

# Carbon, nitrogen, and phosphorus stoichiometry of plankton and the nutrient regime in Cabo Frio Bay, SE Brazil

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**Abstract** This long-term study, performed during the years 2003–2005 and 2008–2009, investigated the carbon (C), nitrogen (N), and phosphorus (P) contents of the phyto- and zooplankton communities and the nutrient regime of Cabo Frio Bay, SE Brazil. The information intends to serve as baseline of the plankton C, N, and P stoichiometry for the calibration of biogeochemical and ecological models in support to future findings related to the local and regional phenomena of climatic change. Cabo Frio Bay is a small semienclosed system set adjacent to a region subject to sporadic coastal upwelling. Zooplankton exhibited average annual C, N, and P contents of  $11.6\pm 6.9\%$ ,  $2.8\pm 1.8\%$ , and  $0.18\pm 0.08\%$ , and phytoplankton ( $>20\ \mu\text{m}$ )  $6.8\pm 6.0\%$ ,  $1.6\pm 1.5\%$ , and  $0.09\pm 0.08\%$ , respectively. The C/N/P ratios correspond to the lowest already found to date for a marine environment. The low C contents must have been brought about by a predominance of gelatinous zooplankton,

like Doliolids/ Salps and also Pteropods. Average annual nutrient concentrations in the water were  $0.21\pm 0.1\ \mu\text{M}$  for phosphate,  $0.08\pm 0.1\ \mu\text{M}$  for nitrite,  $0.74\pm 1.6\ \mu\text{M}$  for nitrate, and  $1.27\pm 1.1\ \mu\text{M}$  for ammonium. N/P ratios were around 8:1 during the first study period and 12:1 during the second. The plankton C/N/P and N/P nutrient ratios and elemental concentrations suggest that the system was oligotrophic and nitrogen limited. The sporadic intrusions of upwelling waters during the first study period had no marked effect upon the systems metabolism, likely due to dilution effects and the short residence times of water of the bay.

**Keywords** Phytoplankton · Zooplankton · C/N/P · Cabo Frio Bay, SE Brazil

## Introduction

Carbon (C), nitrogen (N), and phosphorus (P) correspond to the prime biogenic elements necessary for the sustenance of primary production and the food webs of marine ecosystems, and once established, the autotrophic and heterotrophic plankton communities also control the concentrations of these elements in the marine realm (Elser and Hassett 1994; Tyrrell 1999; Klausmeier et al. 2004). Weber and Deutsch (2010) observed that the N/P ratio is subject to latitudinal variation. They found an N/P ratio of 12:1 in the Southern Ocean and 20:1 in the Polar region. Furthermore, the elemental composition of the plankton communities can change over time in response to nutrient

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availability. Rau et al. (2003) studied a series of 51 years of the isotopic composition  $^{15}\text{N}/^{14}\text{N}$  in the plankton of the region off central California and found that some species alter their  $^{15}\text{N}/^{14}\text{N}$  composition in response to climate change like El Niño. Additionally, Capone (2001) suggest that marine nitrogen fixation is one of the key components in a suite of interactions and feedbacks between the ocean and atmospheric  $\text{CO}_2$ . The marine ecosystems can store 50 times more inorganic carbon than the atmosphere, and, consequently, some marine primary producers can play an important role in controlling the global climate (Downing 1997).

Primary and secondary plankton production sustains over 90 million tons per year of marine organisms used for human consumption (FAO 2008). Information on the carbon (C), nitrogen (N), and phosphorus (P) concentrations of marine plankton (i.e., C/N/P stoichiometry) and associated factors that regulate marine production are a prerequisite for material budgetary assertions, ecological monitoring of the food web, and the detection of likeable climate change effects, being thus also of social and economic value.

Brazil harbors a coastline with an extension of 7367 km ( $5^{\circ}16'19''$  N to  $33^{\circ}45'09''$  S), which stretches along more than 60 % of the Southwest Atlantic Ocean margin (Ekau and Knoppers 1999). In spite of the manifold studies dealing with the species composition of plankton, there is great paucity of information on the elemental composition of phyto- and zooplankton, with some data being restricted to the oligotrophic South Equatorial Current, which impinges upon the continental shelf of the Northeast and the Brazil Current along the East (Schwamborn et al. 1999; Ara 2001).

The southeastern Brazilian coast and shelf between  $22^{\circ}$  S (Cabo de São Tomé) and  $28^{\circ}$  S (Cabo de Santa Marta Grande) are prone to the highest fisheries yields of Brazil. This is in part due to the presence of three local areas of surface coastal upwelling, set off Cabo de São Tomé ( $22^{\circ}$  S), Cabo Frio ( $23^{\circ}$  S), and Cabo de Santa Marta Grande ( $28^{\circ}$  S), and sub-surface shelf-edge upwelling along the entire SE Brazil Shelf (SEBS) (Rossi-Wongtchowski and Madureira 2006; Marone et al. 2010). However, the intensity, spatial coverage, and biological production of the local intermittent surface upwelling systems of SE Brazil does by far not reach those of the large and permanent upwelling regions of the western active continental margins of the world (Walsh 1988).

The Cabo Frio upwelling region is of ecological and economic importance (fisheries and tourism) and serves for the recruitment of species like squids, sardine, and anchovy (Valentin 2001). The abundance of organisms during upwelling events provides a source of food for species at the top of the food chain such as carnivorous fish, seabirds, and marine mammals.

The aim of this study was to investigate the C, N, and P concentrations of the plankton community from the semienclosed Cabo Frio Bay, set slightly eastwards of the main focus of the Cabo Frio upwelling, verify if it is influenced by intrusions of the Cabo Frio upwelling and how they affect the nutrient regime and the C/N/P stoichiometry of the bay's waters.

## Methods

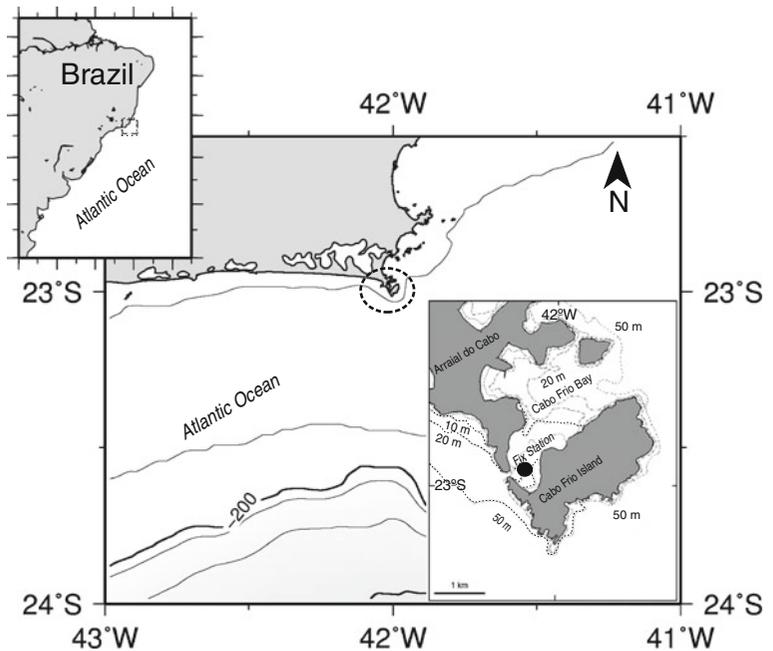
### Study area

Cabo Frio Bay is a small enclosed embayment located along the east–west-oriented coast of Cabo Frio, State of Rio de Janeiro, SE Brazil ( $23^{\circ}01'$  S,  $42^{\circ}00'$  W, Fig. 1). The bay has a surface area of approximately  $7\text{ km}^2$ , a mean depth of 12 m, and is embedded between the Cabo Frio promontory and Cabo Frio Island (Fig. 1). It has access to the sea via two openings. The 150-m wide and 18–38-m deep Boqueirão Channel, set at its southern premises between the promontory and Cabo Frio Island, and the 1.5-km wide and 9–15-m deep opening in the north, between the Cabo Frio and Porcos islands (Fig. 1).

The climate governing the Cabo Frio promontory is typical of a local microclimate being close to Köppen Type BSw, governed by hot and dry north–northeasterly winds in spring and summer and the passage of colder SE polar fronts during autumn and winter, and a low annual average rainfall of 823 mm. The contribution of fresh water inflow is unknown, only few intermittent rivulets mark the area, and the average evaporation/precipitation balance ratio is 1.3 (Barbieri 1984).

