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Distribution of nutrients and chlorophyll across an equatorial reef region: Insights on coastal gradients

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ABSTRACT

We evaluate how the concentrations of inorganic nutrients and chlorophyll *a* vary in a heterogeneous area (Equatorial SW Atlantic), covering a gradient from stations closer to the coast to others more distant associated or not with turbid-zone reefs. Vertical temperature (27.9 ± 0.10 °C; mean ± standard deviation) and salinity (36.2 ± 0.14) profiles showed that the water column is well mixed (0-30 m depth). The oligotrophic condition was marked by low concentrations of phosphate (0.30 ± 0.22 µM) and dissolved inorganic nitrogen (0.64 ± 0.74 µM). Moreover, dissolved reactive silicon (DSi) was low in most samples (< 2.0 µM), but higher (>10 µM) in nearshore stations, probably related to continental runoff and/or resuspension of the bottom sediments. The pelagic phytoplankton biomass indicated that chlorophyll *a* (0.25 ± 0.08 µg L^{-1}) was low, positively correlated with light and negatively correlated with nutrients, indicating possible phytoplankton uptake. Chlorophyll *a* concentrations were lower in stations closer to the coast and higher in some stations near the reefs, indicating that the latter could be more prone to phytoplankton development and depletion of nutrients, especially DSi. Therefore, although oligotrophy is present along this coast, we found some unexpected heterogeneity of nutrient and chlorophyll *a* distributions, which were probably influenced by benthic-pelagic coupling due to the presence of extensive reefs, sponge gardens (18-30 m depth), and the proximity to the coast. These results highlight the importance of understanding the heterogeneity of ocean productivity, especially in lesser known low-latitude areas, which showed distinct nutrient and chlorophyll *a* levels related to the occurrence of tropical reefs that are capable of supporting important fish stocks and unique biological communities.

Descriptors: Oligotrophic seas, Nitrogen, Phosphorus, Chlorophyll, Coral reef.

INTRODUCTION

Coastal regions represent only 10 % of the ocean area but are responsible for at least 25 % of the ocean's primary productivity (Walsh, 1988). Nevertheless, the annual productivity of continental shelves shows remarkable differences worldwide (Gasol et al., 2016; Kudryavtseva et al., 2019) related to the absence or presence of large rivers, continental runoff, depth, vortices, upwelling, and ocean currents that bring nutrients to coastal areas (Simpson and Sharples, 2012;

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Mantellato et al., 2020). Within the shelf region, primary production drives ecosystem production and plays a fundamental role in carbon cycling and budgets (Hofmann et al., 2008). Despite its importance, the coastal pelagic productivity of nutrient-poor arid and semi-arid regions, as in the Equatorial Southwestern Atlantic, is poorly understood in some areas that harbor important tropical reefs and rhodolith beds (Soares et al., 2017, 2019; Costa et al., 2020). These seascapes can influence local productivity and support unique hotspots in oligotrophic areas (Costa et al., 2020; Mantellato et al., 2020). In this regard, it has been observed that the main drivers of the coastal reefs worldwide are nutrients and organic matter supplied by fishes, microorganisms, and sponges (Meyer and Schultz, 1985; Maldonado et al., 2012; Shantz et al., 2015).

The semi-arid coast of the Equatorial Southwestern Atlantic is characterized by low river discharges, absence of upwelling, occurrence of intense trade winds and waves, and low intra- and interannual variation in the sea surface temperature (SST) due to its proximity to the Earth's equator (> 26 °C and variation of less than 4 °C) (Diniz and Oliveira, 2016; Teixeira and Machado, 2013). In this sense, the low intra-annual and inter-annual variations in SST suggests that the stress-tolerant corals here may be acclimatized to these stable environmental conditions (Soares et al., 2019). Indeed, the unique shallow-water reefs of the SW Atlantic have thrived in conditions considered suboptimal for coral (e.g., moderate turbidity and resuspension of sediments) under the optics of classical coral reefs (e.g., Caribbean Sea and Great Barrier Reef) (Burt et al., 2020; Mies et al., 2020). In the low-latitude reef area, stress-tolerant and weedy corals such as *Siderastrea stellata*, *Montastraea cavernosa* and *Mussismilia hispida* (Soares et al., 2019), filamentous algae, and sponges are the main components of the reef assemblages. Other benthic reef fauna (e.g., ascidians) showed lower coverage (< 10%), although their importance may vary depending on the area (Soares et al., 2017).

Some field studies on the productivity of this tropical coast reported the oligotrophic conditions of the region (Knoppers et al., 1999; Souza et al., 2013; Jales et al., 2015; Carvalho et al., 2017; Araujo et al., 2019). Nevertheless, the presence of reef formations in oligotrophic seas is a particularly important source of nonuniformity within the coastal biome (Van Duyl et al., 2002; Longhurst, 2007; Racault et al., 2015; Cotovicz et al., 2020). For example, several studies in oligotrophic waters have reported an increase in primary phytoplankton productivity around islands and reef formations (Elliott et al., 2012; Jales et al. 2015; Vollbrecht et al., 2021). Given the importance of turbid-zone reefs in oligotrophic oceans to ecosystem trophic structure and fisheries (Vollbrecht et al., 2021), here we studied a coastal area in the Equatorial Southwestern Atlantic to evaluate the spatial distribution of the phytoplankton biomass and inorganic nutrients. Knowledge of the productivity and nutrient concentrations in this low-latitude region is pivotal for understanding the characteristics of this environment and will also provide useful and important insights about the benthic-pelagic coupling along equatorial coasts, which can be useful for marine spatial planning and decision making by stakeholders.

