Biota Neotropica 16(3): e20160164, 2016
www.scielo.br/bn

biotaneotropica
ISSN 1676-0611 (online edition)

article

The composition and new records of micro- and mesophytoplankton near the Vitória-Trindade Seamount Chain

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LUBIANA, K.M.F., DIAS JÚNIOR, C. **The composition and new records of micro- and mesophytoplankton near the Vitória-Trindade Seamount Chain**. Biota Neotropica. 16(3): e20160164. http://dx.doi.org/10.1590/1676-0611-BN-2016-0164

Abstract: In spite of the length of the Brazilian coastline, studies of marine phytoplankton species in offshore areas have been largely neglected. Regarding phytoplankton species composition, the aim was to assess biodiversity status, species frequency, and the similarities at different sites along the Vitoria-Trindade Seamount Chain. Phytoplankton net samples were analyzed. One hundred and seventy five infrageneric taxa were identified. They represented four phyla, viz., Cyanobacteria, Bacillariophyta, Dinophyta, and Ochrophyta. Dinophyta was the most diverse, and its genus *Tripos* the largest contributor. This genus also represented more than half of the most common taxa in the sampled area. Thirty-five new infrageneric taxa were recorded, 12 of which are new reports for Brazil. Neritic stations assemblages were markedly different from those of seamounts and deep offshore. The high species diversity, especially among dinoflagellates can be considered typical of tropical oligotrophic waters. The new records demonstrate the gap in knowledge of phytoplankton biodiversity in Brazil.
Keywords: *South Atlantic, Tripos, oceanic islands, phytoplankton, biodiversity.*

LUBIANA, K.M.F., DIAS JÚNIOR, C. **Composição e novos registros do micro e mesofitoplâncton nas proximidades da Cadeia Vitória-Trindade**. Biota Neotropica. 16(3): e20160164. http://dx.doi.org/10.1590/1676-0611-BN-2016-0164

Resumo: O fitoplâncton marinho é negligenciado nas áreas fora da plataforma continental brasileira. Este estudo objetiva avaliar o status da biodiversidade, a frequência de ocorrência das espécies e a relação de proximidade entre as estações amostradas ao longo da cadeia Vitória-Trindade de acordo com a composição de espécies do fitoplâncton. Analisamos amostras de rede e identificamos 175 táxons infra genéricos de quatro filos: Cyanobacteria, Bacillariophyta, Dinophyta e Ochrophyta. Dinophyta teve o maior número de táxons e seu gênero *Tripos* foi o mais diversificado. Esse também representou mais da metade dos táxons muito comuns. Foram identificados 35 novos registros de táxons infra genéricos na área estudada, dentre eles 12 são novos para o Brasil. A composição de espécies nas estações neríticas foi mais distinta das estações oceânicas e sobre os montes da cadeia submersa. A alta diversidade de espécies, especialmente dinoflagelados, é típica de ambiente de águas tropicais oligotróficas. Os novos registros demonstraram a lacuna de conhecimento a respeito da biodiversidade fitoplanctônica nas regiões oceânicas no Brasil.
Palavras-chave: *Atlântico Sul, Tripos, ilhas oceânicas, fitoplâncton, diversidade.*

Introduction

In spite of the long extent of the Brazilian coastline, the study of phytoplankton in offshore areas is incipient, notwithstanding the important role of this marine community as the source of more than 45% of primary production worldwide (Field 1998). Regarding group diversity, a high range in phyla is found, since many organisms are not descended from the same lineage. The greatest species-diversity is found among diatoms (13.776 species) and dinoflagellates (3.281) (Guiry & Guiry 2015), although other groups such as haptophytes, prasinophytes and cyanobacteria, are also significant. According to Barton et al. (2010), phytoplankton composition is driven by a latitudinal gradient of species richness, whereby tropical and subtropical zones prove to be the richest.

The Vitória-Trindade Seamount Chain is located off the central coast of Brazil. Starting 175km off the coast of Espírito Santo State and extending for 950km eastward, the seamounts are disposed almost linearly at 20° and 21°S (Almeida 2006), and situated between the parallels 28° and 38°W. The chain emerged on the seafloor during the Cenozoic, simultaneously with the westward movement of the South America Plate (Almeida 2006). Trindade Island and Martin Vaz Archipelago are located at the eastern end, the farthest location from the coast (Almeida 2006, Motoki et al. 2012). The last 17 submarine banks rise higher than 2.5km from the seafloor, with more than half reaching the euphotic zone (Motoki et al. 2012).

The Brazilian current, originating from the South Equatorial Current at 10°S (Silveira et al. 2000), passes through the region transporting an oligotrophic, warm and highly saline water mass (Brandini et al. 1997, Gaeta et al. 1999). Due to low nutrient availability, these environmental conditions favor phytoplankton species that are mixotrophic, heterotrophic or diazotrophic.