Apart from its climate and physiographical configuration, Cabo Frio Bay still lacks further information on the governing physical–biogeochemical processes. As this contribution addresses for the first time the C/N/P stoichiometry of its plankton and the influence of allochthonous sources upon, it becomes necessary to describe the boundary conditions of the oceanographical processes operating on the shelf, which potentially may

**Fig. 1** Sampling site at the Cabo Frio Bay, RJ, Brazil



affect the bay by the exchange of water through its southern and northern accesses to the sea.

The Cabo Frio coastal-shelf region, including Cabo Frio Bay, constitutes an unusual local realm of the tropical Brazilian coast. The region is located at the oceanographical, geomorphological, and biogeographical transition zone between the East Brazil Shelf (EBS) and the northern portion of the SEBS (Castro and Miranda 1998; Knoppers et al. 1999; Mahiques et al. 2005; Marone et al. 2010). The division between both shelf sectors is particularly marked by a sudden switch in the direction of the coast and shelf from north–south (i.e., EBS) towards east–west (i.e., SEBS) (Fig. 1). When northeasterly trade winds prevail in spring and summer, coastal upwelling of waters off Cabo Frio is induced. The upwelling events are also enhanced by a bathymetrical effect due to the directional shift of the shelf, forcing the northwards deeper flowing colder South Atlantic Central Waters (SACW) to proliferate from the shelf edge along the shelf bottom to the inner shelf (i.e., subsurface upwelling). Concomitant to the interplay between these features, the oligotrophic southwards meandering Brazil current (BC) flows closer to the coast and shear effects by the

sudden shift in direction of the shelf generate local eddies (Castro and Miranda 1998; Carbonel 2003; Calado et al. 2010; Belém et al. 2003).

The water masses that interact on the Cabo Frio shelf, and potentially affect Cabo Frio Bay, are the tropical surface waters (TSW) of the BC (TSW; temperature >20 °C, salinity >36), the coastal waters (CW; temperature >18 °C, salinity <35), and the SACW (temperature 6 to <18 °C; salinity, 34.5–35.9) (Castro and Miranda 1998; Braga and Niencheski 2006). The dissolved inorganic nitrogen (DIN) and phosphorous (DIP) concentrations of SACW at the shelf edge ( $z \approx 150$  m) oscillate around 10–20  $\mu\text{M}$  DIN and 0.3–0.8  $\mu\text{M}$  DIP, which diminish after mixing with the nutrient poor CW and/or TSW during upwelling up to the surface at the inner shelf (Knoppers and Pollehne 1991; Belém et al. 2003). The upwelling waters at the surface are manifested by a slightly colder plume, generally >16 °C after upward mixing, and reaches on average 104 km in a SSE direction (Castro et al. 2006).

The Cabo Frio inner shelf waters exhibit a primary productivity of 2–14  $\text{mg C m}^{-3} \text{ h}^{-1}$  (Gonzalez-Rodriguez et al. 1992). Primary production rates integrated over a

30-m water column from 0.5 to 0.8 g C m<sup>-2</sup> day<sup>-1</sup> have been registered during upwelling in summer (Knoppers and Pollehne 1991). The plankton community is dominated by diatoms (*Asterionella glacialis*, *Skeletonema costatum*, *Chaetoceros* sp., *Rhizosolenia* sp., *Paralia sulcata*, *Melosira nummuloides*, *Diploneis bombus*, *Diploneis didyma*, *Pleurosigma naviculaceum*, *Pleurosigma nomani*, *Pleurosigma elongatum*, *Nitzschia closterium*, *Nitzschia panduriformis*, *Nitzschia sigma*, *Rhaphoneis surirella*, *Navicula pennata*, *Cocconeis scutellum*, *Licmophora abbreviata*, and *Cyclotella stylonum*), the copepods (*Euaetideus giesbrechti*, *Haloptilus longicornis*, *Rhincalanus cornutus*, *Temeropsis mayumbaensis*, *Pleuromamma piseki*, *Heterorhabdus papilliger*, *Calanoides carinatus*, and *Ctenocalanus vanus*), and Tunicates (Salps and Doliolida) (Bassani et al. 1999). Furthermore, the area has a distinct biological community in comparison to other tropical coastal regions of Brazil, with the presence of some cold-water planktonic species, mollusks and fish (i.e., *Sargocentron bullisi*) endemic to this region (Figueiredo and Menezes 1980; Absalão 1989).

### Sample collection

A total of 134 water samples and 24 plankton samples were collected at a fixed station at the southern premises of Cabo Frio Bay (Fig. 1). The water samples were collected at the surface and the bottom layers with a Nansen bottle at weekly intervals during two distinct periods: from September 2003 to January 2005 and from April 2008 to June 2009. The physico-chemical parameters in the water samples were analyzed by the Brazilian Navy Research Institute (Instituto de Estudos do Mar Almirante Paulo Moreira). Temperature was measured with a reversing thermometer and the dissolved inorganic nutrients (phosphate, nitrate, nitrite, and ammonium) were determined according to Grasshoff et al. (1983).

The plankton samples were collected monthly in the Cabo Frio Bay during the same periods (from September 2003 to January 2005 and from April 2008 to June 2009). Only during January of 2009, the sampling was performed weekly. Plankton samples were taken by horizontal hauls with nets with the following mesh sizes: 64 and 100  $\mu\text{m}$  (during 2003–2005), and 20, 64, and 150  $\mu\text{m}$  (during 2008–2009).

### Analytical techniques

The plankton samples were lyophilized during 24 h prior to carbon, nitrogen, and phosphorus determination. The C and N analysis were performed in triplicate using a Perkin-Elmer elemental analyzer CHNS/O 2400 Series II. The equipment calibration and quality control analysis were performed using the certified reference material acetanilide. The results showed recoveries for carbon of 100.5 $\pm$ 0.3 % and nitrogen 100.7 $\pm$ 0.2 %.

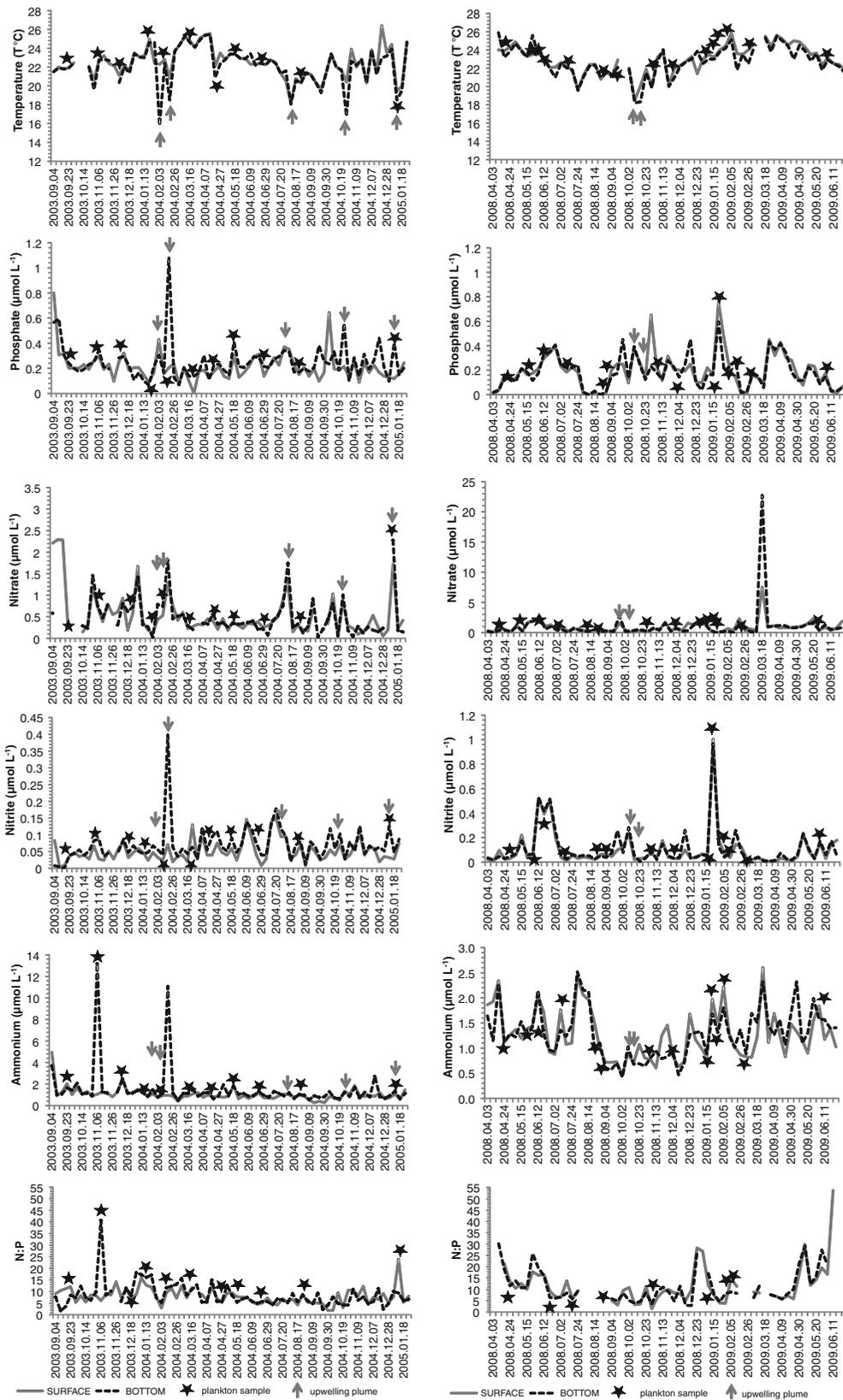
P was analyzed in triplicate employing the colorimetric method adapted of Grasshoff et al. (1983). About 15 mg of plankton was digested for 1 h (150 °C) with oxidative solution (K<sub>2</sub>O<sub>8</sub>S<sub>2</sub>+H<sub>3</sub>BO<sub>3</sub>+NaOH) in a pressure cooker. Thereafter, an ascorbic acid solution containing sulfuric acid H<sub>2</sub>SO<sub>4</sub> (50 %), (NH<sub>4</sub>)<sub>6</sub>Mo<sub>7</sub>O<sub>24</sub>.4H<sub>2</sub>O+K(SbO)C<sub>4</sub>H<sub>4</sub>O<sub>6</sub>, and ultrapure water was added to each sample. Then, samples were rested in the dark for 30 min, and the phosphorus concentration was determined. The quality control of the analysis and spectrophotometer (Shimadzu) calibration was obtained by employing blank samples and standard with phosphate solution of 1,000 mg L<sup>-1</sup> Merck®.