METHODS

Study area

The study area is located in the distinctive and underexplored Brazilian semi-arid coast (BSC) (from almost 2 to 5° S) (Diniz and Oliveira, 2016), in the Tropical Southwestern Atlantic marine province (*sensu* Spalding et al., 2007) (Figure 1). This semi-arid region presents diverse coastal habitats, such as shallow-water and mesophotic reefs, rhodolith and seagrass beds, intertidal beach rocks, sandy beaches, and submerged dunes (Ekau and Knoppers, 1999; Costa et al., 2020; Soares et al., 2017, 2021). In this study, water sampling was concentrated within and around an area of fourteen tropical reefs at Pedra da Risca do Meio Marine State Park (whose acronym in Portuguese is PEMPRIM). PEMPRIM is a marine protected area (MPA) rich in biodiversity and endemism that covers a rectangular area of 33.2 km^2, approximately 18 km off the coast of Fortaleza city,Ceará State's capital (Soares et al., 2017, 2019; Freitas et al., 2019) (Figures 1 and 2).

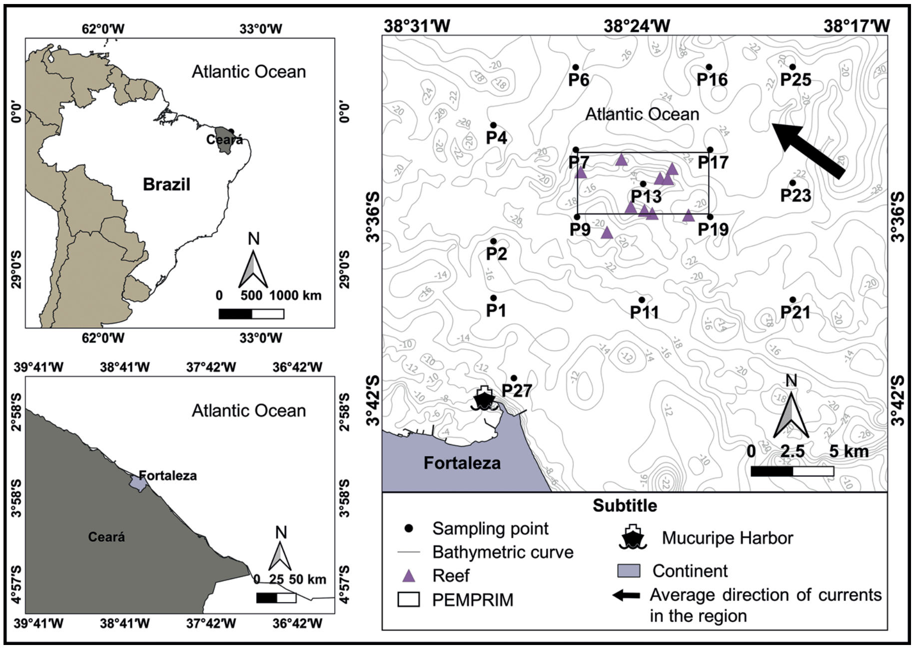

Figure 1. Study area off the Equatorial Southwestern Atlantic coast (Ceará State, Brazil). The marine protected area (PEMPRIM) with tropical coral reefs (18-30m depth) is indicated by the rectangle with corresponding stations (P7, P9, P13, P17, and P19).

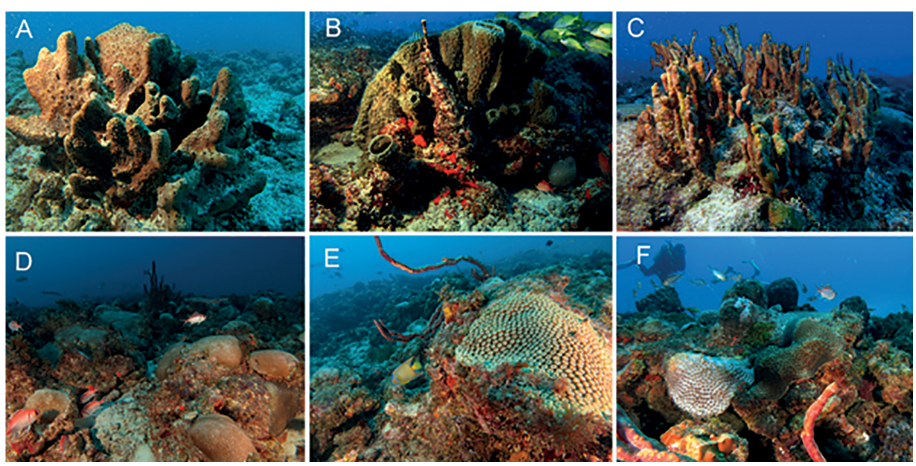

Figure 2. Subaquatic photographs displaying the reefs that inhabit this low-latitude area (SW Atlantic, Brazil). Reef seascapes showing sponge gardens (A, B and C). Dominance of stress-tolerant corals (D, E and F) such as *Siderastrea stellata* (D) and *Montastraea cavernosa* (E and F) atop reefs.

