detected by their signature in a plot of SSC (90° side scatter) vs. FL1 (green fluorescence), and in FL3 (red fluorescence) vs. FL1, as shown in Figure 2 A and B, according to

del Giorgio et al. (1996) and Gasol and del Giorgio (2000). For *Synechococcus* spp. and autotrophic picoeukaryotes, 400 μl non-stained samples were run at hi-speed (ca. 52.3 $\mu\text{l min}^{-1}$). Figures 2C and D show cytograms of SSC vs. FL3, and FL3 vs. FL2 (orange fluorescence) used to detect autotrophic cells. Data were acquired in log mode until around 10000 events or during 3 min. Polysciences latex beads of 1 μm (10 μl) were used for calibration. Data acquisition and analysis were performed with the FlowJo® V10.0.8 software program.

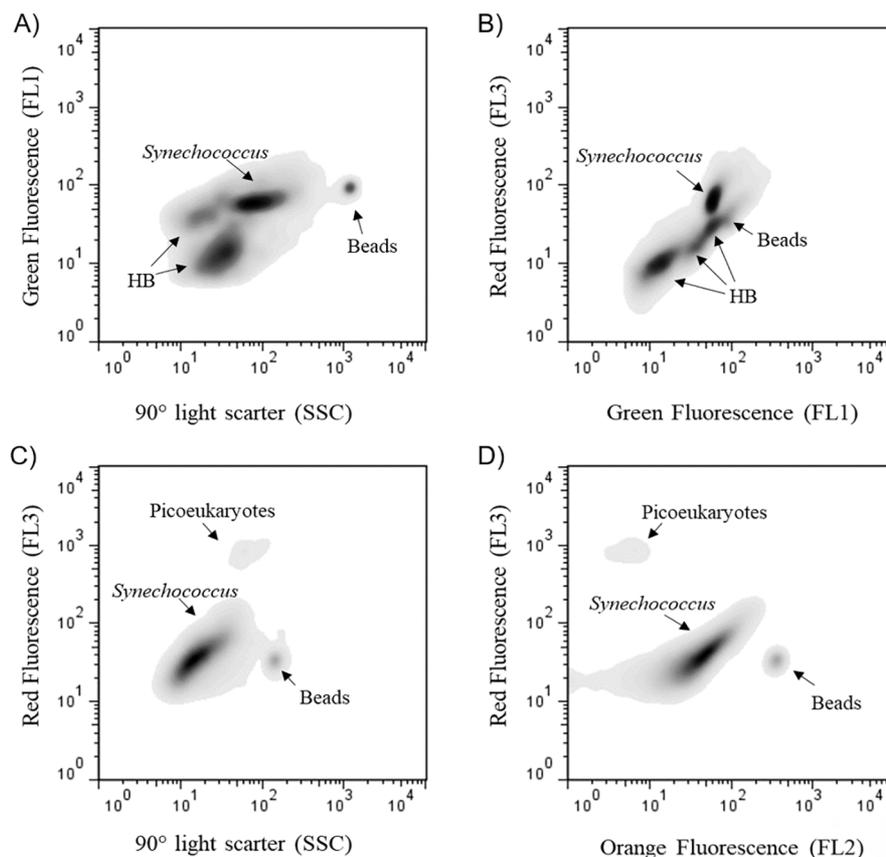


Figure 2. Density plots obtained by flow cytometry Equatorial Atlantic Microbial Observatory (EAMO) water samples. A) and B) Syto-13 stained picoplankton samples. Identification of the three populations of Heterotrophic Bacteria (HB), *Synechococcus* spp. and the polystyrene 1 mm beads. C) and D) Unstained samples showing the red and orange autofluorescence of autotrophic picoplankton groups: *Synechococcus* spp. and picoeukaryotes.

Bacterial production (BP) rates were estimated using the $[3\text{H}]$ -leucine incorporation method (Kirchman, 1992). First, 15 μl of $[3\text{H}]$ -leucine (20 nM final conc.) were added to six 1.2 ml replicates (4 treatments and 2 dead controls – leucine plus TCA addition before sample addition). After the incubation period ($\sim 2.5\text{h}$) in the dark at the *in situ* temperature, leucine incorporation was stopped by adding 90 μl of 100% trichloroacetic acid (TCA) and samples were stored frozen (-80°C) until further analyses. We extracted bacterial protein by washing it with 5% TCA, and 80% ethanol (Smith and Azam, 1992) and reading in a liquid scintillation counter (Beckman LS-6500). Disintegrations were converted to $\mu\text{g C l}^{-1} \text{h}^{-1}$ using the conversion factor of 0.86 from Smith and Azam (1992). Bacterial respiration (BR) rates were estimated by dissolved

oxygen consumption in 5.9 mL exetainers® (10 replicates) during 48h of incubation in the dark at the *in situ* temperature. Initial and final dissolved oxygen concentrations were measured using a microprobe connected to OXY-meter Unisense® (Briand et al., 2004). Estimations were performed assuming a respiratory quotient (RQ) of 1 (see Berggren et al., 2012).

We additionally estimated dissolved nutrients following conventional methods (Grasshoff et al., 1999), conducted by an Autoanalyzer 3 (AA3 HR Seal). Ammonium measurements were performed by the blue indophenol method (Parsons et al., 1984) with detection limits of 0.1 μM . We determined nitrite concentration by the diazotization method. Nitrate and total N were determined by reduction in the Cd-Cu column followed by diazotization.

Soluble reactive P and total P concentrations were determined through the phosphomolybdic method. Total fractions of P and N were digested in an acid medium with potassium persulfate before analyses. We addressed a nutrient limitation (N and P) through the ratio between nitrate + nitrite and soluble reactive P for new production (Cavender-Bares et al., 2001). Dissolved inorganic silicate was determined based on the formation of yellow silicomolybdic acid.

