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Influence of abiotic factors on phytoplankton diversity and distribution in an atoll environment

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ABSTRACT

Taxonomic investigations of phytoplankton community structure are very important for understanding the dynamics of these organisms in places like reefs, which present broad hydro-biological variation. This study aimed to determine and investigate phytoplankton community composition and biomass in natural pools of Atol das Rocas (3°51' S; 33°49' W), and to evaluate the possible influences of abiotic variables throughout different seasons. The oceanographic parameters used to assess the phytoplankton community and its biomass were chlorophyll *a*, salinity, water temperature, dissolved oxygen and dissolved inorganic nutrient content, namely ammonia, nitrate, nitrite, phosphate and silica. A total of 109 species were identified, distributed among four groups: Ochrophyta (52.3 %), Dinophyta (37.6 %), Cyanobacteria (7.33 %) and Haptophyta (2.75 %). Although none of the hydrological parameters were found to be statistically determinant, phytoplankton composition in all the studied pools was primarily associated with nutrient salts and there was a qualitative and quantitative increase in phytoplankton in the rainy season. This increase was due to the positive relationship between phytoplankton composition and nutrient salts when associated with local hydrodynamics, which provides more favorable conditions for the enrichment of diversity with emphasis on species that compose the benthic microflora.

Keywords: chlorophyll *a*, environmental variables, microphytoplankton, natural pool, reef

Introduction

Phytoplankton are mainly autotrophic and very weak swimmers, and therefore flow at the whim of currents. These organisms are mostly single-celled and the main photosynthetic living cells in the marine environment (Lubiana 2015). Phytoplankton have various shapes and sizes and play important global ecological roles as indicators of water quality (Verlecar & Desai 2004), in primary production, and as regulators of climatic and biogeochemical cycles (Vaulout 2001; Winder & Sommer 2012). According to Vaulout (2001), marine phytoplankton colonize the upper part of the water column, above the limit of light penetration, and their community structure and abundance are mainly controlled by inorganic nutrients.

Understanding the factors that control the dynamics and composition of species is important to prevent environmental impacts on aquatic ecosystems (Winder & Sommer 2012). Environmental changes, such as to physical conditions, nutrient input (bottom-up control) and the

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intense pressure of "grazing" (top-down control), affect the diversity, structure and dynamics of phytoplankton communities (Hoppenrath *et al.* 2009; Winder & Sommer 2012). This in turn causes phytoplankton to employ several different ecological defense strategies to ensure population maintenance (Hoppenrath *et al.* 2009).

It is common knowledge that productivity of a reef system is greater for phytobenthos than for phytoplankton due to the presence of symbiotic zooxanthellae in corals and macroalgae (Odum & Odum 1955; Sournia 1968). However, plankton play a key role in the nutrition and maintenance of numerous sessile and sedentary organisms that are filter feeders and cohabit the same environment, including coral polyps.

From an ecological standpoint, studies of taxonomy and community structure are very important to understand the dynamics of phytoplankton of reefs, especially given how phytoplankton composition can vary depending on the hydro-biological characteristics of the studied site (Sridhar *et al.* 2010).

As is the case for Atol das Rocas, there is a scarcity of research on phytoplankton composition and dynamics in remote locations. Only a few studies, conducted by Feitosa & Passavante (2004); Jales *et al.* (2015) and Jales (2015), have addressed phytoplankton of Atol das Rocas.

Therefore, the aim of this paper was to determine and investigate phytoplankton community composition and biomass, and determine if there are any influential abiotic variables in the different seasons, of pools of Atol das Rocas. This study should provide additional information for further research on the trophic capacity of the atoll and its influence on the South Atlantic Ocean, as it has a significant role in the conservation, perpetuation and dispersion of numerous organisms.

Materials and methods

Study area

Atol das Rocas is located south of the equator (3°51' S; 33°49' W) in the Atlantic Ocean, approximately 143 nautical miles from the state of Rio Grande do Norte, Brazil (Gherardi & Bosence 2001). Similar to a series of ocean banks along the coast of Ceará and Rio Grande do Norte, the atoll originated from a fracturing process that created the island of Fernando de Noronha (Medeiros *et al.* 2009).

The atoll is a geological site that consists of carbonate sediments. The site is 3.35 km long (east-west) and 2.49 km wide (north-south), with an area of approximately 6.5 km² and an estimated perimeter of 11 km. While it is one of the smallest atolls in the world (Pereira *et al.* 2013), it comprises two islets, a large sandy plain exposed at low tide, pools of different shapes and sizes, caves, channels, reef fronts, a reef flat, a crest encircling the ring of the reef, and a lagoon on the north-northeast side (Villaça & Jensen 2006). The Atol das Rocas reef complex is influenced by the South Equatorial Current, which runs in a westward direction at an average speed of 30 cm s^{-1} (Richardson & Walsh 1986). Before becoming the Biological Reserve (ReBio) of Atol das Rocas on June 5th, 1979, it was a target of overfishing and sand and coral extraction (Moraes *et al.* 2003). Currently, the site is used for conducting scientific research and educational activities.

Sampling

Samples were collected in five pools in Atol das Rocas (Barretinha, Cemitério, Tartarugas, Rocas and Barretão) (Fig. 1) in two different seasons. In the dry season, sampling was performed between December 3rd and 15th 2012, and in the rainy season, between August 26th and September 09th, 2013. Three collection efforts were carried out in each pool, on different days, for each season.

To observe and identify distribution patterns of phytoplankton, salinity was analyzed using a manual S/Mill-E Atago refractometer, with a scale range of 0 to 100 and increments of 1. Water temperature was determined *in situ* using a common thermometer (alcohol) with a scale of -10 °C to 60 °C, and dissolved oxygen by the modified Winkler method described in Strickland & Parsons (1972). Other analyses included the levels of dissolved inorganic nutrients, namely ammonia, nitrate, nitrite, phosphate (described in Strickland & Parsons 1972), and silica (described in Grasshoff *et al.* 1983). The spectrophotometric analysis described in UNESCO (1966) was used to determine chlorophyll *a* (Tab.1).

The equation of Parsons & Strickland (1963) was applied to calculate chlorophyll *a* concentration. The same method (UNESCO 1966) was also used for size-fractionated chlorophyll *a*; however, before the filtration procedure, using cellulose acetate filters, a prior filtration was done using a 20-µm mesh, separating the fractions containing pico- and nanophytoplankton (≤ 20 µm) from microphytoplankton (> 20 µm).

Samples for determining microphytoplankton composition were collected by filtering 200 L of sea water for each sample through a PVC tube (length 50 cm, diameter 10 cm) enclosed by a 20-µm aperture mesh. A total of 30 samples were collected with three samples for each pool in each season. Following microphytoplankton concentration, samples were transferred to 250 ml plastic bottles and immediately fixed in formaldehyde solution (4%) buffered with sodium tetraborate. Samples were then homogenized and aliquots of 1 ml were removed and placed on a slide to observe all organisms. Two quantitative and two qualitative subsamples were analyzed for each sample. Composition was determined by means of observation using a 400x optical microscope. Quantitative data were used for statistical analysis of frequency of occurrence, relative abundance

(Tab. 2) and specific diversity index. Additional samples were collected to analyze microphytoplankton density.