We evaluated a mixed carbonate-siliciclastic continental shelf region of ~50 km width that is characterized by strong winds (especially from July to December), sediment resuspension, and a mesotidal regime. The cross-shelf geomorphology creates a natural gradient comprising an inner (< 20 m depth), a middle (20-40 m), and an outer shelf (> 40 m to the shelf break, ~ 60-70 m depth) (Morais et al., 2019). This morphological configuration means that most of the continental shelf is in shallow waters (< 40 m depth). A distinctive feature in this region is a warm, fast-flowing coastal current generated by the intense trade winds that flows mostly westward (Dias et al., 2013; Dias et al., 2018; Teixeira and Machado, 2013). The sea surface temperature remains within a range of

26.5-30 °C, with small intra- and interannual variation (Teixeira and Machado, 2013; Soares et al., 2019).

Although annual rainfall in the Brazilian semi-arid coast may be more than 1,000 mm, in areas of the continent far from the coast it is less than 500 mm (Moura et al., 2007), which leads to low river discharges and continental runoff (Dias et al., 2013). The Intertropical Convergence Zone (ITCZ) is considered the most important mechanism in determining the abundance and scarcity of rainfall in the Northeast region (Ferreira and Mello, 2005).

Water sampling and analysis

Water samples were taken from fifteen different stations, comprising five stations within the MPA and ten stations in the surrounding area (Figure 1). The sampling depths within and around the MPA ranged from 16.5 to 29 m, with the shallowest stations (P1 and P27) closest to the coast (Figure 1). A Van Dorn bottle was utilized to collect samples at the subsurface (15 cm below the water surface) and at approximately the middle of the water column (from 8 to 13 m). Oceanographic campaigns occurred at the onset of the dry season (July 2019) on board the Ship Argo Equatorial covering an area of nearly 400 km^2 in a 25 km transect from the station closest to the coast to the most distant. The sampling was conducted only during this period due to logistical limitations (distance from the coast, intense wind speed, and navigation difficulties in other periods). In addition, this oceanographic field sampling was complemented with the use of remote sensing to conduct a longer temporal and spatial analysis (2003-2019). These remote sensing data helped to identify if the water sampling in the dry period is representative of much of the year.

Salinity and temperature were measured *in situ* using a Sontek CastAway CTD. Water transparency was estimated using a Secchi disk, and the depth of the euphotic zone (Zeu) was estimated as 2.7 times the Secchi depth (Cole, 1983). Detailed information on the location of the stations is presented in Table S1 (Supplementary Material). Samples for dissolved nutrient analysis were filtered immediately after collection, whilst still on board. After filtering, the samples were maintained at 4 °C until arrival at the laboratory later the same day. In the laboratory, the samples were stored at −20 °C until analysis. Freezing (to -20 °C) is the recommended method if nutrient samples have to be stored for several days or weeks (Kremling & Briigmann, 1999; Strickland & Parsons, 1972).

Aliquots (1,000 mL) of the water samples were filtered through 0.7-µm-pore size glass-fiber filters (47-mm diameter, type GF-1; Macherey-Nagel, Düren, Germany) for nitrate ($N\text{-}NO_3^-$) plus nitrite ($N\text{-}NO_2^-$), N-ammoniacal ($N\text{-}NH_3$ + $N\text{-}NH_4^+$), and phosphate ($P\text{-}PO_4^{3-}$). Further aliquots (300 mL) of the water samples were filtered through a 0.45-µm pore-size mixed cellulose ester membrane (47 mm diameter, HATF; Millipore, Billerica, MA, USA) for dissolved reactive silicon (DSi). $N\text{-}NO_3^-$, $N\text{-}NO_2^-$, $P\text{-}PO_4^{3-}$ and Si were analyzed according to the protocol of Aminot and Chaussepied (1983) as described in Baumgarten et al. (1996). For N-ammoniacal, we followed the protocol suggested by Strickland and Parsons (1972), as described in Baumgarten et al. (1996). Dissolved inorganic nitrogen (DIN) concentrations were calculated as the sum of $N\text{-}NO_3^-$, $N\text{-}NO_2^-$ and N-ammoniacal. All laboratory analyses were performed in triplicate, with detection limits of 0.05 µM, 0.10 µM, 0.06 µM, and 0.14 µM for $P\text{-}PO_4^{3-}$, $N\text{-}NO_3^-$ plus $N\text{-}NO_2^-$, N-ammoniacal and DSi, respectively.

For chlorophyll *a* quantification, aliquots (5,000 mL) of the water samples were filtered through 0.7-µm-pore size glass-fiber filters (47-mm diameter, type GF-1; Macherey-Nagel) by vacuum pressure of ≤ 5 inches Hg to prevent the disruption of the cells and under low light to avoid degradation of photosynthetic pigments. The particulate materials retained on the filters were frozen at −20 °C for subsequent spectrophotometric determination of chlorophyll *a* using extraction in 90 % acetone under low light, according to the methodology described by Jeffrey and Humphrey (1975).