STATISTICAL ANALYSIS

We initially performed a temporal correlation analysis comparing simple linear models of the dependent variables with residual auto-correlation structure and auto-regressive model of order 1 to investigate potential violations of the independence assumption (Zuur et al., 2008). Only HB showed an auto-correlation structure. However, because of the low correlation index ($\rho = 4.90 \times 10^{-8}$), we assumed the absence of temporal autocorrelation in the data. Furthermore, there was no model improvement with both the auto-correlation (AIC = 24.5, BIC = 31.5) or the autoregressive models (AIC = 24.5, BIC = 31.5) compared with simple linear model (AIC 22.5, BIC = 28.1).

Next, we performed generalized additive models (GAM) models using the Gaussian and gamma distribution errors, and selected the most fitted model considering the Akaike criterion using the 'mgcv' (with functions gam and gamm) and 'bblme' (function AICtab) R packages in order to understand the temporal distribution patterns (intra- and interannual) of the picoplankton populations. We also performed comparative t-tests of environmental and biological (picoplankton) variables to capture seasonal variation between dry and rainy seasons. We tested normality with the Shapiro-Wilk test and homoscedasticity with the Barlett test, and we used Welch t-tests for heteroscedastic variables. Spearman correlation analyses were performed between all environmental parameters and picoplankton components to assess the main variables influencing picoplankton distribution. Multicollinearity between variables was detected through Variance Inflation Factor (VIF), assuming a VIF=5 to exclude collinear variables. An additional

regression analysis was performed to evaluate the relationship between picoplankton populations. All analyses were performed in the R 4.1.1 program (R Development Core Team).

LITERATURE DATA ACQUISITION

We acquired data from seven different microbial observatories to compare variability in abundance of picoplankton in surface waters across different latitudes, namely: Western English Channel – WCO (Tarran and Bruun, 2015); Darwin North Australia – DAR, Maria Island Australia - MAR, Rottneest Island Australia - ROT, Yongala Australia - YON (all from IMOS National Reference Station, available at: <https://portal.aodn.org.au/>); Blanes Bay Microbial Observatory - BBMO (data provided by Gasol, PA); and Northern Gulf of Alaska - NGA (LTR Network - Long Term Ecological Research, data available at: <https://lternet.edu/site/>).

RESULTS

ENVIRONMENTAL SEASONALITY

Rainfall revealed seasonal and interannual variation over the study period. The average rainfall during rainy seasons was more than three times greater than in dry seasons, with maximum values recorded in June-July, and minimum in October-December. We observed a gradual reduction in the average cumulative rainfall of dry and rainy seasons throughout the study period (Figure. 1B). Cumulative rainfall for both seasons in 2016 was below that of previous years, and there was a 74% reduction in total annual average rainfall from 2016 relative to 2013 (data not shown).

Sea surface temperatures ranged from 25.9 to 29.6°C, with higher temperatures during austral summer (January-March), whereas lower temperatures occurred from June to September, with the minimum in the July-August period (Figure. 3a). Rainfall was higher in rainy periods and ranged from 10.1 to 540.4 mm, with an average of 147.3 mm (Figure. 3b). POC concentrations were higher during the rainy season (Figure. 3c) and ranged from 86.36 to 400.22 mgm⁻³. Chlorophyll *a* presented an average of 0.47 µgL⁻¹ (ranged from 0.26 to 0.97 µgL⁻¹) and showed higher concentrations during rainy periods (Figure. 3d).

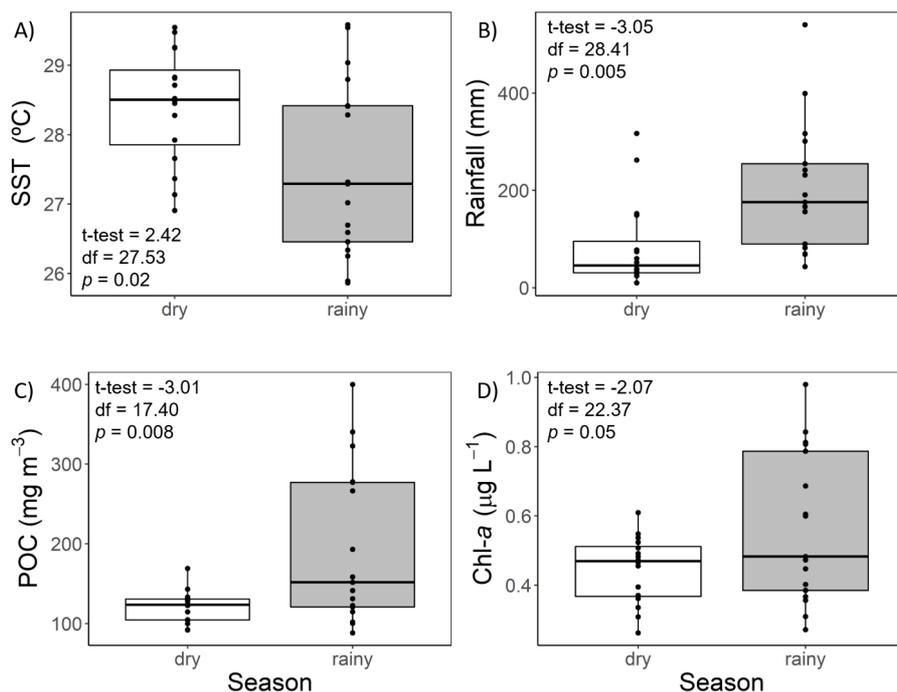


Figure 3. Box plots showing differences in (A) sea surface temperature (SST), (B) rainfall, (C) particulate organic carbon (POC) and (D) Chlorophyll a concentration between dry and rainy seasons in the study area between 2013 and 2016. The central full line indicates the median value, the dotted line indicates the arithmetic mean value, the boxes indicate the lower and upper quartiles, the vertical lines indicate the 10th and 90th percentiles. All differences were significant with p -value ≤ 0.05 .

The euphotic zone depth (range 6.64 - 25.65 m) did not differ between rainy and dry seasons, nor did TDS (range 31.26 - 37.64) or salinity (range 3.27- 3.79). The results for the t-test are shown in [Table S1](#).