A further 30 samples were collected, following the same procedure as the microphytoplankton concentration method. For each sample, one liter of water was collected, conditioned in plastic containers and fixed in Lugol's solution. Phytoplankton were concentrated using sedimentation in the counting chambers and analyzed under a Zeiss Axiovert inverted microscope, using the Utermöhl method described in Hasle (1978), Edler (1979) and Ferrario *et al.* (1995). This count included the entire cuvette, analyzed at a magnification of 400x, and expressed as number of cells.10^3 l^{-1}. Rose bengal was used to better view the samples. Samples were classified with the help of specialized taxonomic literature such as Peragallo & Peragallo (1897-1908), Husted (1930; 1959; 1961-1966), Cupp (1943), Desikachary (1959), Balech (1988), Silva-Cunha & Eskinazi-Leça (1990), Licea *et al.* (1995) and Tomas (1997). Synonymy was identified using AlgaeBase, which is a global database containing information on all algae phyla. Identification refinement criteria and scientific names followed the rating system of Guiry & Guiry (2015).

Table 1. Data for environmental variables measured in pools of Atol das Rocas, and degree of significant correlation (ANOVA, $p \leq 0.05$). Dissolved Inorganic Nitrogen (DIN); Dissolved Inorganic Phosphorous (DIP); Silicate (SiO_2); Cemitério (Cem.); Tartarugas (Tar.); Barretinha (Barret.); Barretão (Bar.).

Environmental variables	Average					Dry Season	Average					Rainy Season	p ≤ 0.05
	Cem.	Tar.	Barret.	Rocas	Bar.	Average	Cem.	Tar.	Barret.	Rocas	Bar.	Average	
Temperature (°C)	27.50	28.33	28.17	28.50	28.17	28.13	30.00	29.00	29.17	28.67	28.67	29.10	**0.01**
Salinity	35.67	35.33	36.00	36.00	35.33	35.67	36.00	36.67	36.00	36.00	36.33	36.20	**0.04**
Dissolved Oxygen (ml L^{-1})	5.53	5.49	4.74	5.46	5.81	5.41	6.69	5.72	5.89	5.53	5.75	5.92	0.07
Total Chlorophyll a (mg m^{-3})	0.13	0.25	0.12	0.10	0.19	0.16	0.91	0.29	0.70	0.32	0.52	0.55	**0.00**
Fracionate Chlorophyll a (mg m^{-3})	0.03	0.01	0.07	0.07	0.04	0.04	0.52	0.16	0.25	0.20	0.18	0.26	**0.00**
DIN (µM)	2.26	1.51	1.51	1.96	1.69	1.79	2.05	1.69	1.53	1.52	1.69	1.70	0.95
DIP (µM)	0.11	0.08	0.08	0.26	0.07	0.12	0.04	0.23	0.21	0.03	0.02	0.11	0.80
SiO_2 (µM)	1.69	151	1.51	2.27	4.31	2.26	0.27	0.19	1.03	0.46	1.69	0.73	0.80

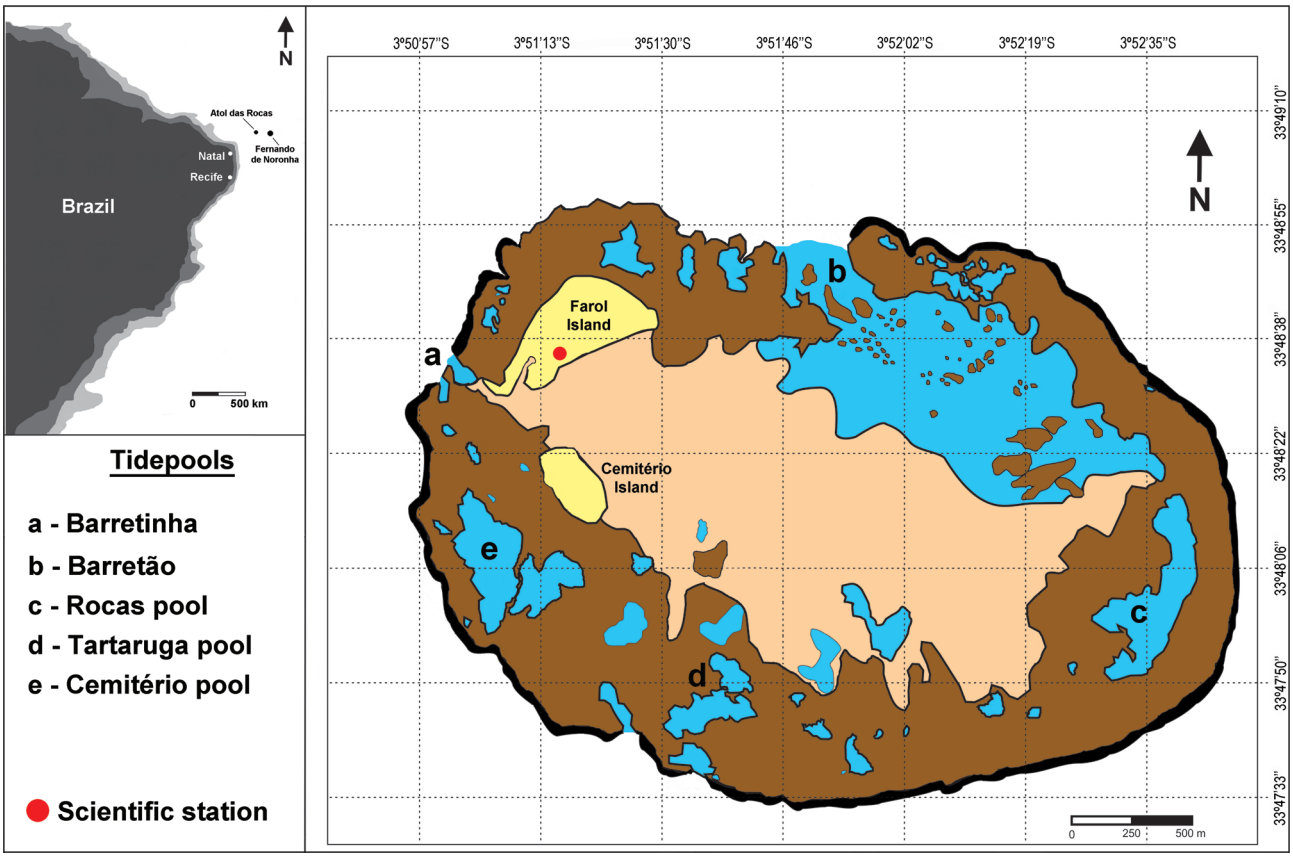

Figure 1. Map of the study area showing the analyzed pools of Atol das Rocas, South Atlantic (3°51' S; 33°49' W). Map modified from Pereira *et al.* 2010.