## Results

### Water properties

Figure 2 shows the results obtained for the physical–chemical parameters during the study periods. During the period of September 2003 to January 2005, the mean water temperature was 22.5 $\pm$ 1.6 °C (varying from 18.2 to 26.4 °C) at the surface and 22.1 $\pm$ 1.9 °C (varying from 15.8 to 25.4 °C) at the bottom. Temperatures below 18 °C were registered five times during this period, indicating the intrusion of upwelling waters in the bay. In contrast, the period from April 2008 to June 2009 exhibited warmer waters with mean temperature of 23.0 $\pm$ 1.5 °C (ranging from of 18.5 to 25.8 °C) at surface and 22.7 $\pm$ 1.6 °C (ranging from 18.2 to 25.9 °C) in the bottom layer, and only one near to negligible intrusion event of upwelling waters was registered (Fig. 2).

**Fig. 2** Temperature and concentrations ( $\mu\text{mol L}^{-1}$ ) of phosphate, nitrate, nitrite, ammonium, and N/P ratio in water during the periods of 2003–2005 ( $n=71$ ) and 2008–2009 ( $n=63$ )



The highest phosphate ( $\text{PO}_4^{3-}$ ) concentration was found during 2003–2005 (mean of  $0.21 \pm 0.1 \mu\text{mol L}^{-1}$  at the surface and  $0.25 \pm 0.1 \mu\text{mol L}^{-1}$  at the bottom). Two phosphate concentration peaks occurred during the intrusion of the upwelling waters (Fig. 2), while during the 2008–2009 period, the mean phosphate concentration was  $0.19 \pm 0.1 \mu\text{mol L}^{-1}$  in both surface and bottom layers.

The mean nitrate ( $\text{NO}_3^-$ -N) concentration of the water was  $0.53 \pm 0.5 \mu\text{mol L}^{-1}$  (range,  $<0.05$ – $2.29 \pm 0.1 \mu\text{mol L}^{-1}$ ) at the surface and  $0.49 \pm 0.4 \mu\text{mol L}^{-1}$  (range,  $<0.05$ – $2.28 \mu\text{mol L}^{-1}$ ) at the bottom during the period September 2003 to January 2005. The period from April 2008 to June 2009 presented higher mean nitrate concentrations of  $0.8 \pm 1.1 \mu\text{mol L}^{-1}$  (range of  $<0.05$ – $7.5 \mu\text{mol L}^{-1}$ ) at the surface and  $1.1 \pm 2.9 \mu\text{mol L}^{-1}$  (range of  $<0.05$ – $22.7 \mu\text{mol L}^{-1}$ ) at the bottom. Four nitrate peaks were found during 2003–2005, being associated with the upwelling waters. In contrast, the peak detected in March of 2009 did not show any association with upwelling events (Fig. 2). No relationship was found between water temperature and nitrate and phosphate concentrations during the period of April 2008 to June 2009.

Nitrite ( $\text{NO}_2^-$ -N) attained mean concentrations of  $0.05 \pm 0.03 \mu\text{mol L}^{-1}$  (ranging from 0.01 to  $0.15 \mu\text{mol L}^{-1}$ ) at the surface and  $0.07 \pm 0.05 \mu\text{mol L}^{-1}$  (ranging from 0.01 to  $0.40 \mu\text{mol L}^{-1}$ ) and at the bottom during the 2003–2005 period. Concomitant to nitrate, higher nitrite concentrations were obtained during the 2008–2009 period, with mean values of  $0.10 \pm 0.16 \mu\text{mol L}^{-1}$  (ranging from 0.05 to  $1.0 \mu\text{mol L}^{-1}$ ) at the surface waters and  $0.11 \pm 0.16 \mu\text{mol L}^{-1}$  (ranging from 0.05 to  $1.0 \mu\text{mol L}^{-1}$ ) at the bottom (Fig. 2).

The ammonium ( $\text{NH}_4^+$ -N) concentrations varied from 0.3 to  $4.9 \mu\text{mol L}^{-1}$  (mean value of  $1.0 \pm 0.6 \mu\text{mol L}^{-1}$ ) at the surface and from 0.5 to  $13.2 \mu\text{mol L}^{-1}$  (mean value of  $1.5 \pm 1.9 \mu\text{mol L}^{-1}$ ) at the bottom during the period of 2003–2005. During 2008–2009, the ammonium concentrations varied from 0.5 to  $2.6 \mu\text{mol L}^{-1}$  (mean value of  $1.3 \pm 0.5 \mu\text{mol L}^{-1}$ ) at the surface and from 0.4 to  $2.5 \mu\text{mol L}^{-1}$  (mean value of  $1.3 \pm 0.5 \mu\text{mol L}^{-1}$ ) at the bottom layer (Fig. 2).

The sum of nitrate, nitrite, and ammonium concentration was employed to express the total dissolved inorganic nitrogen (DIN) concentration of the waters and form the N/P molar ratio. The N/P ratio registered when compared to the ideal demand by phytoplankton expressed by the Redfield ratio of N/P of 16:1

(Redfield 1958) indicates which of these two elements is the potential limiting nutrient for the sustenance of primary productivity. The mean value for N/P ratio during the period of 2003–2005 was  $8.0 \pm 3.5$  (at the surface) and  $8.5 \pm 5.4$  (at the bottom), while during the period of 2008–2009, the mean N/P ratio was  $12.3 \pm 9.7$  at the surface and  $11.6 \pm 8.1$  at the bottom waters (Fig. 2). Henceforth, N was the predominantly limiting nutrient species for the phytoplankton community during the first study period, but only moderately limiting during the second period being attributed to the higher nitrate concentrations.

### C, N, and P composition of plankton

The data interpretation of the plankton samples collected by the nets with different mesh sizes was performed in accordance to the following groups of organisms:  $>20 \mu\text{m}$  (small phytoplankton),  $>64 \mu\text{m}$  (phytoplankton),  $>100 \mu\text{m}$  (zooplankton), and  $>150 \mu\text{m}$  (zooplankton). However, this fractionation using the net mesh size has drawbacks such as a mixture of phytoplankton/zooplankton/inorganic particulate matter in different proportions. Nevertheless, this classification according to the mesh size has been used in many studies (Caetano and Vale 2003; Monterroso et al. 2003; Pempkowiak et al. 2006). This classification is justified because of the environmental characteristics of Cabo Frio Bay and the kind of plankton community in this region. The presence of phytoplankton in the nets with meshes of 100 and  $150 \mu\text{m}$  is possible when longer cylindrical species like *Rhizosolenia* sp. and long-chained diatoms prevail in the region (Bassani et al. 1999). However, the predominant phytoplankton in this region are the diatoms  $<65 \mu\text{m}$  and some dinoflagellates (Valentin and Kempf 1977; Guenther et al. 2008).