The average of total N concentration was 8.93 μM (ranging from 2.67 up to 20 μM) and did not present any clear seasonal pattern, as the others dissolved N and P forms, but revealed a tendency to decrease toward the end of the study (see [Figure. S1](#)). Ammonium presented an average of 0.72 μM (ranging from 0.21 to 4.97 μM), while nitrate concentrations were on average 1.22 μM (ranging from 0.05 to 5.87 μM), and peaks were usually recorded in June-July ([Figure. S1c](#)). Nitrite presented an average of 0.07 μM (ranged <0.01 to 0.34 μM). Most of the N in the water was in the organic form, averaging 66% ($\pm 1.79\%$; reaching up to 95% of TN). The soluble reactive P average was 0.06 μM (range 0.12 - 0.03 μM), while total P average was 0.3 μM (range 0.46 - 0.1 μM , see [Figure. S2](#) for more details). The nitrate + nitrite:

soluble reactive P ratio was an average of 19.2:1, but showed great variation between 80:1 to 1:1. The average total N:Total P ratio was 33:1, ranging from 79.6:1 to 8.5:1.

TEMPORAL DYNAMICS OF EQUATORIAL MARINE PICOPANKTON

Picoplankton was dominated by HB cells, which showed high abundance during the whole study period with an average of $8.10 (\pm 4.34) \times 10^5$ cells mL^{-1} (range 1.4 - 19.5×10^5 cells mL^{-1}), while Syn was one order of magnitude lower, with an average of 0.9×10^5 cells mL^{-1} (range 0.4 - 1.8×10^5 cells mL^{-1}). The lowest abundance in the study was presented by Peuk, with an average of 0.02×10^5 cells mL^{-1} ($0.004 - 0.05 \times 10^5$ cells mL^{-1}). The coefficients of variation for HB, Syn and Peuk were 54%, 35.8% and 71%, respectively. Temporal variation models revealed that only the interannual variation component was significant for HB (r^2 adj.= 0.67; $F = 4.91$; $p = 0.003$, [Figure. 4A](#)), but it is not linked to El Niño (South Oscillation

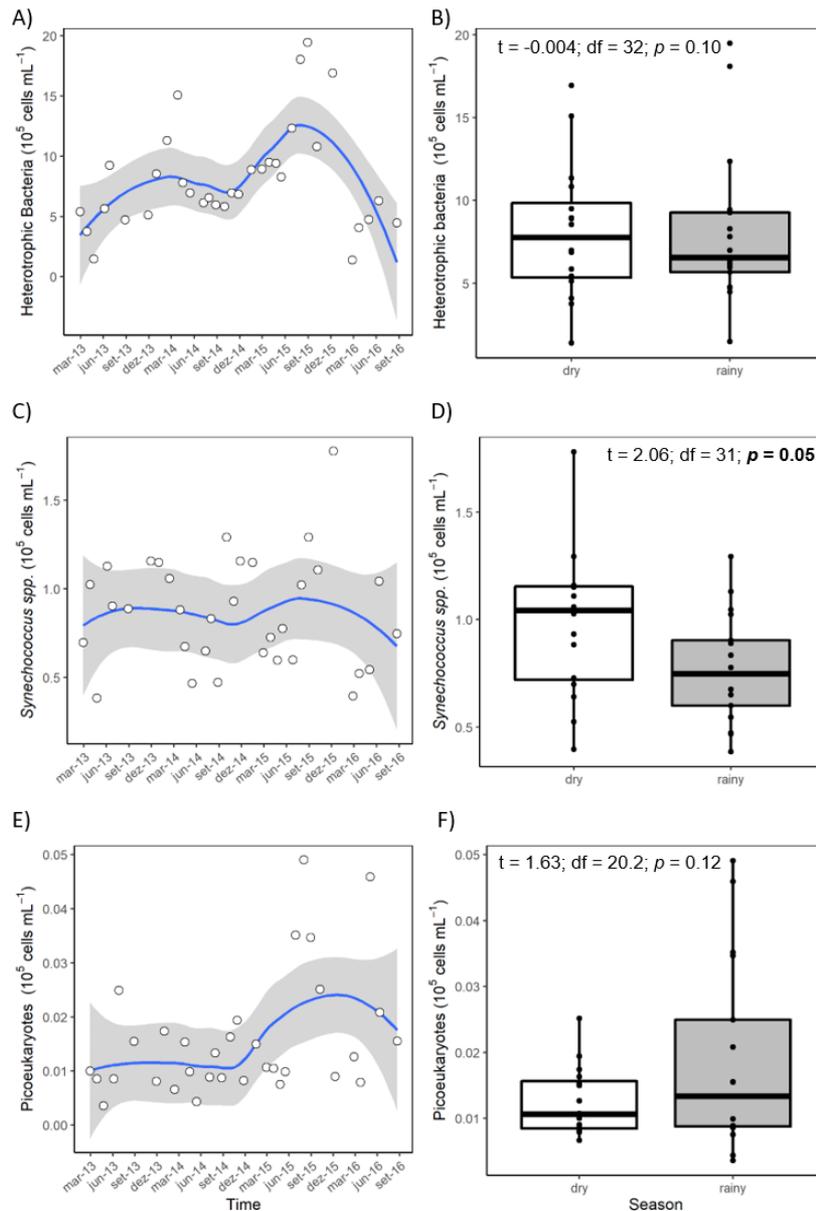


Figure 4. Models of Interannual variation (with smooth) in cell abundance and boxplot showing comparisons between seasons for Heterotrophic Bacteria (A) and (B); *Synechococcus* spp. (C) and (D); and Picoeukaryotes (E) and (F) in Equatorial Atlantic Microbial Observatory - EAMO during 2013-2016. Box-plot information is the same as described in Fig.3.

Index - SOI). The absence of seasonal variation for HB was confirmed by the t-test (Figure. 4B). In contrast, Syn showed a clear seasonal trend, with the model only revealing significance for the seasonal component (r^2 adj. = 0.11; $F = -2.22$; $p = 0.035$; Figure. 4C). A t-test revealed the difference between seasons, with higher abundance during dry seasons (Figure. 4D). Peuk did not show any

seasonal or interannual variation; however, the model revealed the SOI component as a significant influence on its temporal variation (r^2 adj. = 0.61; $F = 4.37$; $p = 0.002$; Figure. 4E and F).