Satellite chlorophyll *a* concentrations were obtained from the Giovanni NASA platform (https://giovanni.gsfc.nasa.gov/giovanni/) and used to determine the time series of long-term space and monthly averages and standard deviation for the sampling equatorial area. We used 8-day chlorophyll concentration values from the MODIS Aqua sensor with a 4 x 4 km spatial resolution covering the period from 2003 to 2019. In order to summarize and note trends in the variance of nutrients and chlorophyll *a* in the study area (Equatorial SW Atlantic, Brazil), a principal component analysis (PCA) was performed using PAST v. 2.12 (Hammer et al., 2001). Firstly, normality was evaluated using the Shapiro-Wilk test, which displayed that only chlorophyll had normally distributed values. Thus, variables were standardized using log (x+1) to linearize the relationship between them, as required for PCA.

RESULTS

Most samples were taken above or just below the maximum limit of the euphotic zone, which ranged from 8.4 to 14.3 m as estimated from the Secchi depth (Table S1). The vertical profiles of temperature (Figure 3) and salinity were homogeneous (Figure 4). Considering the subsurface and middle water column values at all stations (n = 30 samples), the overall mean temperature and salinity values were 27.9 ± 0.10 °C and 36.2 ± 0.14, respectively (Table 1).

The concentrations of chlorophyll *a* ranged from 0.12 to 0.42 µg L^{-1}, DSi from non-detectable to 23.12 µM, P-PO_4^{3-} from non-detectable to 0.66 µM and DIN from non-detectable to 3.11 µM (Table 1, Figure 5). The DIN:PO_4^{3-} ratios were always lower than 5:1, except by P16 on the surface (16:1), where the highest DIN concentration was found (16:1) (Table S1). In turn, the chlorophyll *a* values from Modis Aqua satellite data for this region exhibited small inter- and intra-annual variability with an average value of approximately 0.3 µg L^{-1} (Figure 6). The monthly climatological standard deviations for chlorophyll *a* were also small, usually less than 0.1 µg L^{-1}, except for March when the standard deviation exceeded 0.2 µg L^{-1} (Figure 6). Based on the Modis Aqua data we also see a small spatial variability within the area (Figure S1), with values ranging from 0.2 to 0.6 µg L^{-1} towards deeper regions. Here it is important to mention that the values larger than 1 µg L^{-1}, observed close to the coast, can be noisy values due to shallow water effects in ocean color satellite products, such as chlorophyll (paper submitted).

Although the concentrations of all inorganic nutrients were highly patchy among stations and depths, it is possible to note that the reef area displayed a distinct pattern especially for DSi and Chlorophyll *a* (Figure 5). The highest DSi concentrations were found in the stations closest to the coast (P1 and P27), while the lowest levels were found in the reef zone (MPA area), beyond P2 and P21 (Figures 5C and 5D). The DSi:DIN ratios were generally higher than 1:1, but were lower in some samples from the reef zone, beyond P16 and P21. The highest

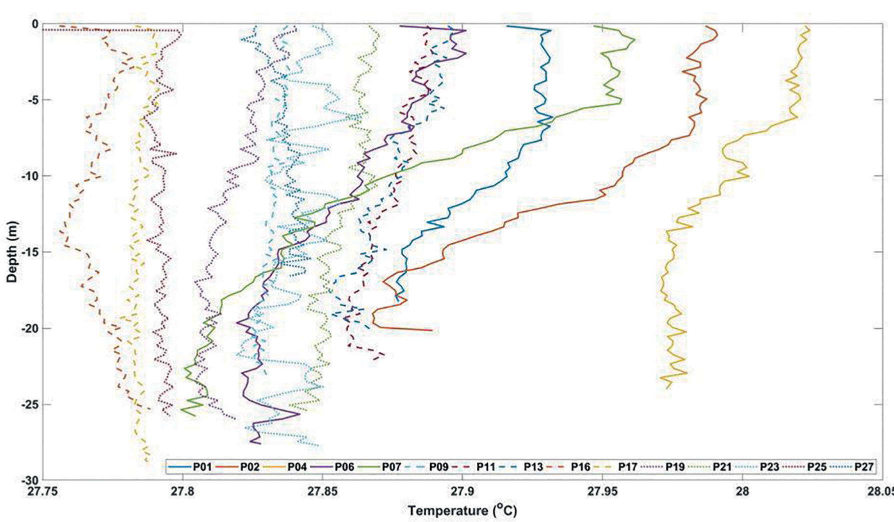

Figure 3. Vertical temperature profiles at sampling stations off the Equatorial Southwestern Atlantic coast (Brazil) showing negligible variation (< 0.1) with depth (0-30 m deep).