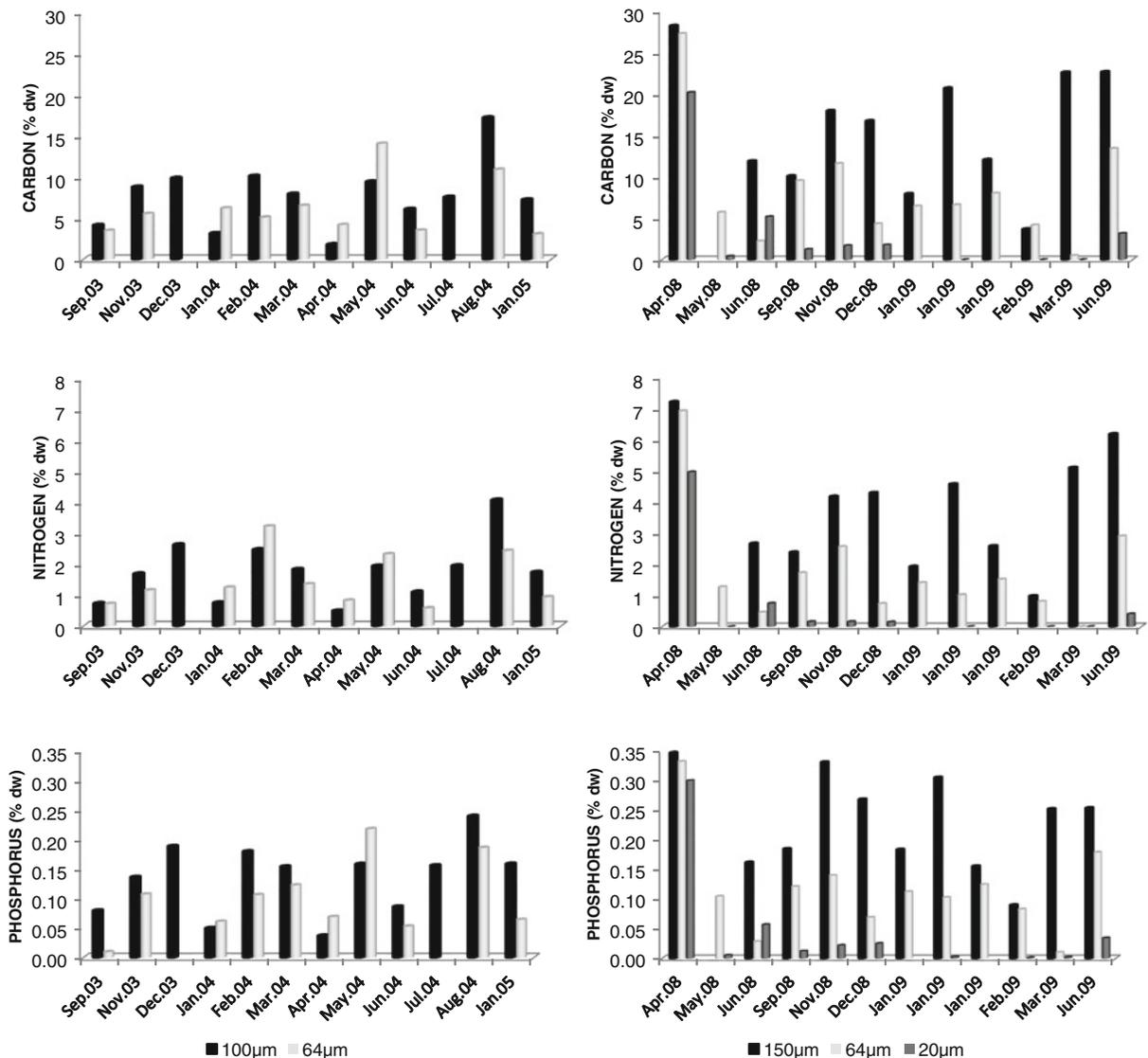
The results from the period of 2003 to 2005 were marked by five events of cooler water intrusions from the Cabo Frio upwelling. Notably, the plankton community showed C and N contents ranging from 1.78 to 17.18 % C and from 0.48 to 4.07 % N for zooplankton ( $100 \mu\text{m}$ ) and from 3.08 to 14.08 % C and from 0.58 to 3.23 % N for the phytoplankton ( $64 \mu\text{m}$ ). In contrast, during the period of 2008–2009, when upwelling intrusion events were negligible, the C and N contents in the plankton community ranged from 3.65 to 28.18 % C and from 0.97 to 7.21 % N for the zooplankton ( $150 \mu\text{m}$ ); from 0.50 to 27.28 % C and from  $<0.07$  to

6.93 % N for the phytoplankton (64  $\mu\text{m}$ ); and from <0.27 to 20.18 % C and from <0.07 to 4.94 % N for the small phytoplankton (20  $\mu\text{m}$ ) (Fig. 3). The range of P contents was from 0.037 to 0.24 % for zooplankton (100  $\mu\text{m}$ ) and from 0.010 to 0.219 % for the phytoplankton (64  $\mu\text{m}$ ) during the 2003–2005 period, while during 2008–2009, the P concentrations ranged from 0.089 to 0.346 % in the zooplankton community (150  $\mu\text{m}$ ), from 0.010 to 0.332 % in the phytoplankton (64  $\mu\text{m}$ ), and from 0.001 to 0.300 % for the small phytoplankton (20  $\mu\text{m}$ ) (Fig. 3).

### Discussion

#### Water properties

A model based on 10 years of data series of weekly water sampling found an average concentration of nutrients in Cabo Frio Bay waters of 0.28  $\mu\text{mol L}^{-1}$  for phosphate, 0.13  $\mu\text{mol L}^{-1}$  for nitrite, 1.0  $\mu\text{mol L}^{-1}$  for nitrate and 0.95  $\text{mg m}^{-3}$  for chlorophyll-a (Pereira et al. 2008). However, during upwelling events at the coast outside of to the bay, concentrations of 5–



**Fig. 3** Carbon, nitrogen, and phosphorous concentrations in zooplankton (100 and 150  $\mu\text{m}$ ), phytoplankton (64  $\mu\text{m}$ ), and phytoplankton/inorganic particulate matter (20  $\mu\text{m}$ ) during 2003–2005 and 2008–2009 sampling periods

10  $\mu\text{mol L}^{-1}$ , (exceptionally  $\geq 15 \mu\text{mol L}^{-1}$ ) for nitrate, 0.6–1  $\mu\text{mol L}^{-1}$  for phosphate,  $\geq 10 \mu\text{mol L}^{-1}$  (occasionally  $\geq 15 \mu\text{mol L}^{-1}$ ) for silicate and temperature between 12 and 16 °C were observed. In contrast, the TSW waters of BC generally exhibit concentrations of  $\leq 1 \mu\text{mol}$  (nitrate), 0.2  $\mu\text{mol L}^{-1}$  (phosphate),  $< 5 \mu\text{mol L}^{-1}$  (silicate), and 22 to 26 °C (Valentin and Kempf 1977; Bassani et al. 1999).

The nutrients concentration found in the water samples during the present work were within the lower range of the historical data series reported in the literature for the Cabo Frio Coast (Moser and Giancesella-Galvão 1997; Bassani et al. 1999; Pereira et al. 2008), and the nutrient concentrations during the intrusion of upwelled waters did by far not attain the above described high concentrations during stronger events of the Cabo Frio upwelling outside the bay. Both the temperature and nutrient records inside the bay indicated that upwelling may sporadically affect the bay's waters, but TSW and CW play a dominant role. It is postulated that these water masses wash out the bay even when moderate north–northeasterly winds prevail, enhancing their intrusion via the larger northwards oriented opening and outflow through the Boqueirão Channel. However, the intrusion of the upwelled waters during the first study period also indicate that both wind regime and the microtides (maximum range of 1.3 m) act in concert for the intrusions via the southwards oriented Boqueirão Channel. In all, the upwelled water intrusions corresponded to diluted waters by TSW and/ or CW.

During the period of 2003–2005, the intrusion of the upwelled waters occurred more frequently in the Bay, the N/P ratio above 16 reached 1.4 % of the samples at the surface and 7.2 % at the bottom. However, the N/P ratio above 16 covered 22.6 % of the samples at the surface and 21.2 % at the bottom during 2008–2009 period, indicating the presence of a higher frequency of events characterized by P limitation during this period in comparison to the former.