BACTERIAL PRODUCTION AND RESPIRATION

Bacterial production ranged from 0.22 to 3.21 $\mu\text{g C L}^{-1}\text{h}^{-1}$, with an average of $1.24 \pm 0.96 \mu\text{g C L}^{-1}\text{h}^{-1}$

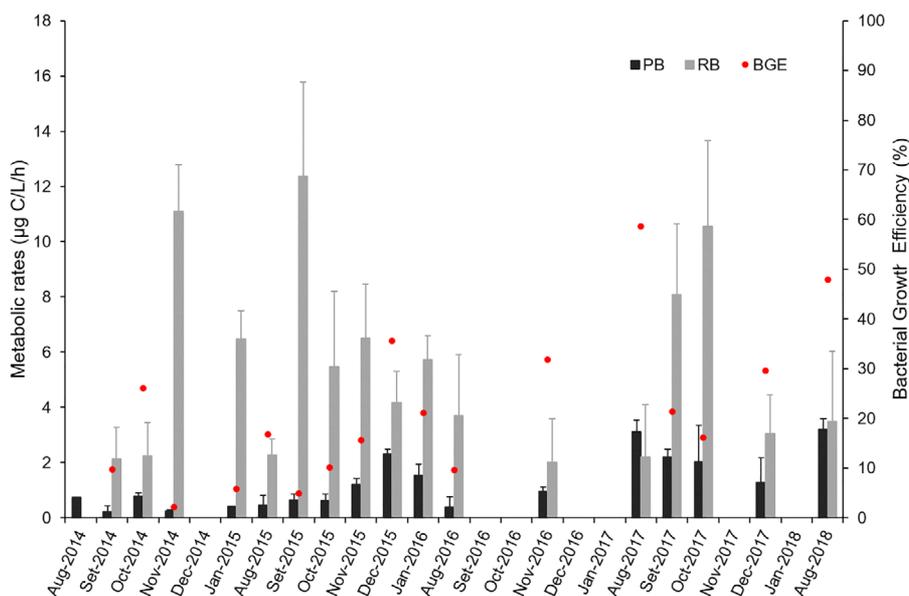


Figure 5. Bacterial Production-BP (black bars); Bacterial Respiration-BR (gray bars) mensal averages (\pm standard deviation) and estimated Bacterial Growth Efficiency - BGE (red dots) in Equatorial Atlantic Microbial Observatory - EAMO during 2013-2016.

(Figure. 5). No seasonal variation was detected during the study period (from August 2014 to August 2016). Bacterial Respiration ranged from 2.01 to 12.37 $\mu\text{g C L}^{-1}\text{h}^{-1}$, with an average of $5.38 \pm 3.3 \mu\text{g C L}^{-1}\text{h}^{-1}$, and did not show seasonal variation like BP. Respiration rates were much higher than those of production. Consequently, bacterial growth efficiency (BGE) presented an average of 21% (ranging from 2% to 59%).

ENVIRONMENTAL DRIVERS OF PICOPLANKTON

None of the environmental variables significantly correlated with HB, except for salinity and POC, with negative and positive correlations, respectively (Figure. 6). Salinity also negatively correlated with Syn and Peuk. Peuk were negatively correlated with SST and SOI, and positively correlated with POC. We recorded positive correlations among HB with Syn and with Peuk. However, no correlation was detected between the two photosynthetic counterparts, Syn and Peuk. Regression analyses revealed stronger relationships of HB with Syn (r^2 adj. = 0.30; slope = 0.89; $F = 14.43$; $df = 31$; $p = 0.0006$) than with Peuk (r^2 adj. = 0.145; slope = 0.395; $F = 6.444$; df

= 31; $p = 0.016$). BP and BR showed no significant correlation with any environmental variable measured in this study.

DISCUSSION

Greater stability in environmental factors and consequently in temporal dynamics of picoplankton is expected in low latitude oceans contrasting with higher latitudes (Heywood et al., 2006; Giovannoni and Vergin, 2012). In fact, our results demonstrate that seasonality is not a major factor driving picoplankton populations over time at Equatorial Atlantic (with the exception of Syn, which showed higher abundance in dry periods; see Figure. 4). On the other hand, an interannual variation trend was well pronounced for HB and Peuk populations, with Peuk dynamics possibly being influenced by the occurrence of El Niño events. These results suggest that each population of picoplankton may have independent temporal dynamics, even though these populations are correlated with each other.