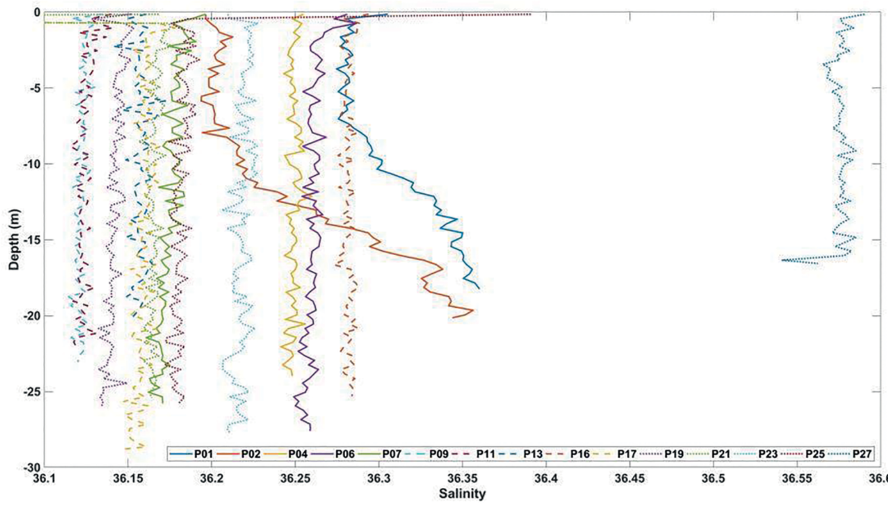

Figure 4. Vertical salinity profiles at sampling stations off the Equatorial Southwestern Atlantic coast (Brazil) showing a homogeneous distribution throughout the water column (0-30 m deep).

Table 1. Minimum, maximum, and mean ± standard deviation values of variables in a tropical reef area in the Equatorial Southwestern Atlantic (Ceará State, Brazil) [DSi: Dissolved reactive silicon; DIN: Dissolved inorganic nitrogen].

Variables	jul/19						
	Surface			Middle			Overall
	Mean	Min	Max	Mean	Min	Max	Mean
Temperature (°C)	27.85 ± 0.13	27.45	28.0	27.85 ± 0.06	27.76	27.97	27.85 ± 0.10
Secchi (m)	4.31 ± 0.84	3.1	5.6	-	-	-	-
Salinity	36.2 ± 0.16	35.8	36.6	36.2 ± 0.11	36.1	36.6	36.2 ± 0.14
Euphotic zone (m)	-	-	-	11.65 ± 2.28	8.4	15.1	-
Maximum depth (m)	-	-	-	23.7 ± 3.6	16.5	28.8	-
P-PO_4^{3-} (μM)	0.24 ± 0.18	≤ 0.05	0.56	0.37 ± 0.25	≤ 0.05	0.66	0.30 ± 0.22
DSi (μM)	4.2 ± 7.4	≤0.14	23.12	4.01 ± 5.25	0.26	14.07	4.11 ± 6.31
DIN (μM)	0.63 ± 0.76	≤ 0.10	3.11	0.64 ± 0.74	≤ 0.10	2.24	0.64 ± 0.74
Chlorophyll *a* (μg L^{-1})	0.22 ± 0.08	0.12	0.37	0.27 ± 0.08	0.15	0.42	0.25 ± 0.08

DSi:DIN (> 5:1) ratios were found in stations closest to the coast (P1 and P27) (Table S1).

A PCA was performed to summarize the general spatial variation in the data set. The first four principal components captured 79.5% of the variance, successfully representing the variability of our data. The first two PCA axes explained 48.8 % of the variation in environmental variables and chlorophyll *a* (Figure 7). PCA axis 1 showed an inverse correlation between chlorophyll *a* and DIN and DSi, which were positioned on opposite sides of this axis. In PCA axis 1, we also observed that chlorophyll *a* was positively influenced by light availability (using Secchi depth and euphotic zone as proxies) and temperature, while being negatively influenced by salinity.

Most samples from the middle water column layer were positioned on the positive side of PCA axis 2, and were related to higher phosphate values. PCA loadings and eigenvalues are presented in Tables S4 and S5.