As the period of 2003–2005 exhibited five events of colder upwelling water intrusions, it is envisaged that dissolved inorganic phosphate could have been released from the surface pore waters from the bottom sediments by the process of density displacement, resulting in a decrease in the N/P ratio. The period of 2008–2009 with negligible upwelling water intrusions exhibited higher N/P ratios. Ammonia, a logical candidate to support the release of bottom sediment pore

waters, did not behave in a similar fashion as phosphate. Its presence is likely due to ammonification in the water column. It must be borne in mind that the sediments are largely composed of sands (Kütter, personal communication). The periods marked by the presence of warmer water masses (i.e., TSW and/or CW) lacked stratification of the water column, permitting a closer coupling of the water column and the sediments and nitrogen remineralisation in both compartments. Metzler et al. (1997) reports that most of the production in the warm waters of the Brazilian shelf (i.e., TSW) is regenerated primary production with  $f$  ratios of 0.16 in the surface waters.

One should not discard the presence of planktonic marine nitrogen fixing cyanobacteria, which are regarded as a relevant source of atmospheric nitrogen to the euphotic zone (Capone 2001). The presence of the cyanobacteria *Phormidium* and *Trichodesmium* along the Cabo Frio inner shelf during the prevalence of TSW has been observed, but has as yet to be published (Kütter, personal communication). Along the Northeast Brazil Shelf (NBS); governed by the impingement TSW from the ultraoligotrophic South Equatorial Current (SEC) (Castro and Miranda 1998; Ekau and Knoppers 1999), other cyanobacteria like *Oscillatoria eurythraeum* together with phytoflagellates dominated the phytoplankton community (Medeiros et al. 1999). In the same region, Schwamborn et al. (1999) also reports on the predominance of the same cyanobacterial species together with low  $\delta^{15}\text{N}$  values of the zooplankton indicating that  $\text{N}_2$ -fixing cyanobacteria might be ingested by zooplankton. Susini-Ribeiro et al. (1999) also reported on the presence of several species of cyanobacteria, including two of the genus *Oscillatoria* sp. Moreover, the diatom species (e.g., *Hemiaulus hauckii*) was also found in Cabo Frio Bay, which may contain endosymbiotic cyanobacteria capable of  $\text{N}_2$  fixation (Carpenter et al. 1999). It is thus postulated that cyanobacteria might play a role in the nitrogen cycle of Cabo Frio Bay during predominance of TSW. However, the sampling technique of phytoplankton with the net of mesh size  $> 20 \mu\text{m}$  did not reveal any massive conglomerations of organic matter derived from cyanobacteria and is of course inapt to sample cyanobacteria when present in lower densities.

Table 1 depicts a comparison among water nutrient concentrations in Cabo Frio Bay and other areas. The Cabo Frio Bay is nutrient poor being similar to the concentrations of TSW from the BC and the SEC of the

**Table 1** Concentrations ( $\mu\text{mol L}^{-1}$ ) of nutrients in water from Cabo Frio Bay compared with different areas

Site	Deep measured (m)	Mean (min–max) ( $\mu\text{mol L}^{-1}$ )					Reference
		$\text{PO}_4^{2-}$	$\text{NO}_2^-$	$\text{NO}_3^- \text{N-N}$	$\text{NH}_4^+$	N/P	
Sargasso Sea— Bermuda	<50	<0.05	<0.05	<0.05	<0.05	35.0	A, B, C
Inland Sea— Japan	<10	0.43 (0.2–8.9)	–	(0.5–15.0) <sup>a</sup>	27.6 (3.7–123.0)	14.3 (2.2–61.3)	D, E, F
Iberian Peninsula	<20	(<0.2–0.7)	(0.3–0.5)	(<0.5–6.0)	(0.1–2.0)	(17.0–18.7)	G, H, I, J
Benguela upwelling	<30	(1.36–1.65)	–	(0.03–30.0)	–	(10.0–40.0)	K, L, M
Baltic Sea	<10	(0.05–2.5)	–	(1.0–35.0) <sup>a</sup>	–	(6.0–70.0)	N, O, P
Cabo Frio Bay	<10	0.21 (<0.02–1.08)	0.09 (0.01–1.0)	0.84 (<0.05–22.7)	1.27 (0.3–13.2)	9.8 (1.5–53.7)	This study

Data are represented by mean (minimum and maximum)

A Babiker et al. (2004); B Lipschultz (2001); C Michaels et al. (1994); D Nakamura et al. (1993); E Nishikawa et al. 2010; F Magni and Montani (2000, 2002); G Varela et al. (2010); H Casas et al. (1997); I Prego et al. (2012); J Alvarez-Salgado et al. (1997); K Silió-Calzada et al. (2008); L Andrews and Hutchings (1980); M Calvert and Price (1971); N Wan et al. (2011); O Wasmund et al. (2001); P HELCOM (2009)

<sup>a</sup>Nitrate+nitrite

northeastern and eastern shelves. The exception was found in the area of the Sargasso Sea in the North of Atlantic showing lower nutrient concentrations than the Cabo Frio Bay.

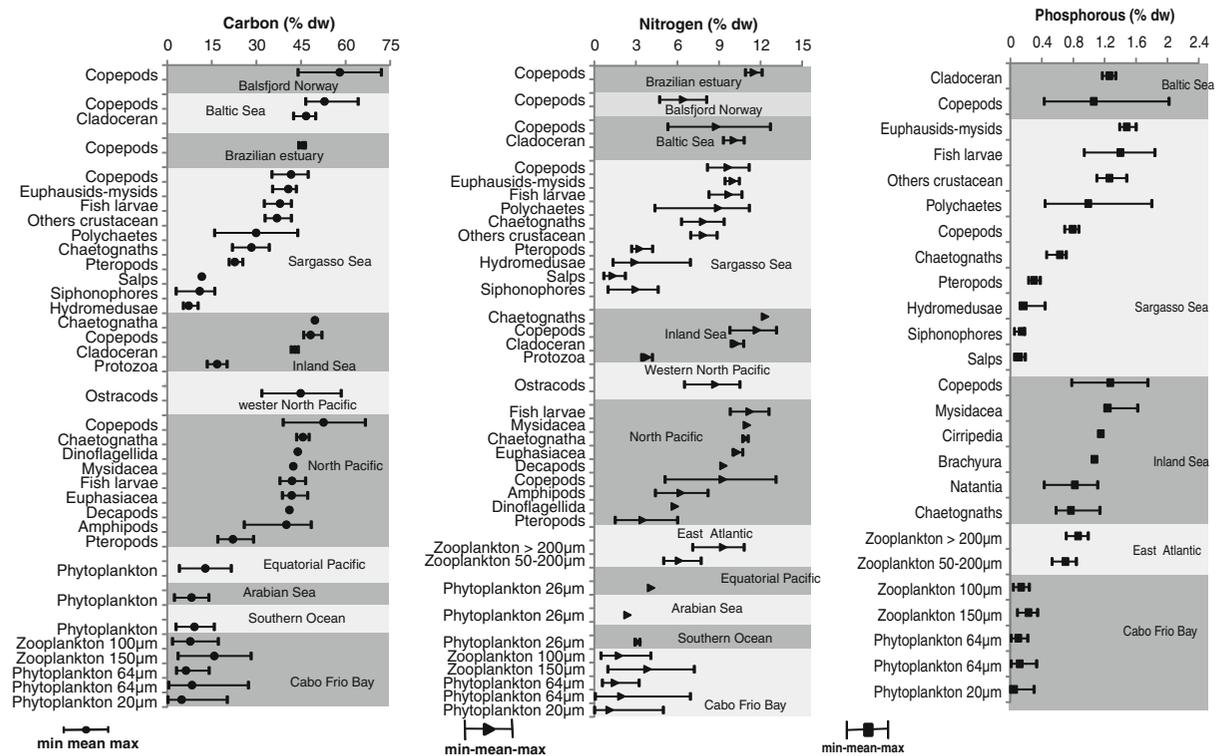
The rather low nutrient concentrations monitored in Cabo Frio Bay not only suggest that the bay is oligotrophic but also that anthropogenic inputs of effluents or even surface runoff of fertilizers are negligible.

### C, N, and P composition of plankton

The mean C content of 7.7 % (100  $\mu\text{m}$  net) and 15.8 % (150  $\mu\text{m}$  net) found in the zooplankton of Cabo Frio Bay are two to five times lower in comparison to other sites (Fig. 4). The average data of C content was 52.1 % (Copepods and Cladocerans) in the Baltic Sea, 45.1 % (Pteropods+Copepods+Anphipods+Euphasiacea+Decapods+Chaetognatha+Mysidacea+fish larvae) in the North Pacific, 45.6 % of copepods in the estuary of Cananéia, SE Brazil, 44.6 % (Protozoa+copepods+cladoceran+Chaetognatha) in the Inland Sea of Japan and 28.5 % (Copepods+Euphausids-mysids+Chaetognatha+Hydromedusae+Pteropods+Fish larvae) in the Sargasso Sea (Fig. 4). The phytoplankton (64 and 20  $\mu\text{m}$  net) in the Cabo Frio Bay

showed mean C content of 7.2 and 3.1 %, respectively, indicating the same behavior found for the zooplankton, and with values two to three times lower in comparison to phytoplankton in the Equatorial Pacific (21.5 %), Arabian Sea (14.0 %), and Southern Ocean (14.9 %) (Fig. 4).