TEMPORAL PATTERNS OF PICOPLANKTON

The dominance of HB cells marked the structure of the picoplankton community at

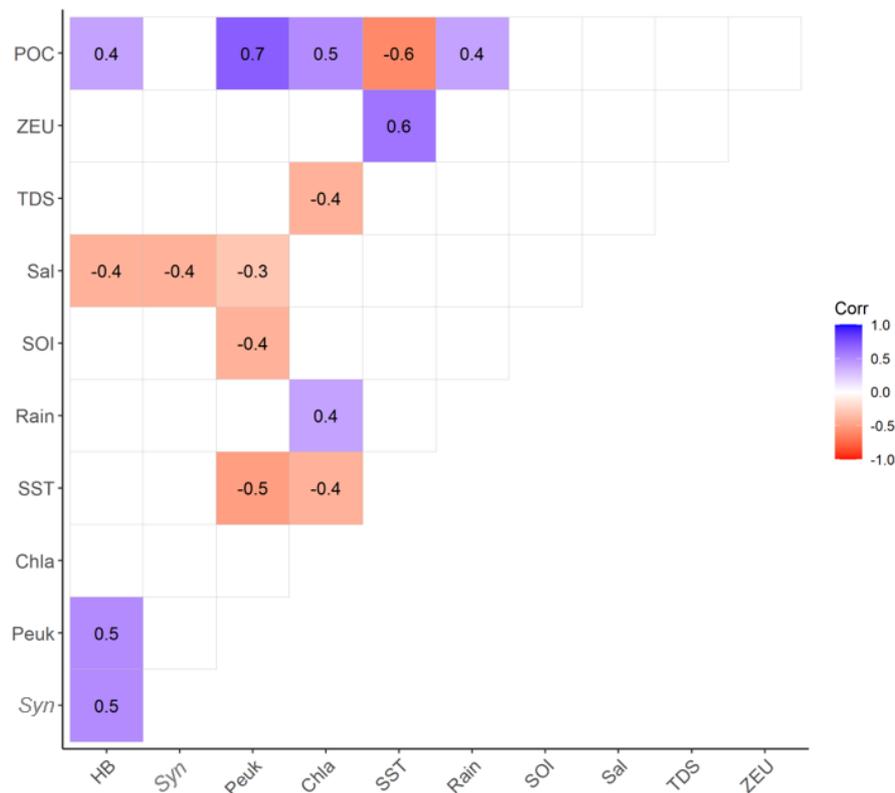


Figure 6. Correlation Plot showing Spearman coefficients between picoplankton components and environmental variables. Plot showing only significant correlations (p -value ≤ 0.05). (HB= Heterotrophic Bacteria; Syn= *Synechococcus*; Peuk= Picoeukaryotes, Chla= Chlorophyll a; SST= Sea surface temperature; SOI= South Oscillation Index; Sal= Salinity; TDS = Total Dissolved Solids; ZEU= Euphotic zone).

EAMO throughout the entire study period. HB abundance showed fluctuations which were independent of environmental seasonality, with an interannual variation being pointed out in the GAM model (Table 1). Even with these fluctuations, the contribution of HB cells for total picoplankton abundance (sum of all 3 populations) was 88% on average (ranging from 77% to 95%), emphasizing the importance of microbial processes mediated by heterotrophs at *EAMO*. These results are consistent with other studies along the Brazilian coast (Andrade et al., 2004; Ribeiro & Lopes et al., 2016) and in the South Atlantic Ocean, where HB represents 50% to 70% of the picoplankton community in oligotrophic waters (Landry et al., 1996; Zubkov et al., 1998). HB importance is enhanced in ecosystems where photosynthetic biomass is low ($chl_a \leq 0.05 - 1 \mu\text{g. L}^{-1}$), as recorded at *EAMO*. Allochthonous C subsidies

(i.e. river discharge for coastal regions) and decreased bacterivory are possible reasons for HB dominance in oligotrophic systems. Additionally, HB access to nutrients which are not available to phytoplankton (Cotner and Biddanda, 2002) is another possible explanation supported by our nutrient concentration results, which revealed that most N is available in organic form (quickly processed by bacterial extracellular enzymes).

The unique picoplankton component that presented seasonal variation was cyanobacteria Syn (Figure. 4B), revealing a minor variation throughout the study (CV = 35.8%) compared to other picoplankton components (CV = 53% for HB and 71% for Peuk). Peaks occur in dry seasons, especially in austral summer (from November to January). This pattern also occurs in temperate coastal environments, which revealed high picoplankton contributions (especially of Syn) to

Table 1. Generalized additive models-GAM coefficients for models fitted and selected by AIC criterion to evaluate temporal patterns of picoplankton populations in Equatorial Atlantic Microbial Observatory EAMO.

	Variables	t/F value*	p value	Adj. R ²	Distribution family
Heterotrophic Bacteria	Season	0.824	0.419	0.67	Gamma
	Smooth (Time)	4.909	0.003**		
	Smooth (SOI)	2.186	0.216		
<i>Synechococcus</i> spp.	Season	-2.219	0.035*	0.11	Gaussian
	Smooth (Time)	0.135	0.716		
	Smooth (SOI)	0.855	0.531		
Picoeukaryotes	Season	0.924	0.366	0.61	Gaussian
	Smooth (Time)	1.702	0.205		
	Smooth (SOI)	4.368	0.002**		

total phytoplankton biomass during summer due to higher solar radiation and nutritional restriction related to thermal stratification (i.e. Gasol et al., 2002). Summer peaks of Syn were also recorded in coastal waters of the subtropical East China Sea (Jiao et al., 2005), although the same study recorded peaks in winter at open ocean sites (Kushiro water). Syn peaks predominantly occur in mid-latitudes, primarily associated with a period of deepening of mixed-layer depth (Campbell et al., 1997; Durand et al., 2001; Liu et al., 2007). Moreover, no stratification indicator was observed at EAMO (considering the physicochemical parameters). The low depth of the area (~20 m) allows constant mixing along the water column. Despite this, the more oligotrophic conditions of dry seasons may favor Syn in superficial waters in this region (see Figure. 4).

During this study, *Prochlorococcus*, a cyanobacteria commonly found in oligotrophic waters, was not detected in our cytometry analyzes. Although we did not detect it, we have evidence of its existence in our samples by 16S amplicon sequencing (Kavagutti et al. 2016). *Prochlorococcus* usually dominates over Syn in most parts of the oligotrophic oceans due to selective advantages in absorption characteristics and photosynthetic performances (Blanchot and Rodier, 1996; Zubkov et al., 2000; Heywood et al., 2006; Karl and Church, 2014). However, Syn can dominate in surface waters since *Prochlorococcus* appears to be quite sensitive to high irradiance (Partensky et al., 1999; Crosbie and Furnas, 2001; Bergo et al., 2017). The light absorption properties (i.e. low pigment content

and low chl_a concentration) of *Prochlorococcus* cells also interfere with the ability to detect populations in marine surface samples analyzed by flow cytometry. This detection problem may depend on the adopted method (Partensky and Garczarek, 2010) and the type of instrument (i.e. BD FACSCanto, BD Accuri C6) (Ribeiro & Marie et al., 2016), and could be the reason for the lack of *Prochlorococcus* in our samples.