Statistical analysis

Environmental variables and average diversity of microphytoplankton composition were tested for significance by comparing the different seasons (dry and rainy) and pools (Barretinha, Cemitério, Tartarugas, Rocas and Barretão) using an ANOVA. Variables for which $p \leq 0.05$ were considered significant. Univariate analyses were carried out using STATISTICA 8.0. To better explore the relationships between environmental variables and phytoplankton community structure, multivariate analyses, namely Prinncipal Component Analysis (PCA), Cluster Analysis and BIOENV, were conducted using PRIMER 6.0.

Raw data of samples collected using the microphytoplankton concentration method were considered for the indexes of frequency, abundance and diversity. Frequency of occurrence was calculated by applying the formula described in Mateucci & Colma (1982), considering the number of samples in which each taxon occurred and the total number of analyzed samples. Relative abundance was estimated according to Lobo & Leighton's criteria (Lobo & Leighton 1986). The Shannon index (Shannon 1948) was used to calculate specific diversity using PRIMER 6.0, and obtained values were classified according to Valentin *et al.* (1991).

Results

Water temperature in the study area varied from 27.5 °C to 30 °C, with the extreme values being found for Cemitério during the dry and rainy seasons, respectively. Salinity varied from 35.33 in the dry season to 36.67 in the rainy season, with both extremes being for Tartarugas. Dissolved oxygen ranged from 4.74 ml l^{-1} in Barretinha in the dry season to 6.69 ml l^{-1} in Cemitério during the rainy season. The lowest average total chlorophyll *a* value in the dry season was 0.10 mg m^{-3} in Rocas, and 0.01 mg m^{-3} for size-fractionated chlorophyll *a* in Tartarugas. Chlorophyll *a* values were higher in the rainy season, with the highest average chlorophyll *a* being for Cemitério, reaching 0.91 mg m^{-3} and 0.52 mg m^{-3} for total and size-fractionated values, respectively. In relation to fractionation, pico- and nanophytoplankton components that corresponded to the ≤ 20-µm fraction had the lowest contribution to biomass in the environment, with 28.4 % in the dry season and 47.5 % in the rainy season (Tab. 1).

Unlike the variables described above, in terms of average values for all pools, nutrient salts and silica had their highest averages during the dry season. Dissolved inorganic nitrogen (DIN) content was calculated as the sum of nitrate, nitrite, and ammonia. Average values for DIN, DIP (Dissolved Inorganic Phosphorous) and SiO_2 were 1.79, 0.12 and 2.26 µm in the dry season and 1.70, 0.11 and 0.73 µm in the rainy season, respectively.

There was a significant difference in temperature, salinity and total and size-fractionated chlorophyll *a* in relation to season (Tab. 1). Dissolved oxygen and nutrient salts did not differ significantly between seasons. With regard to spatiality, there was no significant difference for any of the analyzed parameters.

The PCA revealed three axes explaining 71 % of the variation in environmental parameters in the study area. The first axis showed a direct relationship between temperature and total and size-fractionated chlorophyll *a*, and an inverse relationship with SiO_2. The second axis showed a direct relationship between salinity and DIP, while the third axis revealed a direct relationship between dissolved oxygen and DIN. These axes explained 40 %, 16 % and 14 % of the variation, respectively. Figure 2 shows the pattern between samples of the different seasons, with the rainy season having the higher values (Fig. 2).

A total of 109 species were identified, distributed among four major groups: the predominant group Ochrophyta (52.3 %), followed by Dinophyta (37.6 %), Cyanobacteria (7.33 %) and Haptophyta (2.75 %) (Tab. 2). The dry season had high densities of *Protoperidinium* sp. (261.10^3 cells l^{-1}), *Prorocentrum balticum* (389.10^3 cells l^{-1}), *Prorocentrum lima* (932.10^3 cells l^{-1}) and *Pyrophacus* sp. (143.10^3 cells l^{-1}). The highest densities were found for Tartarugas, although these species also occurred in the other pools. In addition to having a high density in Tartarugas, *Prorocentrum lima* was also found at a high density in Barretão (366.10^3 cells l^{-1}).

The species with the highest densities in the rainy season were *Lyngbya* sp. (127.10^3 cells l^{-1}), *Amphora arenari*a (113.10^3 cells l^{-1}), *Bellerochea malleus* (97.10^3 cells l^{-1}), *Cylindrotheca closterium* (218.10^3 cells l^{-1}), *Navicula* sp. (120.10^3 cells l^{-1}), *Ostreopsis ovata* (362.10^3 cells l^{-1}), *Protoperidinium* sp. (572.10^3 cells l^{-1}), *Prorocentrum compressum* (79.10^3 cells l^{-1}), *Prorocentrum hoffmannianum* (89.10^3 cells l^{-1}), *Prorocentrum mexicanum* (88.10^3 cells l^{-1}), *Prorocentrum lima* (862.10^3 cells l^{-1}) and *Pyrophacus* sp. (503.10^3 cells l^{-1}). While the density of most species was higher in the rainy season, *Prorocentrum balticum* was an exception, reaching a markedly low density of 36.10^3 cells l^{-1}, over ten times lower than in the dry season (389.10^3 cells l^{-1}).

With regard to the occurrence and abundance frequency indexes, species classified as dominant and very frequent were *Pyrophacus* sp. and *Prorocentrum lima*. *Ostreopsis ovata*, which was also classified as dominant, was frequently, being present in 40 % of the analyzed samples.

Shannon's specific diversity index (Shannon 1948) varied widely, with samples ranging from 0.43 to 3.00 bits $cell^{-1}$ for Tartarugas in the dry and rainy seasons, respectively. Therefore, according to the classification of Valentin (1991), some values for samples were classified as of very low diversity (< 1.0 bits $cell^{-1}$) and others as high diversity (≥ 3.0 bits $cell^{-1}$), but most (21 of 30 analyzed samples) were classified as medium diversity (2.0 ≤ medium diversity < 3.0 bits $cell^{-1}$), with indexes of 2 to 2.90 bits $cell^{-1}$ (Fig. 3).