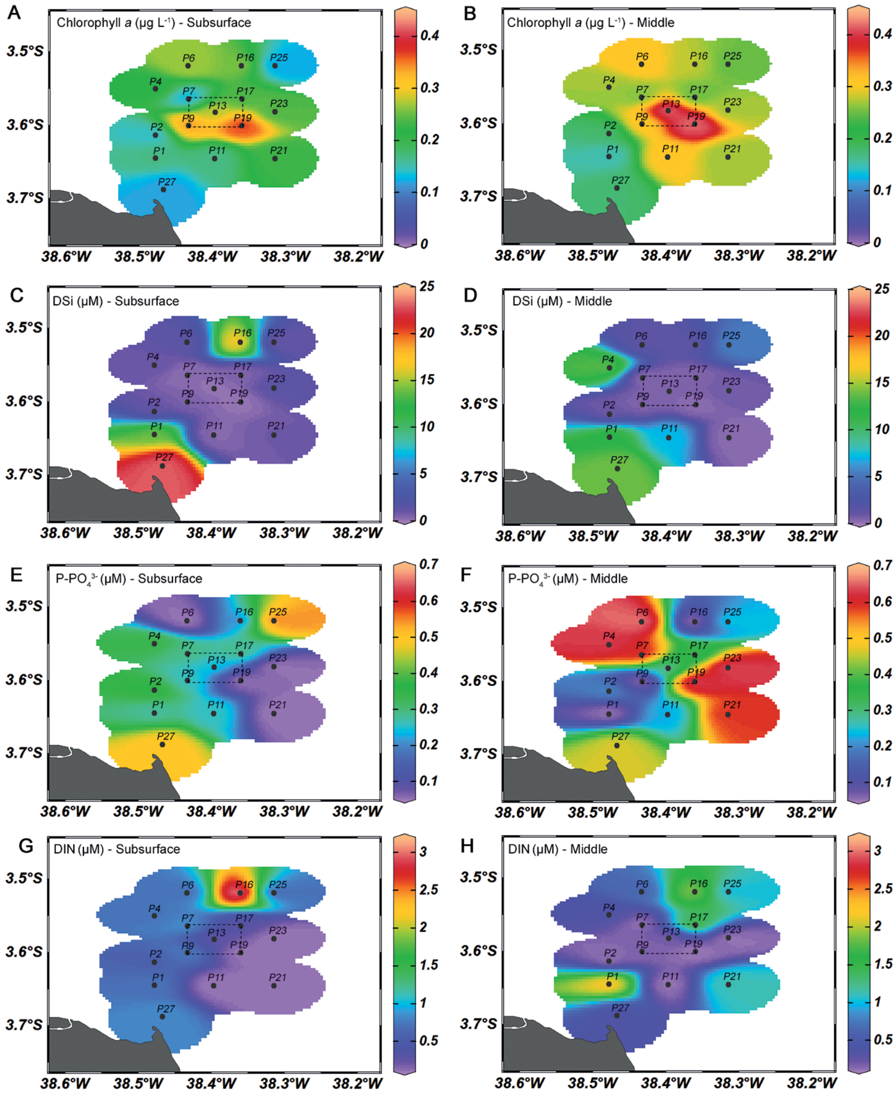

Figure 5. Chlorophyll a and nutrient concentrations in subsurface (left) and middle water (right) samples from the Equatorial Southwestern Atlantic coast (Brazil): (A) and (B) Chlorophyll a; (C) and (D) dissolved reactive silicon (DSi), (E) and (F) phosphate and (G) and (H) dissolved inorganic nitrogen (DIN). The marine protected area (PEMPRIM) with extensive reefs and sponge gardens is indicated by the dotted rectangle at each figure center with corresponding stations (P7, P9, P13, P17, and P19).

DISCUSSION

Our results showed the local wind speed and strong marine currents prevented water column stratification, as evident from the homogeneous vertical profiles of temperature and salinity. Temperature and salinity values were within the ranges reported for equatorial marine well-mixed waters (Souza et al., 2013). Also, the concentrations of chlorophyll *a*, DSi, P-PO_4^{3-} and DIN were within the ranges previously found in the tropical southwestern Atlantic, including the Brazilian semi-arid coast (chlorophyll *a* 0.01-0.63 µg L^{-1}, DSi 0.07-70.0 µM, P-PO_4^{3-} 0.001-0.92 µM, DIN 0.05-3.2 µM; Carvalho et al., 2017; Araujo et al., 2019) (Table S2).

Nevertheless, the distinct pattern especially for DSi and Chlorophyll *a* in reef area suggests an unexpected increase in the biological uptake of DSi in the equatorial reef zone. Traditionally, a decrease in DSi levels in the water column has been associated with increased growth in diatom

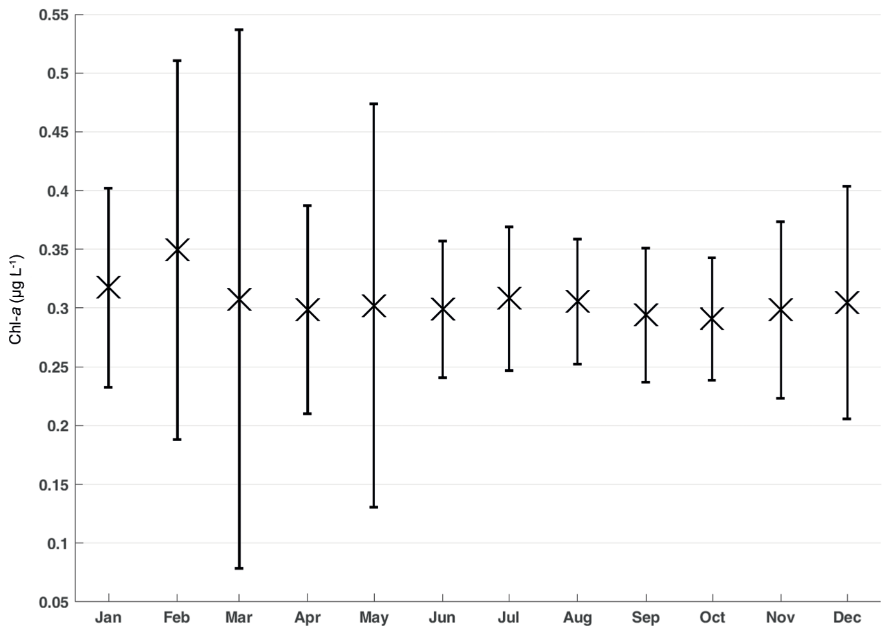

Figure 6. Climatological monthly averages and standard deviations (vertical bars) for chlorophyll *a* concentration based on MODIS Aqua data from 2003 to 2019 in a tropical coral reef region in the Equatorial Southwestern Atlantic (Ceará State, Brazil).