Peuk showed the lowest abundance values throughout the entire study period. Our results revealed a low relative contribution of Peuk to total picoplankton abundance, but probably because Peuk thrives better where light is scarce and the nutrient concentration is higher, near the bottom of the euphotic zone (Partensky et al., 1996; Vázquez-Domínguez et al., 2008). Thus, our surface sampling may have underestimated the contribution of Peuk to picoplankton in the study area. Although a minor numerical contribution to the abundance of picoplankton cells, Peuk can substantially contribute in terms of carbon standing stock, showing lower abundance just due to higher grazing pressure (Worden et al., 2004). Even though Peuk showed low abundance, its range of variation was the largest among the picoplankton components at EAMO (CV = 71%) and occurred independently of seasonality. Peuk abundance peaks occurred between 2015 and 2016, coinciding with the El Niño event (Figure. 4C). The model analysis confirmed the influence of El Niño on its distribution (Table 1). El Niño may positively affect Peuk on the NE Brazilian coast by two main processes: (1) by reducing precipitation as a result of tropospheric warming

that suppresses atmospheric convection; and (2) by inducing cross-equatorial SST anomalies related to increased upwelling events (i.e. the Benguela system on the African east coast) caused by southeasterly wind anomalies near the Equator (Xie and Carton, 2004). Although El Niño influences on the Brazilian NE are well recognized, its effects on picoplankton still require more studies, as the effects on hydrology may vary depending on the intensity of El Niño (Rodrigues et al., 2011).

In applying our picoplankton variability results to a global context, we compared picoplankton community abundance data from seven microbial observatories located at different latitudes. In comparing these results (see Figure. 7 and Table 2), we observed that each picoplankton component has a specific variation pattern across latitudes. The variation in cell abundance of HB is equivalent

to that found in temperate (BBMO and WCO) and polar (NGA) regions (Figure. 7A). On the other hand, Syn cell abundance at *EAMO* showed the highest mean value and lowest variation (see CV% values in Table 2) related to other observatories of higher latitudes, suggesting that the importance of this cyanobacteria increases towards the Equator. Meanwhile, the opposite occurs with Peuk, which decreases in abundance towards the Equator, although it shows superior variation to that found in other subtropical latitudes (DAR, YON and ROT), suggesting that Peuk may have a lower relative contribution to the total biomass of picoplankton in tropical regions relative to prokaryotic components. In only comparing the photosynthetic picoplankton components (Syn and Peuk), it is possible to observe that the proportion of Syn to total abundance is much higher at *EAMO* (above 80%), related to temperate and subtropical observatories

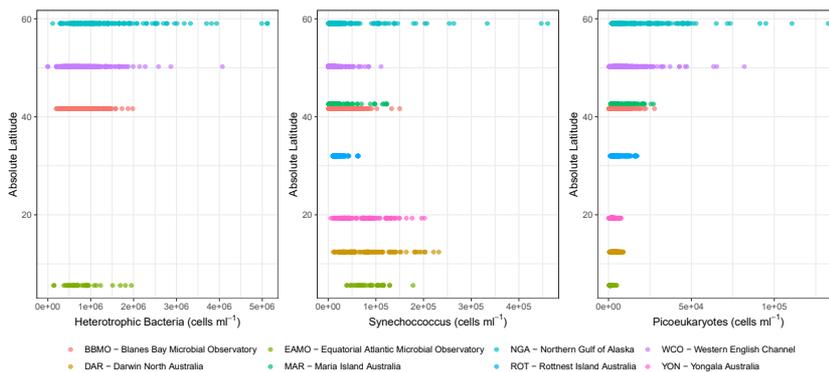


Figure 7. Scatter plot of the three picoplankton populations abundances against absolute latitude. This dataset includes flow-cytometric abundance data from eight microbial observatories (including our new observatory - *EAMO*) covering a wide range of absolute latitudes (from 0 to 50°). Literature data acquisition is described in the methods section.

Table 2. Comparison of picoplankton components registered by microbial observatories of different latitudes showing mean values ± standard deviation and coefficient of variation (%). NGA - Northern Gulf of Alaska; WCO - Western English Channel; MAR - Maria Island Australia; BBMO - Blanes Bay Microbial Observatory; ROT - Rottneest Island Australia; YON - Yongala Australia; DAR - Darwin North Australia; *EAMO* - Equatorial Atlantis Microbial Observatory.

Microbial Observatories	Latitude	Longitude	H.Bacteria (cells x10 ⁵)		Synechococcus (cells x10 ⁴)		Picoeukaryotes (cells x 10 ³)	
			Mean ±sd	CV(%)	Mean ±sd	CV(%)	Mean ±sd	CV(%)
NGA	59.51 N	149.28 W	13.3 ±9.24	69.3	4.77 ±7.40	155.06	22.82 ± 21.42	93.82
WCO	50.25 N	4.22 W	8.19 ±4.72	57.6	1.09 ±1.53	139.72	10.46 ±10.11	96.64
MAR	42.59 S	148.23 E	-	-	2.43 ±3.02	124.15	7.86 ±6.35	80.70
BBMO	41.66 N	2.5 E	8.21 ±2.85	37.4	2.50 ±2.23	89.11	3.89 ±4.31	110.67
ROT	32 S	115.41 E	-	-	2.22 ±1.22	54.93	7.04 ±4.37	62.14
YON	19.30 S	147.62 E	-	-	7.14 ±4.30	60.23	2.57 ±1.41	55.01
DAR	12.4 S	130.77 E	-	-	7.94 ±5.26	66.29	4.00 ±1.95	48.65
<i>EAMO</i>	5.59 S	35.05 W	8.10 ±4.34	53.6	8.71 ±3.12	35.82	1.57 ±1.12	71.22