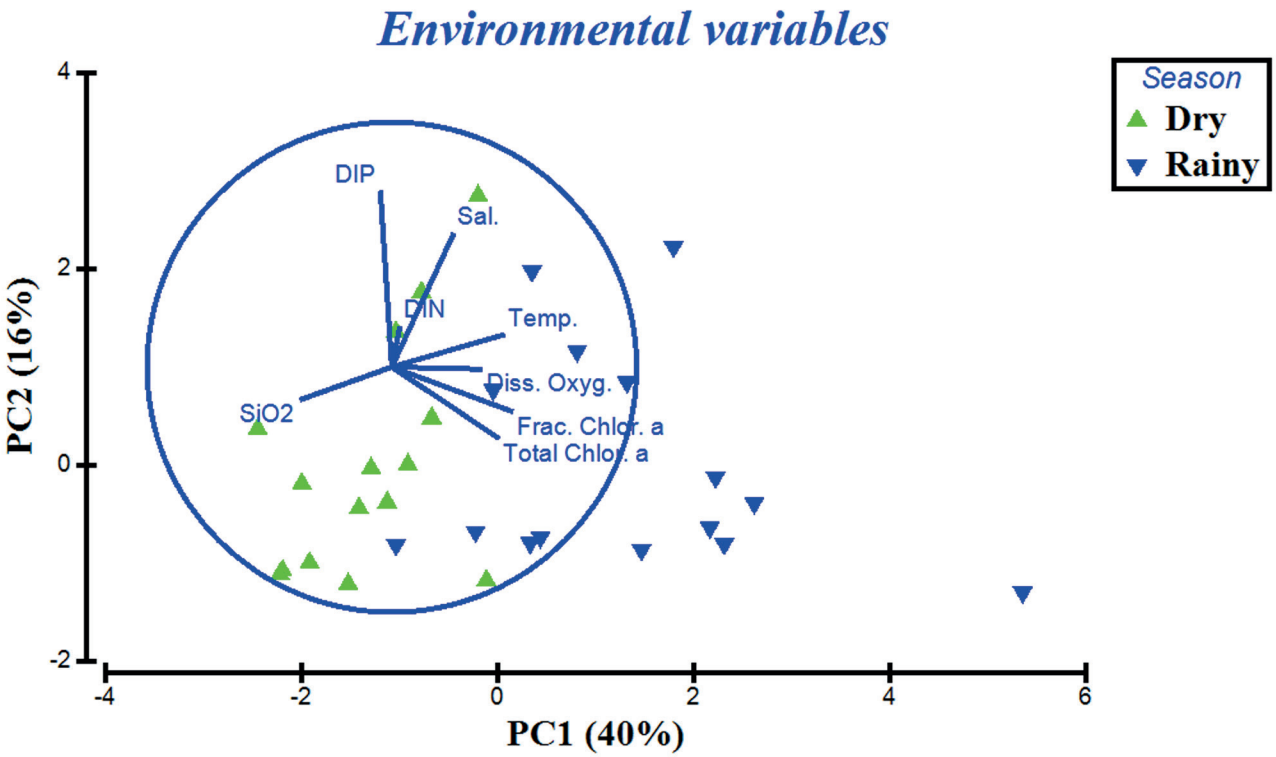

Figure 2. Principal Component Analysis of pools of Atol das Rocas (South Atlantic) in different seasons (dry and rainy). Environmental variables: Dissolved Inorganic Nitrogen (DIN); Dissolved Inorganic Phosphorous (DIP); Salinity (Sal.); Temperature (Temp.); Dissolved Oxygen (Diss. Oxyg.); Total Chlorophyll *a* (Total Chlor. *a*); Fractionated Chlorophyll *a* (Frac. Chlor. *a*); Silicate (SiO_2).

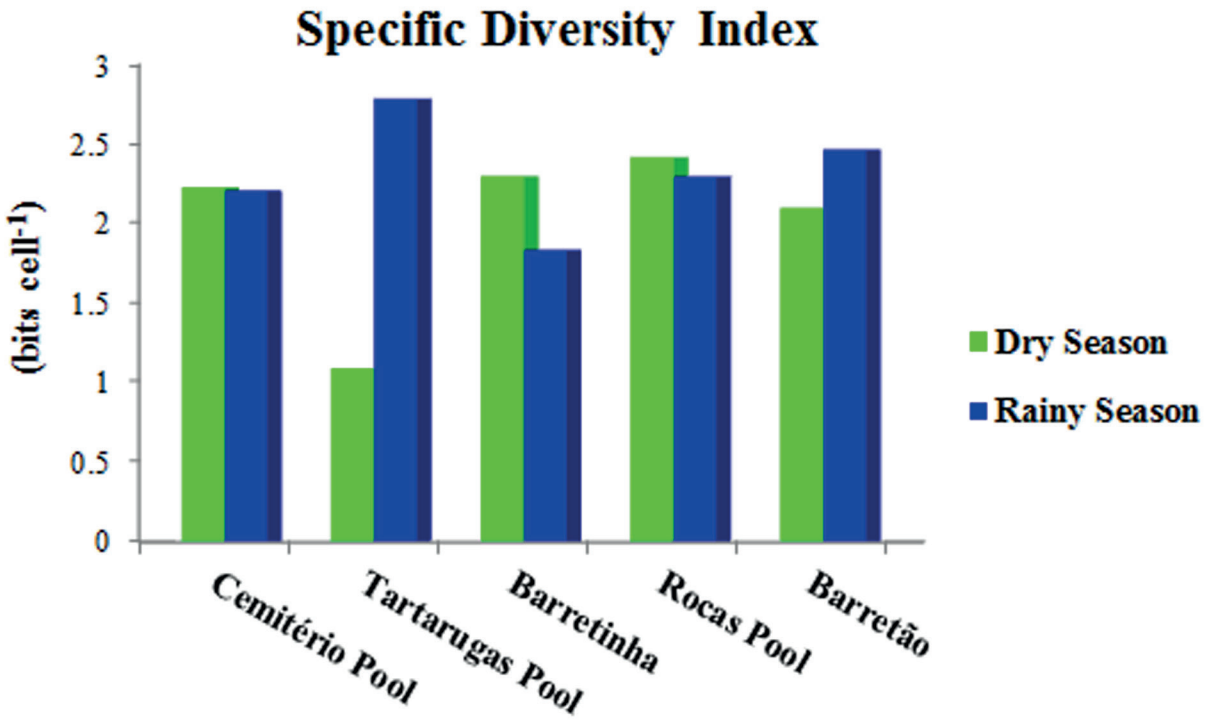

Figure 3. Specific diversity index for pools of Atol das Rocas (South Atlantic) in different seasons (dry and rainy).

Table 2. Microphytoplankton community composition of pools of Atol das Rocas. Cemitério (Cem.); Tartarugas (Tar.); Barretinha (Barret.); Barretão (Bar.).