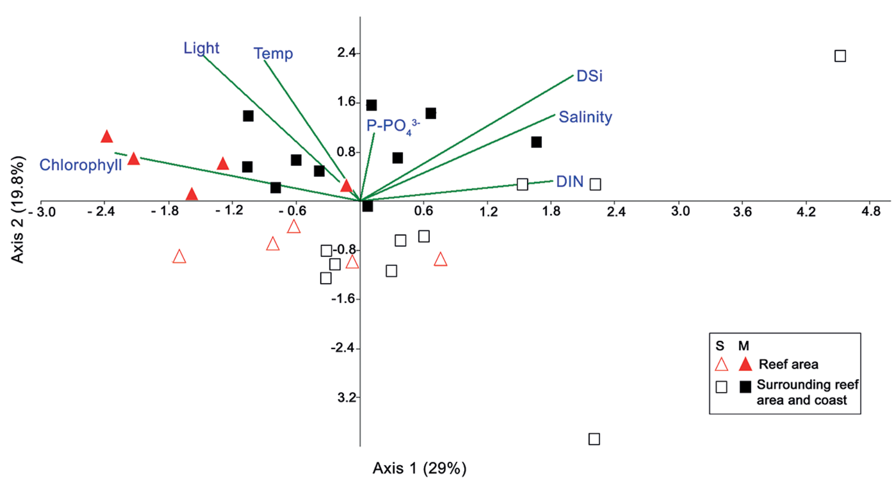

Figure 7. Principal component analysis of environmental variables and chlorophyll a in the Equatorial Southwestern Atlantic (Ceará State, Brazil). Triangle symbols indicate stations within the PEMPRIM marine protected area with tropical reefs (red color). Secchi depth (subsurface) and euphotic zone depth (middle water) were used as proxies for light availability. S: subsurface and M: middle.

populations (cell divisions) (Maldonado et al., 2012), which was suggested by the inverse correlation between chlorophyll *a* and DSi (see PCA). In this same study area, Bezerra (2021) evaluated the composition and biomass of phytoplankton by the HPLC-CHEMTAX method and found that, in the reef area, while the mean relative abundance of diatoms ranged from 30 to 55%, the picocyanobacteria (*Prochlorococcus* and *Synechococcus*) ranged from 18 to 27% (averages for subsurface and middle water column layer). These results are contrasting with those expected for an oligotrophic region, in which the phytoplankton assemblage likely would be dominated by picocyanobacteria

(Charpy et al., 2012; Farias et al., 2022). Taking into account the benthic-pelagic coupling, organic nutrients released by sessile suspension feeders (e.g., sponges) may also be contributing to sustain primary production in tropical reefs (Cochlan et al., 2008; Wawrik et al. 2009; Ferrier-Pagès et al., 2012; Maldonado et al., 2012; Morando & Capone, 2018), and should be further investigated.

In this regard, large sponges are present in high abundance and dominance (~25% of benthic cover) in this shallow-reef area (Soares et al. 2017, 2019) (Figures 2A to 2C), and may also play a significant role in the decrease of DSi in this area. However, this hypothesis needs further study. Sponges are benthic suspension feeders that play an important role in the global ocean Si cycle and in benthic-pelagic coupling, as siliceous sponges require silica for their growth and might also act as a significant silica sink, at least regionally (Maldonado et al., 2011; Maldonado et al., 2012; Tréguer and De La Rocha, 2013). Alternatively, the higher DSi levels in nearshore stations could be attributed to greater continental runoff or sediment resuspension due to waves and trade winds (Braga et al., 2018), in addition to the lower biological uptake suggested by the lower chlorophyll *a* at stations P27, P02, and P01 (Figures 5A and 5B).

The *in situ* chlorophyll *a* values are close to the climatological values found using the Modis Aqua satellite data for this region, corroborating the field oceanographic sampling throughout the low-latitude area. Thus, water sampling in the dry period can be representative of much of the year. Nevertheless, a higher standard deviation for March in satellite data is associated with the rainy season that occurs in this region from February to May and concentrates 70 % of the annual local precipitation (Sakamoto et al., 2015).

PCA results showed an inverse correlation between chlorophyll *a* and DIN, in addition to DSi, suggesting a higher phytoplankton uptake (Furnas et al. 2005), especially in some stations located above the tropical reef area (MPA). In turn, the observed inverse correlation of chlorophyll *a* with salinity was probably due to lower concentrations of chlorophyll *a* in stations closer to the coast, instead of a salinity effect *per se*.

In this context, the decrease of DIN and mainly of DSi in the reef area could be related to the intensification of pelagic-benthic coupling processes in low-latitude reefs, which may create niches that favor a higher inorganic nutrient uptake by the phytoplankton (Furnas et al., 2005). Additionally, nutrient sources from sediments and/or other organic compounds from reef habitats may be playing an important role in the enhancement of phytoplankton growth (Meyer and Schultz, 1985; Wild et al., 2008; Alongi et al., 2015, Racault et al., 2015; Shantz et al., 2015), and further investigations are required to shed light on these potential mechanisms to explain the higher phytoplankton growth in equatorial reef areas.