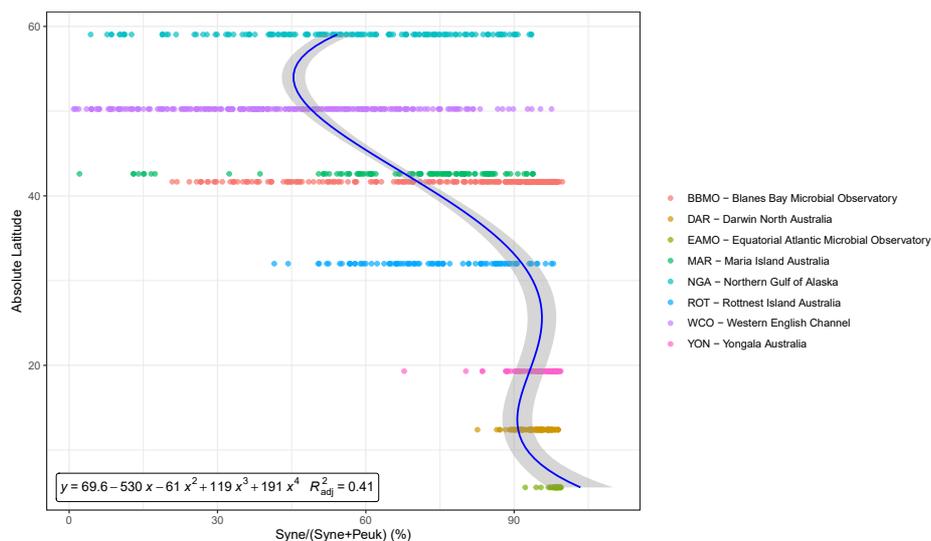


Figure 8. Scatter plot of the ratio between *Synechococcus* and PPP (photosynthetic picoplankton) abundances against absolute latitude. Data acquisition is the same described in Fig.7. The polynomial equation and the R^2 are shown in the plot. The relationship was significant (p -value < 0.01).

(Figure. 8). This proportion is equivalent, or even very low, with a predominance of eukaryotic organisms composing the picophytoplankton in some cases, which points out the importance of prokaryotes towards the Equator. Our results support the idea that microbial dynamics may exhibit less marked seasonal fluctuations in the tropics compared to mid-high latitude regions. However, when considering the interannual variability, the abundance of picoplankton in this most central portion of the globe can be as expressive as that found towards the poles, and mostly that prokaryotes are central players in picoplankton's ecological role in tropical waters.

BACTERIAL C METABOLISM

Our estimates of BP rates were predominantly high ($\sim 36 \mu\text{g C L}^{-1} \text{d}^{-1}$), exceeding previous estimates made in South and Central Atlantic open waters (0.03 - $24.3 \mu\text{g C L}^{-1} \text{d}^{-1}$ in Vázquez-Domínguez et al., 2008). Nevertheless, these results are within the range of rates measured on the southeast coast of Brazil (4.8 - $175.0 \mu\text{g C L}^{-1} \text{d}^{-1}$), which has more eutrophic conditions (Paranhos et al., 2001). The high BP rates found at *EAMO*, where oligotrophy conditions dominate, reinforce the idea that the heterotrophic portion of picoplankton has high relevance in tropical waters considering carbon biomass production. Both the

high HB cell concentrations and the high BP rates found at *EAMO* evidence the net heterotrophy condition in microbial metabolism occurring in this region as a consequence of a high carbon demand for bacterial growth and respiration, surpassing the primary production performed by phytoplankton (Hoppe et al., 2002).

Like most biotic variables, BP and BR did not present seasonal signals. The estimates of BR rates recorded ($\sim 6 \mu\text{g C l}^{-1} \text{h}^{-1}$) were close to those estimated from surface coastal waters by del Giorgio and Williams (2005) of $3.7 \mu\text{g C L}^{-1} \text{h}^{-1}$, and vastly surpassed the BP rates, which resulted in a low BGE (Figure. 5). The BR variation during the study period was inferior to BP (CV = 58% and 64%, respectively). Indeed, there is consensus that respiration is less variable than other processes in aquatic ecosystems (del Giorgio and Duarte, 2002). The fact that several distinct sources of organic matter can subsidize BP reflects its higher potential variability compared with BR, which is usually influenced by temperature.

BP, BR and BGE rates measured at *EAMO* agree with previous studies for tropical coastal oceans (Lee et al., 2009), and such studies evidence lower BGE in tropical environments as a result of higher temperatures, higher light exposure, and nutrient limitation (Amado et al., 2013). An additional explanation relates to the

negative relationship between BGE and the C:N ratio, which denotes that low-quality substrate (high C:N ratios) reduces bacterial efficiency to produce biomass (Pradeep Ram et al., 2003). Low BGE (<25%) were recorded even in a hypereutrophic estuarine ecosystem of Northeast Brazil where BP and BR (2.88 and 20.64 $\mu\text{g C L}^{-1} \text{h}^{-1}$ on average, respectively) were approximately two-fold higher than the rates in the present study (1.51 and 5.81 $\mu\text{g C L}^{-1} \text{h}^{-1}$, respectively) (Guenther et al., 2017). This corroborates our hypothesis of low efficiency in the energy use of bacteria at low latitudes, as reported in a study by Hoppe et al. (2002) performed in transects from North to South in the Atlantic. We also detected increased BP/BR ratios related to chlorophyll *a* concentration (slope = 6.03, $R^2=0.41$), suggesting an increase in HB utilization efficiency of substrate during higher chlorophyll *a* concentration periods, and higher photosynthetic biomass. Increased BGE with increasing chlorophyll *a* concentration suggest that phytoplankton substrate release may be the primary source of organic matter for bacteria in such cases, even in shallow coastal waters.

ENVIRONMENTAL DRIVERS OF PICOPLANKTON

Coastal environments are influenced by diverse factors such as river and continental discharges, atmospheric changes, wind force, adjacent water masses, and a highly heterogeneous ecosystem. The salinity at *EAMO* was the critical factor with a negative impact on the abundance of the entire picoplankton community (Figure. 6). Therefore, mechanisms related to salinity reduction and riverine inputs, intensive rainfall episodes or less saline outer shelf water mass entrance in the coastal zone might positively affect picoplankton. This influence may arise from the covariation between salinity and nutrients. We found a negative relation between salinity and ammonia ($r= -0.37$; $p=0.05$), which is expected since ammonium is often related to a regenerated production, specifically of the direct exchange between phytoplankton and HB.

Riverine inputs can reduce salinity and bring POC to the coast. However, according to Vital et

al. (2010), river discharges are insignificant in the study area, since nearby rivers are small and do not contribute to significant amounts of organic matter. We believe that this hypothesis requires further investigation, especially considering the effects of the tide because freshwater entrance into the coastal region can be intensified during the ebb tide.