Microphytoplankton composition	Dry season						Rainy season					
	Conc. 20 µm	Density (cells.10^3 l^{-1})					Conc. 20 µm	Density (cells.10^3 l^{-1})				
		Cem.	Tar.	Barret.	Rocas	Bar.		Cem.	Tar.	Barret.	Rocas	Bar.
CYANOBACTERIA												
Cyanophyceae 1 [a, C]	X	1			3		X	7				
Cyanophyceae 2								2				
Cyanophyceae 3 [r, C]	X						X			91		
Cyanophyceae 4 [r, I]	X						X					
Anabaena sp. [a, I]	X						X					
Lyngbya sp. [a, VC]	X	8	3		1		X	48	3	63	4	9
Oscillatoria sp. [a, VC]	X	3			3	1	X	7	1	20	13	14
Trichodesmium thiebautii [r, S]	X						X					
OCHROPHYTA												
Amphitetras antidiluviana Ehrenberg 1840											1	
Amphiprora alata (Ehrenberg) Kützing 1844 [r, S]	X						X					
Amphiprora sp. [r, S]	X						X	1				1
Amphora arenaria Donkin 1858 [a, VC]	X	1	3		2		X	61	2	41	1	8
Amphora sp. [a, C]	X			1		3	X	1		3	2	17
Asterionellopsis glacialis (Castracane) Round in Round, R.M.Crawford & D.G.Mann 1990 [a, I]							X					
Asterolampra marylandica Ehrenberg 1844 [r, S]							X					
Auricula sp. [r, S]							X					
Bacillaria paxillifer (O. F. Müller) T. Marsson 1901 [r, I]	X						X		10			
Bellerochea malleus (Brightwell) Van Heurck 1885 [a, C]	X			4		2	X	9	8	72	5	3
Biddulphia biddulphiana S. F. Gray 1821 [r, I]	X						X					
Biddulphia regia (Schultze) Ostenfeld 1908			1									
Campylodiscus clypeus (Ehrenberg) Ehrenberge x Kützing 1844 [r, S]							X					8
Campyloneis grevillei (W.Smith) Grunow & Eulenstein in Grunow 1868 [r, S]	X											
Chaetoceros sp. [r, S]	X						X					
Climacosphenia elongata Mereschkowsky [r, C]	X						X		2	1		1
Cocconeis scutellum Ehrenberg 1838 [a, VC]	X		1				X	5	2	2	1	4
Cylindrotheca closterium (Ehrenberg) Reimann & J.C.Lewin 1964 [a, C]							X		192		26	
Dictyocha fíbula Ehrenberg 1839 [r, S]	X											
Dimerogramma sp. [r, S]							X					

Table 2. Cont.

Microphytoplankton composition	Dry season						Rainy season					
	Conc. 20 µm	Density (cells.10^3 l^{-1})					Conc. 20 µm	Density (cells.10^3 l^{-1})				
		Cem.	Tar.	Barret.	Rocas	Bar.		Cem.	Tar.	Barret.	Rocas	Bar.
Diploneis bombus (Ehrenberg) Ehrenberg 1853								1	1			
Diploneis sp. [r, C]	X					1	X					1
Diploneis sp.1 [r, I]	X		2				X					
Grammatophora oceanica Ehrenberg 1840									1			
Grammatophora sp. [a, I]							X					
Isthmia enervis Ehrenberg 1838 [r, I]	X						X					2
Lampriscus sp. A. Schmidt 1882 [r, I]	X						X				3	1
Licmophora sp. [r, C]	X								17	6	2	
Lithodesmium undulatum Ehrenberg 1839	X											
Lyrella lyra (Ehrenberg) Karajeva 1978 [r, C]	X	1	1				X			2		1
Melchersiella hexagonallis C. Teixeira [r, C]	X						X				2	3
Navicula sp. [a, C]	X	3	1		7		X	27	19	33	345	380
Navicula sp.1 [a, I]							X		120			
Nitzschia distans W. Gregory 1857 [r, S]							X					
Nitzschia longissima (Brébisson) Ralfs in Pritchard 1861 [a, VC]	X						X					
Nitschia pacifica Cupp 1943 [r, S]	X											
Nitzschia punctata (W.Smith) Grunow 1878 [r, S]							X					
Nitzschia sigma(Kützing) W.Smith 1853 [a, C]			1				X		10		16	2
Nitzschia spathulata W.Smith 1853 [a, C]	X						X				11	25
Nitzschia sp. [r, VC]											16	1
Paralia sulcata (Ehrenberg) Cleve 1873 [a, I]	X											
Pleuro/ Gyrosigma sp. [r, C]	X						X		9	1	4	5
Podocystis adriatica (Kützing) Ralfs in Pritchard 1861 [r, C]	X							3		3		2
Psammodictyon panduriforme (W.Gregory) D.G.Mann in Round, Crawford & Mann 1990 [r, S]							X			1		
Rhabdonema adriaticum Kützing 1844 [r, I]	X						X					
Rhizosolenia imbricata Brightwell 1858 [r, S]							X					
Rhizosolenia styliformis T. Brightwell 1858 [r, S]							X					
Streptotheca tamesis Shrubsole 1891 [r, S]	X											
Surirella fastuosa Ehrenberg [r, S]	X						X					

Table 2. Cont.

Microphytoplankton composition	Dry season						Rainy season					
	Conc. 20 µm	Density (cells.10^3 l^{-1})					Conc. 20 µm	Density (cells.10^3 l^{-1})				
		Cem.	Tar.	Barret.	Rocas	Bar.		Cem.	Tar.	Barret.	Rocas	Bar.
Synedra formosa Hantzsch 1863 [r, C]	X						X					
Synedra sp.									8			
Thalassiosira sp. [a, C]	X						X		1		2	5
Toxarium undulatum Bailey 1854 [r, I]							X					
Trachyneis aspera (Ehrenberg) Cleve 1894 [r, C]	X	1	1	1			X	9	5	2		6
Triceratium antediluvianum (Ehrenberg) Grunow 1868 [r, S]	X				1							
Triceratium pentacrinus (Ehrenberg) Wallich 1858 [r, S]							X					
Tropidoneis sp. [r, I]							X				1	
DINOPHYTA												
Ceratocorys horrida Stein 1883 [r, S]							X					
Dinophysis caudata Saville-Kent 1881 [r, S]	X											
Dinophysis sp. [r, S]							X					
Gymnodinium catenatum H.W.Graham 1943 [a, C]	X						X					
Gymnodinium sp. [a, VC]	X						X	4	17	3	3	2
Gonyaulax birostris Stein 1883 [r, S]	X											
Gonyaulax minuta Kofoid & Michener 1911 [r, I]	X						X					
Gonyaulax polyedra F.Stein 1883 [r, S]							X					
Gonyaulax polygramma Stein 1883 [r, C]	X	1					X					
Gonyaulax spinifera (Claparède & Lachmann) Diesing 1866 [r, S]	X											
Neoceratium declinatum (Karsten) F. Gomez, D. Moreira & P. Lopez-Garcia 2010 [r, I] = *Tripos declinatus* (G. Karsten) F.Gómez 2013							X					
Neoceratium fusus (Ehrenberg) F.Gomez, D.Moreira & P.Lopez-Garcia 2010 [r, S] = *Tripos fusus* (Ehrenberg) F.Gómez, 2013							X					
Neoceratium horridum (Gran) F. Gomez, D. Moreira & P.Lopez-Garcia 2010 = *Tripos horridus* (Cleve) F. Gómez, 2013											1	
Neoceratium lineatum (Ehrenberg) F. Gomez, D. Moreira & P. Lopez-Garcia 2010 [r, S] = *Tripos lineatus* (Ehrenberg) F. Gómez, 2013	X											
Neoceratium macroceros (Ehrenberg) F. Gomez, D. Moreira & P. Lopez-Garcia 2010 [r, S] = *Tripos macroceros* (Ehrenberg) F.Gómez, 2013							X					
Neoceratium pentagonum (Gourret) F. Gomez, D. Moreira & P. Lopez-Garcia 2010 [r, I] = *Tripos pentagonus* (Gourret) F.Gómez, 2013	X						X					

Table 2. Cont.