In spite of the surprisingly low C contents found for the zooplankton in Cabo Frio Bay, recent studies dealing with the sedimentation of particulate matter from the deployment of sediment traps in 50- and 100-m depth at the Cabo Frio shelf edge (Albuquerque et al. 2014) recorded zooplankton C contents within the lower range of other regions. For example, the *Swimmers* captured by the sediment traps were the Salpidae with 29 % C, Hydromedusae with 9.1 % C, Bivalves with 19.2 % C, and Pteropods ranging from 16 to 22 % C. Other *Swimmers* including Copepods, Appendicularia, Ostracods, and Polychaete larvae harbored C contents ranging from 40 to 50 %, being similar to the contents of other regions (Botero, unpublished MSc thesis). Unfortunately, the C, N, and P analyses correspond to the bulk values of the net fractionated plankton. However, during summer, Salpidae, Doliolids, Cnetophores, and Pteropods form a large fraction of the zooplankton (Valentin 2001) and are massively washed upon the



**Fig. 4** Carbon, nitrogen, and phosphorous contents (% dw) in plankton from Cabo Frio Bay in comparison with other sites [data from: Ara (2001), Gronvik and Hopkins (1984), Walve and

Larson (1999), Beers (1966), Hedges et al. (2002), Kaeriyama and Hikedada (2004), Uyet and Matsuda (1988), Omori (1969), Hirota (1981), and Le Borgne (1982)]

beaches of the Rio de Janeiro coast during summer (Knoppers, personal communication). It is postulated that the low zooplankton C contents encountered were in part brought about by the presence of the more gelatinous organisms.

The zooplankton communities of Cabo Frio Bay harbored mean N content of 1.77 % (100  $\mu\text{m}$  net) and 3.82 % (150  $\mu\text{m}$  net) being two to five times lower than those found in zooplankton of other oceans, such as the Inland Sea of Japan with N contents of 10.8 %; the Baltic Sea with 10.1 %; the Cananéia estuary, SE Brazil, with 11.45 %; the East Atlantic Ocean, Africa, with 9.3 % (net 200–5,000  $\mu\text{m}$ ) and 6.1 % (50–200  $\mu\text{m}$  net); and the North Pacific and Sargasso Sea with 8.66 % and 7.1 %, respectively (Fig. 4). The phytoplankton of Cabo Frio Bay showed a mean N concentration of 1.7 % (64  $\mu\text{m}$  net) and 1.1 % (20  $\mu\text{m}$  net), and these were two to four times lower than mean contents in phytoplankton of Equatorial Pacific (4.0 %), Southern Sea (3.1 %), and Arabian Sea (2.38 %) (Fig. 4). The mean P content of the zooplankton of Cabo Frio bay of 0.14 % (net 100  $\mu\text{m}$ ) and

0.23 % (net 150  $\mu\text{m}$ ) was also considerably lower than other regions (Fig. 4).

However, the mean C/N ratio found in the Cabo Frio Bay zooplankton was similar to those reported by Schwaborn et al. (1999). The author encountered a mean value of  $5.4 \pm 0.7$  for zooplankton (>300  $\mu\text{m}$ ) along the northeast coast of Brazil. In comparison to other regions (Fig. 5), the Cabo Frio Bay results of the C/N ratios were also similar. Le Borgne (1982) found no differences in the C/N ratios among samples during upwelling and no upwelling periods in the East Atlantic Ocean. In contrast, the phytoplankton (>20  $\mu\text{m}$ ) of Cabo Frio Bay showed a higher C/N ratio in comparison to other sites (Fig. 5). Phytoplankton showed higher N/P ratios than the zooplankton, except for the fraction of 20  $\mu\text{m}$ . The zooplankton N/P ratio lied in the same order of magnitude as found for the Sargasso Sea (31.5:1; Fig. 5)

**Fig. 5** C/N, C/P, and N/P ratios of plankton from the Cabo Frio Bay in comparison with other sites [data from Ara (2001), Gronvik and Hopkins (1984), Walve and Larson (1999), Beers (1966), Hedges et al. (2002), Kaeriyama and Hikedada (2004), Uyet and Matsuda (1988), Omori (1969), Hirota (1981), Le Borgne (1982)]



Hasset et al. (1997) reported for the North Atlantic Ocean an N/P ratio higher in the marine zooplankton than for seston with mean values of 24:1 (range, 19:1 to 27:1). Copepods, for example, in the Sargasso Sea showed an N/P ratio of 27:1, the zooplankton in Antarctic waters 40:1 for copepods, 30–39:1 for Salpidae, and 20–30:1 for krill. Information on the geographical variation of N/P ratios of seston has been compiled by Sterner et al. (2008), and further data on the C/P ratios are depicted in Fig. 5. Hasset et al. (1997) also reported that the N/P ratio in marine zooplankton has been found to be consistently higher than the Redfield ratio of 16:1, suggesting that this group of organisms selectively stores more nitrogen than phosphorous in comparison to its phytoplankton food source, likely to avoid impoverishment of nitrogen under nitrogen limiting conditions as is the case for the majority of oligotrophic oceanic currents.

The major finding of this study was that the C, N, and P contents were surprisingly low, but the C/N, N/P, and C/P ratios of the zooplankton were within the same range reported in other studies.

Furthermore, the bulk C, N, and P values can be related to the fact that the Cabo Frio Bay has a mixture of taxa, since the abundance of a particular group is very important in the elemental composition of the sample. Cabo Frio Bay showed an abundance of zooplanktonic gelatinous species (*Doliolida* and *Salps*) that have low carbon in its composition (Beers 1966; Small et al. 1983), and diatoms were predominant (>80 %). According to Weber and Deutsch (2010), the N/P ratios observed in marine phytoplankton span at least an order of magnitude and vary two distinct levels of biological organization: phylogenetic differences between species and large taxonomic groups and phenotypic variability between populations of the same species that are adapted to different physical or chemical environments.

Cabo Frio bay exhibited low nutrient contents and nitrogen limitation in the water column and low carbon, nitrogen, and phosphorous concentrations of the planktonic communities, suggesting the presence of oligotrophic conditions, similar to those of the northeast and east Brazilian shelf waters, which are washed out by warm TSW from the nutrient poor and nitrogen limited western boundary currents. The C/N/P ratios of Cabo Frio Bay should serve as a baseline for the future monitoring of the impact of temperature increases derived from climate change, as well as probable anthropogenic activities, as the system is still oligotrophic.

The lower C contents of the phytoplankton could also be partly the result of the presence of nitrogen fixation. According to Klausmeier et al. (2004), the N<sub>2</sub> fixation is energetically costly, leading to less C incorporated per unit light energy absorbed. The latter corresponds to relevant issue to be further pursued as reports on N<sub>2</sub>-fixing cyanobacteria are emerging, but have to as yet to be published.

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## References

- Absalão, R. S. (1989). Padrões distributivos e zoogeografica dos moluscos da plataforma continental brasileira. Parte III. Comissão Oceanográfica Espírito Santo I. *Memórias do Instituto Oswaldo Cruz*, 84(4), 1–6.
- Albuquerque, A. S., Belém, A. L., Zuluaga, F. J. B., Cordeiro, L. G. M., Mendoza, U., Knoppers, B., Gurgel, M. H. C., Meyers, P. A., Capilla, R. (2014). Particle fluxes and bulk biogeochemical characterization of the Cabo Frio Upwelling System in southeastern Brazil. *Revista da Academia Brasileira de Ciências*, Rio de Janeiro, 86 (2).
- Alvarez-Salgado, X. A., Castro, C. G., Perez, F. F., & Fraga, F. (1997). Nutrient mineralization patterns in shelf waters of the Western Iberian upwelling. *Continental Shelf Research*, 17(10), 1247–1270. doi:10.1016/S0278-4343(97)00014-9.
- Andrews, W. R. H., & Hutchings, L. (1980). Upwelling in the Southern Benguela Current. *Progress in Oceanography*, 9, 1–81. doi:10.1016/0079-6611(80)90015-4.
- Ara, K. (2001). Length-weight relationships and chemical content of the planktonic copepods in the Cananéia Lagoon estuarine system. *Plankton Biology & Ecology*, 48(2), 121–127. São Paulo, Brazil.
- Babiker, I. S., Mohamed, M. A. A., Komaki, K., Ohta, K., & Kato, K. (2004). Temporal variations in the dissolved nutrient stocks in the surface water of the Western North Atlantic Ocean. *Journal of Oceanography*, 60, 553–562.
- Barbiere, E. (1984). Cabo Frio e Iguaba Grande, dois microclimas distintos a um curto intervalo espacial. In L. D. Lacerda, D. S. D. Araújo, R. Cerqueira, & B. Turcq (Eds.), *Restingas: Origem, estrutura, processos* (pp. 3–14). Niterói, Brazil: CEUFF.