Also, according to PCA most samples from the middle water column layer were characterized by higher phosphate values, which suggests that the remineralization in the bottom layers could be a phosphate source for this pelagic environment in the reef area. In turn, closer to the coast, continental phosphate contributions would act as phosphate sources (Araujo et al., 2019). Particularly, in the area under the influence of turbid-zone reefs, due to the distance from the coast, remineralization is probably the main source of nutrients. In fact, there is an estimate that in reef areas, benthic organisms release 10-50% of their gross organic production as mucus, which stimulates the heterotrophic microbial metabolism in the water column and consequently the regeneration of inorganic nutrients (Silveira et al., 2017). Although benthic exudates are rich in carbon and mostly devoid of nitrogen and phosphorus (Naumann et al., 2010; Silveira et al., 2017), studies have shown that not only the growth of heterotrophic bacteria is stimulated in the case of coral exudates, but also the phytoplankton (Ferrier-Pagès et al., 2000).

The apparent phosphate accumulation at some stations in the middle layer, while DSi and DIN were inversely correlated with chlorophyll *a*, suggests a greater demand for these two nutrients. A previous study in the Tropical Southwestern Atlantic showed a similar tendency of higher phosphate in relation to DIN and silicate (Araujo et al., 2019). The DIN:PO_4^{3-} ratios on the Brazilian Northeast coast were lower than 10:1, indicating a nitrogen limitation for primary production in the area, and a greater removal of DIN and silicate, in relation to phosphate (Araujo et al., 2019). Similarly, in our area, the DIN:PO_4^{3-} ratios were generally lower than 5:1, suggesting that phytoplankton is limited by nitrogen. In turn, the DSi:DIN ratios were generally higher than 1:1, indicating DSi availability for diatoms, especially in stations closest to the coast due to continental influence on coastal waters (Sospedra et al., 2018). On the other hand, in some stations from the reef zone, the DSi:DIN ratios were below the Redfield molar ratios, probably because of higher diatom growth (Bezerra, 2021) that led to the decrease in DSi concentrations in the water. The Si:N:P atomic ratio of marine diatoms is about 16:16:1 under optimal nutrient conditions (Redfield, 1963, Brzezinski, 1985). Considering that the deviation of the Redfield ratio in water indicates a limiting potential of N, P or Si for phytoplankton growth, in our area the main limiting nutrient is probably the nitrogen.

A distinctive feature of the South Atlantic reefs would be a high concentration of nutrients (Table S3), which is different from the low levels found in the Caribbean and Australian reefs (Mies et al., 2020). However, in this study, we found low levels of nutrients (inorganic nitrogen) (Table 1) compared to other studies on Brazilian coral reefs (Mies et al., 2020). Most of the reefs analyzed by Mies et al. (2020) were located off the coast of Pernambuco and Bahia (other Northeast states), which are under the effect of large rivers with high quantities of nutrients (Costa et al., 2000, 2008). This contrasts with the short and low-inflow estuaries of the semi-arid equatorial region, where our study was performed, which can act more as importers than exporters of nutrients (Dias et al., 2013, 2018).

Due to the semi-arid climate, dams and frequent droughts, the exportation (e.g., nutrients and organic matter) of the estuaries to the inner continental shelf is greatly reduced during most of the year (Dias et al., 2013, 2018). Moreover, a combination of factors, such as the absence of upwelling in the Brazilian semi-arid coast (Teixeira and Machado, 2013) and a permanent thermocline in the oceanic area, which prevents water column mixing (Lalli and Parsons, 1997), contribute to the oligotrophy in the studied coastal area (Teixeira and Machado, 2013).

Finally, the equatorial reef areas analyzed herein are located at depths varying between 18-30 m, much deeper and farther offshore than most documented reef studies along the Brazilian coast (Mies et al., 2020). This shows that the tropical reefs of the South Atlantic have high heterogeneity with respect to nutrient levels.

CONCLUSION

Our results show an unexpected heterogeneous spatial distribution of the phytoplankton biomass and inorganic nutrients in an equatorial coastal area, probably influenced by benthic–pelagic coupling due to the presence of extensive reefs and sponge gardens. Low-Latitude reefs were an area more prone to phytoplankton development and nutrient depletion, mainly DSi. Although some previous studies have addressed these variables (Souza et al, 2013; Carvalho et al., 2017; Araujo et al., 2019), there is still a need to maximize the spatial and inter-annual sampling resolution in Equatorial SW Atlantic, including vertical depth sampling, in areas around reefs, which are known to be rich in biodiversity and endemism (Soares et al., 2017, 2019). Furthermore, this work represents an unprecedented baseline record for the reefs along the semi-arid coast and should support further studies to determine the temporal variation of nutrients and chlorophyll *a* along the low-latitude ecosystems, one of the least known tropical habitats of the world.

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AUTHOR CONTRIBUTIONS

H.S.B.: Conceptualization; Investigation; Writing – original draft; Writing – review & editing;

I.O.L., A.D.A.B., R.S.A., E.F.S.J., C.E.P.T.: Methodology; Formal Analysis; Investigation; Writing – review & editing;

T.M.G., T.C.L.T.: Writing – review & editing;

M.B.V.: Supervision; Resources; Writing – review & editing.

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