Microphytoplankton composition	Dry season						Rainy season					
	Conc. 20 µm	Density (cells.10^3 l^{-1})					Conc. 20 µm	Density (cells.10^3 l^{-1})				
		Cem.	Tar.	Barret.	Rocas	Bar.		Cem.	Tar.	Barret.	Rocas	Bar.
Neoceratium teres (Kofoid) F. Gomez, D. Moreira & P. Lopez-Garcia 2010 [r, C]	X						X					
Neoceratium tripos (O.F.Müller) F. Gomez, D. Moreira & P. Lopez-Garcia 2010 [r, S] = *Tripos muelleri* Bory de Saint-Vincent, 1824							X					
Ornithocercus magnificus Stein 1883 [r, S]							X					
Ornithocercus quadratus Schütt 1900 [r, S]							X					
Ornithocercus sp. [r, S]							X					
Ostreopsis ovata Fukuyo 1981 [d, C]							X		9	339	4	10
Oxytoxum sceptrum (F.Stein) Schröder 1906 [r, S]							X					
Oxytoxum scolopax Stein, F. 1883 [r, S]	X											
Phalacroma rotundatum (Claparéde & Lachmann) Kofoid & Michener 1911 [r, I]	X						X					
Podolampas palmipes Stein 1883 [r, S]	X											
Podolampas spinifera Okamura 1912 [r, I]							X	1	1		2	
Protoperidinium obtusum (Karsten) Parke& Dodge 1976 [r, S]	X											
Protoperidinium pyriforme (Paulsen) Balech 1974 [a, I]	X						X					
Protoperidinium sp. [a, C]	X	24	174	4	50	9	X	270	17	229	2	54
Protoperidinium sp. 1 [a, I]	X						X					
Protoperidinium sp.2 [r, S]							X					
Prorocentrum balticum (Lohmann) Loeblich 1970 [a, C]	X	2	379	2	1	5	X	19	6	4	3	4
Prorocentrum compressum (Bailey) Abéex Dodge 1975 [a, C]	X	4	19			1	X	26	8	35	2	8
Prorocentrum emarginatum Fukuyo 1981 [r, C]	X						X					
Prorocentrum hoffmannianum M. A. Faust 1990 [a, VC]	X	4	3	1			X	3	23	51	3	9
Prorocentrum lima (Ehrenberg) F.Stein 1878 [d, VC]	X	6	474	49	37	366	X	375	7	57	14	409
Prorocentrum mexicanum Osorio-Tafall 1942 [a, I]							X		3	85		
Prorocentrum micans Ehrenberg 1834 [a, I]	X		9		3		X					
Prorocentrum sigmoides Böhm 1933												1
Pyrophacus sp. [a, VC]	X	3	105	14	3	18	X	72	97	184	11	139
HAPTOPHYTA												
Coccolithus sp. [a, VC]	X	10	8	1	6	13	X	14	7	2	5	3
Coccolithus sp. 1 [a, C]	X						X					
Coccolithus sp. 2 [r, C]	X		1	1			X	1	1			

There was no significant difference between seasons for average diversity of microphytoplankton composition. Spatially, the only significant difference among pools was between Cemitério and Tartarugas in the dry season ($p \leq 0.04$).

The dendrogram regarding microphytoplankton composition shows the formation of two large groups associated with seasonality. It also shows that the pools had were very similar during the rainy season, with the exception of a sample from Rocas that was grouped with Cemitério. A clear pattern among pools was not observed in the dry season (Fig. 4). Phytoplankton density in the pools followed the same pattern as microphytoplankton composition, with a distinction between seasons. However, in this case, a single Tartarugas sample in the rainy season was grouped with the dry season samples (Fig. 5).

The BIOENV analysis using Spearman's correlation resulted in different groupings than did the cluster analysis. Correlation between phytoplankton composition and environmental variables was relatively low (r = 0.337), with composition correlating with salinity and SiO_2. Correlations between phytoplankton composition and environmental variables were also analyzed for each season and pool. For seasons, the highest correlation was during the rainy season (r = 0.492), with composition correlating with DIP and SiO_2. The lowest correlation was during the dry season (r = 0.261) with composition correlating with total chlorophyll *a*, DIN, DIP and SiO_2.

Analyses of biotic and abiotic interactions for each pool revealed that phytoplankton composition in Cemitério was highly correlated with salinity, total chlorophyll *a*, DIN, DIP and SiO_2 (r = 0.846). There was an even a higher correlation with temperature, total and size-fractionated chlorophyll *a*, DIN and DIP for Tartarugas (r = 0.932). Phytoplankton composition of Barretinha, Rocas and Barretão correlated with nutrient salts and SiO_2, with the correlation being higher (r = 0.850) for Barretinha and Rocas than for Barretão (r = 0.598) (Tab. 3).

Spearman's correlation and BIOENV revealed that the most representative species found in this study (*Prorocentrum balticum*, *Prorocentrum lima, Pyrophacus* sp. and *Ostreopsis ovata*), were correlated with size-fractionated chlorophyll *a* and DIN (r = 0.438).

Discussion

Ocean surface waters vary widely in temperature, reaching averages from -1.8 °C up to 30 °C depending on the location (Toseland *et al*. 2013). Phytoplankton are found in all of these different temperature zones, with temperature being an environmental parameter that influences their growth and diversity (Thomas *et al*. 2012). This study found temperature to be one of the parameters with a significant seasonal difference and a direct relationship with chlorophyll *a*, according to the PCA. The highest and lowest average