- Bassani, C., Bonecker, A. C. T., Bonecker, S. L. C., Nogueira, C. R., Reis, J. M. L., & Nascimento, L. R. (1999). Plâncton do litoral norte do estado do Rio de Janeiro (21°00' a 23°30'S)—Análise e síntese do conhecimento. *Oecologia Brasiliensis*, 7, 99–120. doi:10.1590/S0100-736X2010000600003.
- Beers, J. R. (1966). Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. *Limnology and Oceanography*, 11(4), 520–528.
- Belém, A. L., Castelão, R. M., & Albuquerque, A. L. (2003). Controls of subsurface temperature variability in a western boundary upwelling system. *Geophysical Research Letters*, 40, 1362–1366. doi:10.1002/grl.50297.
- Braga, E. S., & Niencheski, L. F. H. (2006). Composição das massas de água e seus potenciais produtivos na área entre Cabo de São Tomé (RJ) e o Chuí (RS). In C. L. D. B. Rossi-Wongtschowski & L. S. Madureira (Eds.), *O ambiente oceanográfico da plataforma continental e do talude na região sudeste-sul do Brasil* (pp. 161–218). São Paulo: Universidade de São Paulo.
- Caetano, M., & Vale, C. (2003). Trace-element Al composition of seston and plankton along the Portuguese coast. *Acta Oecologica*, 24, S341–S349.
- Calado, L., da Silveira, I. C. A., Gangopadhyay, A., & de Castro, B. M. (2010). Eddy induced upwelling off Cape São Tomé (22°S, Brazil). *Continental Shelf Research*, 30, 1181–1188. doi:10.1016/j.csr.2010.03.007.
- Calvert, S. E., & Price, N. B. (1971). Upwelling and nutrient regeneration in the Benguela Current, October, 1968. *Deep-Sea Research*, 18, 505–523.
- Capone, D. G. (2001). Marine nitrogen fixation: what's the fuss? *Current Opinion in Microbiology*, 4, 341–348.
- Carbonel, C. A. A. H. (2003). Modelling of upwelling downwelling cycles caused by variable wind in a very sensitive coastal system. *Continental Shelf Research*, 23(16), 1559–1578. doi:10.1016/S0278-4343(03)00145-6.
- Carpenter, E. J., Montoya, J. P., Burns, J., Mulholland, M., Subramaniam, A., & Capone, D. G. (1999). Extensive bloom of a N-fixing diatom/cyanobacterial association in the tropical Atlantic Ocean. *Marine Ecology Progress Series*, 185, 273–283.
- Casas, B., Varela, M., Canle, M., González, N., & Bode, A. (1997). Seasonal variations of nutrients, seston and phytoplankton, and upwelling intensity off La Coruña (NW Spain). *Estuarine Coastal Shelf Series*, 44, 767–778. doi:10.1006/ecss.1996.0155.
- Castro, B. M., Miranda, L. B. de (1998). Physical oceanography of the Western Atlantic continental shelf located between 4°N and 34°S. In A. R. Robinson, K. H. Brink (Eds.), *The sea*, Vol. 11 (pp. 209–251). New York: Wiley.
- Castro, B. M., Lorenzetti, J. A., Silveira, I. C. A., & Miranda, L. B. (2006). Estrutura termohalina e circulação na Região entre Cabo de São Tomé (RJ) e o Chuí (Rs). In C. L. D. B. Rossi-Wongtschowski & L. S. Madureira (Eds.), *O ambiente oceanográfico da plataforma continental e do talude na região sudeste-sul do Brasil* (pp. 11–120). São Paulo: Universidade de São Paulo.
- Downing, J. A. (1997). Marine nitrogen: phosphorus stoichiometry and the global N:P cycle. *Biogeochemistry*, 37, 237–252.
- Ekau, W., & Knoppers, B. (1999). An introduction to the pelagic system of the North-East and East Brazilian Shelf. *Archive of Fisheries and Marine Research*, 47(2/3), 113–132.
- Elser, J. J., & Hassett, R. P. (1994). A stoichiometric analysis of the zooplankton–phytoplankton interaction in marine and freshwater ecosystems. *Nature*, 370, 211–213. doi:10.1038/370211a0.
- FAO. (2008). *Yearbook. Fishery and aquaculture statistic*. Rome: Food and Agriculture Organization.
- Figueiredo, J. L., Menezes, N. A. (1980). Manual de peixes marinhos do sudeste do Brasil III, Teleostei (2). Museu de Zoologia: Universidade de São Paulo.
- Gonzalez-Rodriguez, E., Valentin, J. L., André, D. L., & Jacob, S. A. (1992). Upwelling and downwelling at Cabo Frio (Brazil): Comparison of biomass and primary production responses. *Journal of Plankton Research*, 14(2), 289–306. doi:10.1093/plankt/14.2.289.
- Grasshoff, K., Ehrhardt, M., Kremling, K. (1983). *Methods of seawater analysis*. Weinheim: Verlag Chemie.
- Gronvik, S., & Hopkins, C. C. E. (1984). Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: Generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). *Journal Experts Marine Biology Ecology*, 80, 93–107. doi:10.1016/0022-0981(84)90096-0.
- Guenter, M., Gonzalez-Rodriguez, E., Carvalho, W. F., Rezende, C. E., Mugrabe, G., & Valentin, J. L. (2008). Plankton trophic structure and particulate organic carbon production during a coastal downwelling–upwelling cycle. *Marine Ecology Progress Series*, 363, 109–119. doi:10.3354/meps07458.
- Hassett, R. P., Cardinale, B., Stabler, L. B., & Elser, J. J. (1997). Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton–phytoplankton interaction. *Limnology and Oceanography*, 42(4), 648–662.
- Hedges, J. I., Baldock, J. A., Gélinas, Y., Lee, C., Peterson, M. L., & Wakeham, S. G. (2002). The biochemical and elemental compositions of marine plankton: A NMR perspective. *Marine Chemistry*, 78(1), 47–63. doi:10.1016/S0304-4203(02)00009-9.
- HELCOM (2009). Eutrophication in the Baltic Sea—An integrated thematic assessment of the effects of nutrient enrichment in the Baltic Sea region. Helsinki Commission. Baltic Sea Environment Proceeding No. 115B.
- Hirota, R. (1981). Dry weight and chemical composition of the important zooplankton in the Setonaikai (Inland Sea Japan). *Bulletin Plankton Society Japan*, 28(1), 19–24.
- Kaeriyama, H., & Ikeda, T. (2004). Metabolism and chemical composition of mesopelagic ostracods in the western North Pacific Ocean. *ICES Journal Marine Sciences*, 61, 535–541. doi:10.1016/j.icesjms.2004.03.009.
- Klausmeier, C. A., Litchman, E., Daufresne, T., & Levin, S. A. (2004). Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature*, 429, 171–174. doi:10.1038/nature02454.
- Knoppers, B., & Pollehne, F. (1991). The transport of carbon, nitrogen and heavy metals to the offshore sediments by plankton sedimentation. In W. Ekau (Ed.), *Joint Oceanographic Projects (JOPS I), Cruise Report* (pp. 25–30). Bremerhaven: Alfred Wegener Institute for Polar and Marine Research (AWI).
- Knoppers, B., Ekau, W., & Figueiredo, A. G. (1999). The coast and shelf of east and northeast Brazil and material transport. *Geo-Marine Letters*, 19(3), 171–178.