Rainfall influence was predominantly weak on picoplankton, but it may represent simultaneous impacts with indirect effects. The impacts of rainfall are significant in the upper layers (the top 5 m) of the water column (Li et al., 1998). For example, rainfall can favor increased POC by organic matter entrance into the coast from rivers and continental sources. In addition, it reduces available radiation through cloud cover. In this sense, positive correlations between Peuk and Chla with POC and TDS reflect that eukaryotic phytoplankton may constitute a significant portion of this organic matter in higher turbulence and suspended particles during rainy seasons (Figure. 6). Water transparency decreased shortly during rainy seasons when higher POC and Chla concentrations were recorded, preventing solar radiation from reaching the ocean floor. Ruiz-González et al. (2012) and Durand et al. (2001) argue that POC configures as a good predictor of phytoplankton carbon and demonstrate that eukaryotic components of phytoplankton seem to be more strongly related to POC than to prokaryotic ones.

Coastward intrusions bringing cold and nutrient-rich waters have never been reported for this region (Castro et al., 2005). However, this may occur if dispersion is efficient enough to transport nutrients in a cross-equatorial gradient. Strong winds prevail almost the whole year-round in NE Brazil, mixing nearby water masses (Vital et al., 2010). Wind-induced transport of surface waters controlled by seasonal displacement of ITCZ (Castellanos et al., 2015) may transport surface water masses westward on a meridional scale across the Atlantic and mix adjacent ones (i.e. South Atlantic Central Waters with Tropical or Coastal Waters) in shallow coastal regions. Furthermore, Barth and Hauila (1968) reported

topographically-induced small-scale upwelling events which can enhance primary and secondary production at the surface divergent zones between 5°S and 7°S.

Such hydrodynamic mechanisms are likely weak nutrient sources for picoplankton in this coastal region. The provision of allochthonous nutrients can eventually support new plankton production. Nitrate revealed peaks during most rainy seasons (June and August 2014, 2015, and 2016), and eventual high concentrations were recorded for other N forms, which would be linked to other processes mentioned above. N concentrations are typically low in oligotrophic oceans (ammonia < 0.5 µM; nitrite = 0.1 µM; nitrate = 0.2 µM), while according to Sharper (1983), most coastal waters present higher values (ammonia = 25 µM, nitrite = 2 µM; nitrate = 30 µM). Mean concentrations recorded here (ammonia = 1.72 µM, nitrite = 0.07 µM, nitrate = 1.22 µM) were predominantly close to inferior limits of coastal amplitude. Thus, as nutrient concentration variability was independent of seasonal influences, the mechanisms responsible for these eventual increases of nutrients are still unclear, but can be linked to biological supply and assimilation, meaning by picoplankton in such case.

Despite eventual nutrient supplies, we are led to believe that autotrophic picoplankton exudates predominantly supply secondary bacterial production. Stronger couplings between bacterial and phytoplankton production (BP: PP) are expected under nutrient limitation conditions (Shiah et al., 2001). The link between HB and photosynthetic picoplankton occurs through feedback interaction mechanisms based on the exchange of organic and inorganic compounds (Mague et al., 1980; Karl et al., 1998). This interaction may configure significant energy sources for both in certain conditions. It suggests that the microbial loop may profoundly contribute to energy flow in aquatic food webs in these oligotrophic coastal waters. Although we found weak positive relations between components of picoplankton here, we highlight the need for new studies to describe these relationships better in an underexploited area in plankton research. In addition, it is necessary to evaluate the effects of

interactions with other components of plankton, such as virioplankton and microzooplankton. The predation by protists (heterotrophic nano flagellates and ciliates) and virus infection can reduce the abundance of the entire picoplankton community (Sherr and Sherr, 1994; Brunn et al., 2015). We only evaluated the environmental effects herein, which are complex and poorly explained picoplankton distribution.

Finally, increased picoplankton importance towards the equator (in warmer conditions) has been discussed when faced with current climate change (Morán et al. 2010; Sarmiento et al. 2010; Sathicq et al. 2020) and our data provide evidence of these assumptions. Future projections suggest SST increase and rainfall reduction (Marengo et al. 2016), and the expected increased picoplankton importance in these conditions lead us to believe that the future climatic scenarios could promote a gradual shift towards smaller primary producers and reduction in BGE, which in turn would have profound implications for marine biogeochemistry and carbon sequestration in the deep ocean (Litchman et al. 2015). The implications of picoplankton dominance would be great in the sense of weakening the energy flow by adding new trophic levels to aquatic food chains, which reduces the efficiency of energy transfer to higher trophic levels (Sarmiento 2012), and these trophic interactions may be decisive in driving picoplankton dynamics in tropical regions since weak environmental relationships were pointed out here.

CONCLUSION

Although there is a clear environmental seasonality in the study area (predominantly related to rainfall dynamics), this seasonality as well as other environmental factors evaluated in this study were not good predictors of the temporal variability found in picoplankton abundance and activity in this western Atlantic coastal station. Our results confirmed that picoplankton in equatorial regions might show great temporal stability on a seasonal scale. However, it can vary significantly over major time scales influenced by broader climatic factors such as El Niño Southern Oscillation. These

inter-annual influences can be decisive in favoring picoplankton, even in environments where nano-micropikton would prevail, as in coastal regions. We found that HB may significantly contribute to the total picoplankton biomass in the tropics. Also, HB influences a possible net heterotrophy in carbon cycling even in a coastal environment, where high efficiency in productivity (BP>BR) is expected. Faced with these results, we have shown the importance of picoplankton to carbon cycling in tropical oceans and highlight the need for more studies in this central portion of the planet, especially given the increasing importance of these microbes for maintaining the global climate and the marine trophic chain in a scenario of global warming.

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AUTHOR CONTRIBUTIONS

M.M.: Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing - original draft.

P.J.: Visualization; Formal analysis; Writing - review & editing.

V.S.K.: Methodology; Writing - review & editing.

B.W.: Data curation; Methodology; Writing - review & editing.

A.S.C.; R.P.: Methodology; Writing - review & editing.

F.U.; A.M.A.: Validation; Writing - review & editing.

H.S.: Conceptualization; Funding acquisition; investigation; Methodology; Project Administration; Supervision; Writing - review & editing.

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