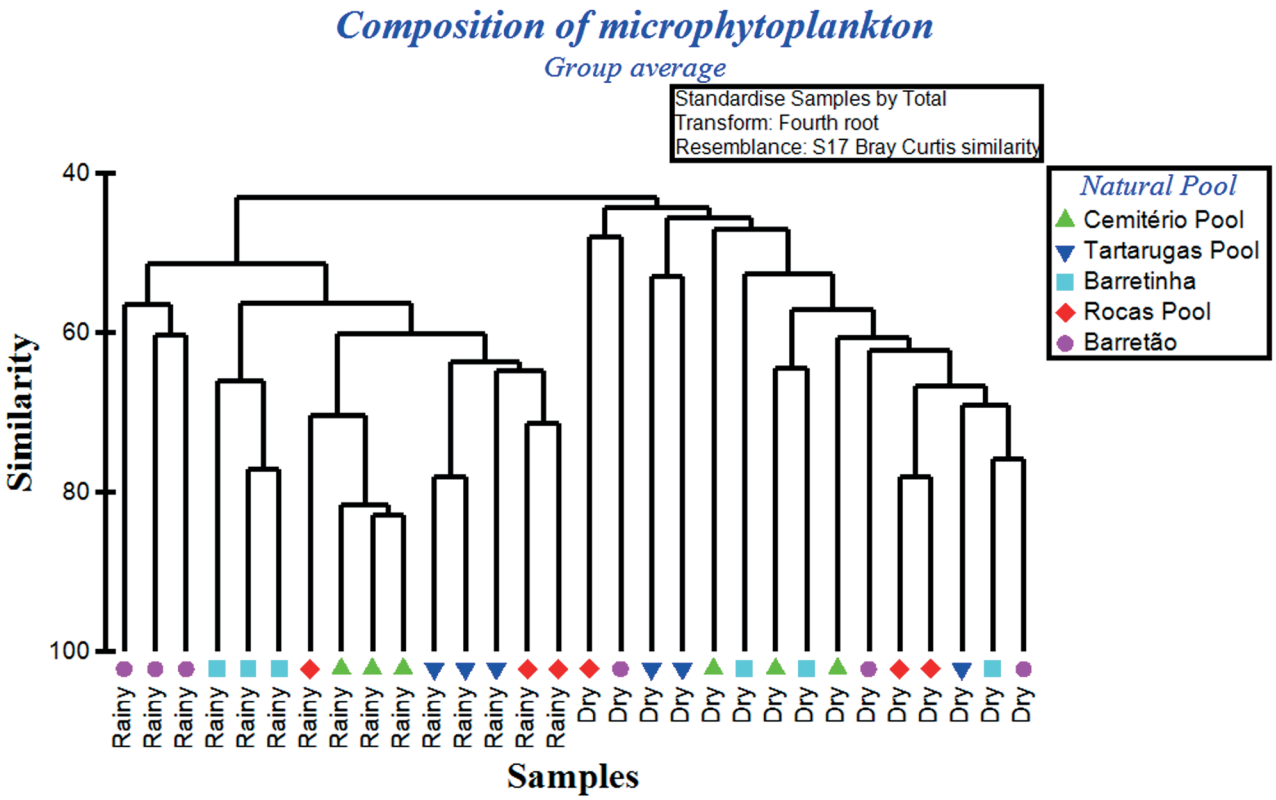

Figure 4. Associations of samples for determining microphytoplankton composition between seasons (dry and rainy), and among pools (Cemitério, Tartarugas, Barretinha, Rocas and Barretão) in Atol das Rocas (South Atlantic).

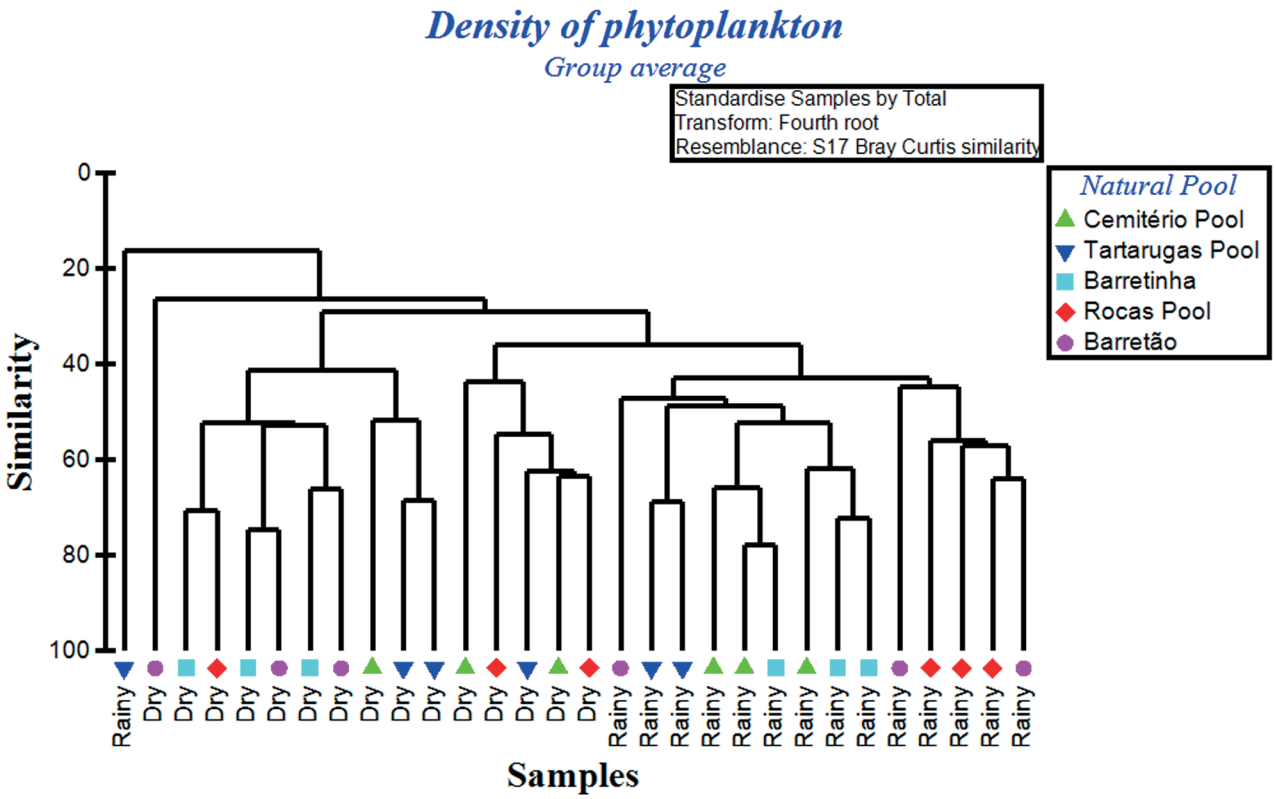

Figure 5. Associations of samples for determining microphytoplankton density between seasons (dry and rainy), and among pools (Cemitério, Tartarugas, Barretinha, Rocas and Barretão) in Atol das Rocas (South Atlantic).

Table 3. Spearman's correlation of environmental variables (r) for groupings (General, Pools, Seasons) of Atol das Rocas. Salinity (Sal.); Temperature (Temp.); Dissolved Inorganic Nitrogen (DIN); Dissolved Inorganic Phosphorous (DIP); Silicate (SiO_2).

Groupings		Spearman (r)	Environmental variables correlated
General	Phytoplankton composition and environmental variables	0.337	Sal. and SiO_2
Natural pools	Cemitério Pool	0.846	Sal., total chlorophyll *a*, DIN, DIP and SiO_2
	Tartarugas Pool	0.932	Temp., total and size-fractionated chlorophyll *a*, DIN and DIP
	Barretinha	0.850	DIN; DIP and SiO_2
	Rocas Pool	0.850	DIN; DIP and SiO_2
	Barretão	0.598	DIN; DIP and SiO_2
Seasons	Rainy season	0.492	DIP and SiO_2
	Dry season	0.261	total chlorophyll *a*, DIN, DIP and SIO_2

temperatures of 30 °C and 27.5 °C, respectively, were recorded in Cemitério. However, average temperatures in August and September 2013 ranged from 28.67 °C to 30 °C in pools of Cemitério and Rocas and Barretinha, respectively. Pereira (2015) reported average temperatures of 27 °C and 27.5 °C for the same climatic period and explained that daily temperature can vary by up to 3 °C due to tidal regime.