- Le Borgne, R. (1982). Zooplankton production in the eastern tropical Atlantic ocean: net growth efficiency and P:B in terms of carbon, nitrogen, and phosphorus. *Limnology and Oceanography*, 27(4), 699–706.
- Lipschultz, F. (2001). A time-series assessment of the nitrogen cycle at BAT5. *Deep-Sea Research II*, 48, 1897–1924. doi:10.1016/S0967-0645(00)00168-5.
- Magni, P., & Montani, S. (2000). Water chemistry variability in the lower intertidal zone of an estuary in the Seto Inland Sea, Japan: Seasonal patterns of nutrients and particulate compounds. *Hydrobiologia*, 432, 9–23.
- Magni, P., Montani, S., & Tada, K. (2002). Semidiurnal dynamic of salinity, nutrients and suspended particulate matter in an estuary in the Seto Inland Sea, Japan, during spring tide cycle. *Journal of Oceanography*, 58, 389–402.
- Mahiques, M. M., Bicego, M. C., Silveira, I. C. A., Sousa, S. H. M., Lourenço, R. A., & Fukumoto, M. M. (2005). Modern sedimentation in the Cabo Frio upwelling system, Southeastern Brazilian shelf. *Anais Academia Brasileira de Ciencias*, 77(3), 535–548.
- Marone, E., Knoppers, B., Souza, W. F. L., Silveira, I. C., & Godoi, S. S. (2010). The Brazil current: Physical and biogeochemical domains. In K. K. Liu, L. Atkinson, R. Quiñones, & L. Talaue-McManus (Eds.), *Carbon and Nutrient Fluxes in Continental Margins. A Global Synthesis. The IGBP Series, Global Change* (pp. 153–171). Berlin Heidelberg: Springer-Verlag.
- Medeiros, C., Macedo, S. J., Feitosa, F. A. N., & Koenig, M. L. (1999). Hydrography and phytoplankton biomass and abundance of North-East Brazilian Waters. *Archive of Fisheries and Marine Research*, 47(2/3), 133–151.
- Metzler, M. M., Glibert, P. M., Gaeta, S. A., & Ludlan, J. M. (1997). New and regenerated production in the South Atlantic off Brazil. *Deep Sea Research Part I: Oceanographic Research Papers*, 44(3), 363–384. doi:10.1016/S0967-0637(96)00129-X.
- Michaels, A. F., Knap, A. H., Dow, R. L., Gundersen, K., Johnson, R. J., Sorensen, J., et al. (1994). Seasonal patterns of ocean biogeochemistry at the U.S. JGOFS Bermuda Atlantic time-series study site. *Deep-Sea Research I*, 41(7), 1013–1038. doi:10.1016/0967-0637(94)90016-7.
- Monterroso, P., Abreu, N. S., Pereira, E., Vale, C., & Duarte, A. C. (2003). Estimation of Cu, Cd and Hg transported by plankton from a contaminated area (Ria de Aveiro). *Acta Oecologica*, 24, S351–S357. doi:10.1016/S1146-609X(03)00033-X.
- Moser, G. A. O., & Gíanesella-Galvão, S. M. F. (1997). Biological and oceanographic upwelling indicator of Cabo Frio (RJ). *Revista Brasileira de Oceanografia*, 45(1–2), 11–23.
- Nakamura, Y., Sasaki, S., Iromi, J., & Fukami, K. (1993). Dynamics of picocyanobacteria in the Seto Inland Sea (Japan) during summer. *Marine Ecology Progress Series*, 96, 117–124.
- Nishikawa, T., Hori, Y., Nagai, S., Miyahara, K., Nakamura, Y., Harada, K., et al. (2010). Nutrient and phytoplankton dynamics in Harima-Nada, Eastern Seto Inland Sea, Japan during a 35-year period from 1973 to 2007. *Estuaries and Coasts*, 33, 417–427. doi:10.1007/s12237-009-9198-0.
- Omori, M. (1969). Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. *Marine Biology*, 3, 4–10.
- Pempkowiak, J., Walkusz-Miotk, J., Beldowski, J., & Walkusz, W. (2006). Heavy metals in zooplankton from the Southern Baltic. *Chemosphere*, 62, 1697–1708. doi:10.1016/j.chemosphere.2005.06.056.
- Pereira, G. C., Coutinho, R., & Ebecken, N. F. F. (2008). Data mining for environmental analysis and diagnostic: A case study of upwelling ecosystem of Arraial do Cabo. *Brazilian Journal of Oceanography*, 56(1), 1–12. doi:10.1590/S1679-87592008000100001.
- Prego, R., Varela, M., de Castro, M., Ospina-Alvarez, N., Garcia-Soto, C., & Gómez-Gesteira, M. (2012). The influence of summer upwelling at the western boundary of the Cantabrian Coast. *Estuarine Coastal Shelf Series*, 98, 138–144. doi:10.1016/j.ecss.2011.12.009.
- Rau, G. H., Ohman, M. D., & Pierrot-Bults, A. (2003). Linking nitrogen dynamics to climate variability off central California: A 51 year record based on 15N/14N in CalCOFI zooplankton. *Deep-Sea Research II*, 50, 2431–2447.
- Redfield, A. C. (1958). The biological control of chemical factors in the environment. *American Scientist*, 46(3), 205–221.
- Rossi-Wongtschowski, C. L. D. B., & Madureira, L. S. (2006). *O ambiente oceanográfico da plataforma continental e do talude na região sudeste-sul do Brasil*. São Paulo: Universidade de São Paulo.
- Schwaborn, R., Voss, M., Ekau, W., & Saint-Paul, U. (1999). Stable isotope composition of particulate organic matter and zooplankton in NE Brazilian shelf waters. *Archive of Fisheries Marine Research*, 47(2/3), 201–210.
- Silió-Calzada, A., Bricaud, A., & Gentili, B. (2008). Estimates of sea surface nitrate concentrations from sea surface temperature and chlorophyll concentration in upwelling areas: A case study for the Benguela system. *Remote Sensing of Environment*, 112, 3173–3180. doi:10.1016/j.rse.2008.03.014.
- Small, L. F., Fowler, S. W., Moore, S. A., & Larosa, J. (1983). Dissolved and fecal pellet carbon and nitrogen release by zooplankton in tropical waters. *Deep-Sea Research*, 30(12A), 1199–1220. doi:10.1016/0198-0149(83)90080-8.
- Sturner, R. W., Andersen, T., Elser, J. J., Hessen, D. O., Hood, J. M., Mccauley, E., et al. (2008). Scale-dependent carbon:nitrogen:phosphorus seston stoichiometry in marine and freshwaters. *Limnology and Oceanography*, 53(3), 1169–1180.
- Susini-Ribeiro, S. M. M. (1999). Biomass distribution of pico-, nano- and microphytoplankton on the continental shelf of Abrolhos, East Brazil. *Archive of Fisheries and Marine Research*, 47(2/3), 271–284.
- Tyrrell, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature*, 400, 525–531. doi:10.1038/22941.
- Uyet, S., & Matsuda, O. (1988). Phosphorous content of zooplankton from the Inland Sea of Japan. *Journal of Oceanographical Society Japan*, 44, 280–286.
- Valentin, J. L. (2001). The Cabo Frio Upwelling System. In U. Seeliger & H. Kjerfve (Eds.), *Coastal marine ecosystems of Latin America* (pp. 97–105). São Paulo: Springer.
- Valentin, J. L., & Kempf, M. (1977). Some characteristics of the Cabo Frio Upwelling (Brazil). *Coastal upwelling Ecosystems Analysis Newsletter*, 6(2), 18–21.
- Varela, M., Álvarez-Ossorio, M. A., Bode, A., Prego, R., Bernárdez, P., & Garcia-Soto, C. (2010). The effects of a winter upwelling on biogeochemical and planktonic components in an area close to the Galician upwelling core: the sound of Corcubión (NW Spain). *Journal of Sea Research*, 64, 260–272. doi:10.1016/j.seares.2010.03.004.

- Walsh, J. J. (1988). *On the nature of continental shelves*. San Diego: Academic.
- Walve, J., & Larsson, U. (1999). Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: Implications for nutrient recycling. *Journal of Plankton Research*, 21(12), 2309–2321. doi:[10.1093/plankt/21.12.2309](https://doi.org/10.1093/plankt/21.12.2309).
- Wan, Z., Jonasson, L., & Bi, H. (2011). N/P ratio of nutrient uptake in the Baltic Sea. *Ocean Science*, 7, 693–704.
- Wasmund, N., Andrushaitis, A., Łysiak-Pastuszek, E., Müller-Karulis, B., Nausch, G., Neumann, T., et al. (2001). Trophic status of the South-Eastern Baltic Sea: A comparison of coastal and open areas. *Estuarine, Coastal and Shelf Science*, 53, 849–864. doi:[10.1006/ecss.2001.0828](https://doi.org/10.1006/ecss.2001.0828).
- Weber, T. S., & Deutsch, C. (2010). Ocean nutrient ratios governed by plankton biogeography. *Nature*, 467, 550–554. doi:[10.1038/nature09403](https://doi.org/10.1038/nature09403).