There was significant seasonal differences in salinity in the reef ecosystem of Atol das Rocas. However, the limited variation (a little more than 1), suggests that the phytoplankton community adapts to this variation without compromising the community. Similar salinities and higher values of chlorophyll *a* were also reported by Feitosa & Passavante (2004) for Atol das Rocas.

Ke *et al.* (2018) describes little variation in temperature and salinity for atoll lagoons in the South China Sea, with averages of 29.39 °C and 33.46 °C, and a resembling chlorophyll *a* values. They also reported a linear correlation between chlorophyll *a* and phytoplankton abundance, as also found in the present study.

Characteristics of planktonic organisms that do not change easily, as far as the morphological, mechanical and general physiological properties of the cells are concerned, are less sensitive to temperature, salinity and light intensity, and much more dependent on turbulence and general nutrient availability (Margalef 1978). It is generally accepted that inorganic nutrient concentrations exert great control over phytoplankton biomass, productivity, and species composition (Dugdale & Wilkerson 1992). Although there

was no significant difference, nutrient salt content was positively correlated with phytoplankton composition in all pools. According to Furnas *et al*. (2005), in oligotrophic ecosystems, newly introduced dissolved inorganic nutrients are often rapidly taken up and turned over by phytoplankton communities. Corroborating the present study, Ke *et al*. (2018) showed there was little variation in nutrient concentrations in the different zones of an atoll lagoons in the South China Sea.

Regarding diversity, the only significant difference found for the diversity index. was between the pools Cemitério and Tratarugas during the dry season. Both pools correlated with DIN and DIP and BIOENV revealed that, during the dry season, DIN and DIP levels were higher in the Cemtério than Tartarugas.

Studying the global pattern of phytoplankton diversity driven by temperature and environmental variability, Righetti *et al*. (2019) states that there is a gap in the understanding of phytoplankton species richness and ecologists have been intrigued with the global pattern of phytoplankton species diversity and the underlying drivers in open water.

The most representative group found at Atol das Rocas was Ochrophyta with 57 species. According to Silva-Cunha & Eskinazi-Leça (1990) and Lacerda *et al*. (2004), ochrophytes are aquatic organisms that substantially contribute to marine productivity and are considered abundant in tropical waters. In spite of the greater occurrence of diatoms, species classified as being the most representative were dinoflagellates, including *Prorocentrum balticum, Prorocentrum lima, Pyrophacus* sp. and *Ostreopsis ovata*, since, with the exception of the last, they were strongly represented in both seasons.

According to Faust *et al*. (1996), the identification of benthic dinoflagellates is of fundamental importance because they have the potential to produce toxins that can be harmful to humans. Species of Ostreopscidaceae are commonly found in benthic microflora and in reef pools. The genus *Ostreopsis* is widely distributed and associated with several blooms annually, in addition to having new locations of occurrence identified (Rhodes 2011). Similar to Atol das Rocas, in this study *Ostreopsis* has also been identified in the Archipelago of São Pedro and São Paulo (Nascimento *et al*. 2012), and in coastal reef environments of northeastern Brazil, such as Tamandaré (Silva 2015) and Porto de Galinhas (Machado 2015).

Although *Ostreopsis ovata* is mostly found in protected environments (Faust *et al*. 1996), in Atol da Rocas, this species was reported only in the rainy season and with a greater occurrence in the collection point connected to the open sea and influenced by local hydrodynamics. A study carried out in 2008 in unprotected rocky areas at La Réserve beach in Nice, France (Tichadou *et al*. 2010), agrees with the surveys conducted by Dias (2004), Pereira *et al*. (2013) and Pinheiro (2016), and affirms that local hydrodynamics can potentiate energy levels and consequently cause environmental changes in an atoll. According to Guerrini *et al*. (2010) and Tichadou *et al*. (2010), studies in the Mediterranean Sea have confirmed the occurrence of *O. ovata* blooms. This species has been the cause of human health problems because it produces palytoxin (PTX) and ostreocine (PTX-like), which are highly toxic. In tropical environments, these toxins are produced by various marine organisms, and can accumulate throughout the food web. *Ostreopsis ovata* was widely observed in Atol das Rocas, but at densities insufficient for producing blooms.

Ostreopsis ovata is usually found in association with other potentially toxic dinoflagellates, such as *Prorocentrum lima*. These organisms form epiphytic communities associated with coral reefs or with seaweed on the surfaces of these corals (Vila *et al*. 2001). According to a study performed in Greece (Aligizaki *et al*. 2009), *Prorocentrum lima*, in addition to being toxic, was found to vary greatly in size and shape, and its density was higher in the dry season when the lowest values for temperature and salinity were recorded.

Unlike other representative species in this study, *Prorocentrum balticum* is also abundant in waters that surround Atol das Rocas (Jales 2015), and it is not benthic nor toxic (Faust & Gulledge 2002). This species is classified as neritic, oceanic and planktonic and is usually found in cold and tropical waters (Faust & Gulledge 2002). Its presence in the studied pools can be explained by the constant renovation during high tide.

The genus *Pyrophacus* is widely distributed and contains only three difficult-to-distinguish species (Hoppenrarth *et al*. 2009). Studies conducted at Jeju Island in Korea (Kim *et al*. 2013), in the Mediterranean (Balkis & Koray 2001), in the Archipelago of São Pedro and São Paulo (Koening & Oliveira 2009) and in the estuary of the Timbó river in Brazil (Silva-Cunha *et al*. 1989) reported the occurrence of this genus.

The microphytoplankton composition of Atol das Rocas exhibited a seasonal distribution pattern, even though not statistically significant. Despite the spatial difference in composition among pools, there was no determinant hydrological parameter during the dry season. However, according to BIOENV, the composition of all pools was chiefly associated with DIN, DIP and SiO_2.

Although local hydrodynamics were not analyzed in the present study, Dias (2004), Pereira *et al*. (2013) and Pinheiro (2016) affirm that hydrodynamics can influence the environment. It should be noted that the pools analyzed in the present study are relatively shallow (average depth of 5 m), and the most representative species in the area are part of the benthic microflora. From this perspective it is possible to deduce that the level of energy impacted the distribution and density of the phytoplankton community during the rainy season.

According to Gherardi & Bosence (2001), waves that occur in the atoll are concentrated in the southeast portion

(windward), although wave refraction in the atoll basement can generate large wave breaks in the west and southwest (leeward) portions. Moreover, high tidal amplitude ensures that a large part of the atoll profile is affected by breaking waves twice a day, with the area being exposed at low tide and bathed by strong tidal currents during ebb tide. In terms of density, only one seasonal pattern was clearly identified — a qualitative and quantitative increase of phytoplankton in the rainy season. This pattern is due to the positive relationship between microphytoplankton composition and nutrient salts when associated with local hydrodynamics, as proposed by Gherardi & Bosence (2001) and Rodriguez (1940), thus providing more favorable conditions for increased density with emphasis on species that compose the benthic microflora.

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