The only two studies available of phytoplankton close to the Vitória-Trindade Seamount Chain, both as a part of the REVIZEE program (Tenenbaum et al. 2006, 2007), were published in Portuguese, thereby precluding access by the international scientific community. Other organisms from this region, such as cetaceans (Wedekin et al. 2014), fishes (Pinheiro et al. 2009, 2015), barnacles (Young 1999), rhodolites (Pereira-Filho et al. 2012), etc, received more attention.

On considering the extreme importance of investigating the fundamental role of phytoplankton community in marine ecosystems, their high biodiversity in tropical waters, and the few studies currently available, the aims of this study were to assess: *(i)* biodiversity status, *(ii)* frequency of occurrence of each taxon, and *(iii)* station similarity, as regards taxonomic composition of micro- and mesophytoplankton communities, close to the Vitória-Trindade Seamount Chain.

Material and Methods

Samples were collected during November of the austral spring of 2003, aboard R.V. Antares of the Brazilian Navy. Collection was by vertical trawling up to 100m deep, using a specific net (20µm mesh size). After sample concentration, a formaldehyde solution was added (final concentration 2%). The samples were then incorporated into the Phytoplankton Collection of the Federal University of Espírito Santo. Vertical profiles of salinity, temperature, and dissolved oxygen were obtained with a CTD and oximeter coupled to a rosette.

Sixteen sampling stations were arranged in two transects (Figure 1), the first comprising nine stations located over the seamount chain (19°S), and the second, seven, most of which close to individual seamounts (20°S). Distances between stations varied from 150 to 200km. One station was located at the southern end of the Abrolhos Bank (E26), another two on the continental slope (E23 and E27), and two more over the Vitória and Montague seamounts (E30 and E32, respectively). A further three were relatively close to the Jasur, Dogaressa and Columbia seamounts (E34, E36, and E38, respectively), and just one station close to Trindade Island (E40). The last seven were situated in deep offshore areas (E14, E15, E16, E17, E18, E19 and E20). The Geographical Information System (GIS) approach with Diva-Gis program v7.5 (http://www.diva-gis.org/), as well as a shape file from the Brazilian Institute of Geography and Statistics (IBGE) (http://mapas.ibge.gov.br/en/interativos/arquivos/downloads), were applied to assessing submarine bathymetry at the sampled sites.

Phytoplankton species diversity was analysed with an Olympus CX41 light microscope. Detected organisms were drawn, measured and photographed under 200x and 400x magnification (USB camera Bel IS500 5.0mp and TSView 7 images acquisition program). Digital images and drawings are available upon request. Three slides were observed for each sample using transect methodology under 100x magnification. In sequence, these taxa were identified with the appropriate bibliography (Kofoid 1905, Cupp 1943, Wood 1954, Abé 1967a, b, Balech 1967, 1971, 1979, Hallegraeff 1987, Balech 1988, Hernández-Becerril 1991, Fernández & García 1998, Botes 2002, Polat & Koray 2002, Gómez 2005, Koening & Lira 2005, Tenenbaum et al. 2006, Haraguchi & Odebrecht 2007, Islabão & Odebrecht 2011, Garcia & Odebrecht 2012, Okolodkov 2014).

The International Code of Nomenclature for Algae, Fungi and Plants (IAPT) was applied to taxonomic classification, and AlgaeBase (Guiry & Guiry 2015) to checking nomenclature. In sequence, a table was set up for indicating taxa occurrence per station, whereby percentages were obtained. This facilitated classification into categories as, *(i)* very common (≥ 70% of stations); *(ii)* common (<70% and ≥ 30%); *(iii)* uncommon (<30% and ≥ 10%); and *(iv)* rare (<10%).

Subsequently, the search focused on phytoplankton species already reported in marine waters of Brazil, with the aim of finding new records (Koening & Lira 2005, Procopiak et al. 2006, Tenenbaum et al. 2006, 2007, Haraguchi & Odebrecht, 2007, Sousa et al. 2008, Villac et al. 2008, Villac & Tenenbaum 2010, Islabão & Odebrecht 2011, Proença et al. 2011, Tiburcio et al. 2011, Garcia & Odebrecht 2012, Jardim & Cardoso 2013, Menezes et al. 2015). All species synonyms were checked through AlgaeBase, in order to confirm the records in the publications consulted.

Hierarchical clustering methods are useful for evaluating species-composition correlations between stations, thereby revealing biogeographical connections with subjacent processes (Kreft & Jetz 2010). The pvclust package v1.32 (Suzuki & Shimodaira 2006), available in R program (http://www.r-project.org/), was applied in the present case. The Ward agglomerative method, based on the binary distance of taxonomic composition among stations, was employed for inferring hierarchical clustering. Statistical confidence of dendrogram nodes was defined by approximately unbiased (AU) support values that are less biased than the traditional bootstrap (Suzuki & Shimodaira 2006).

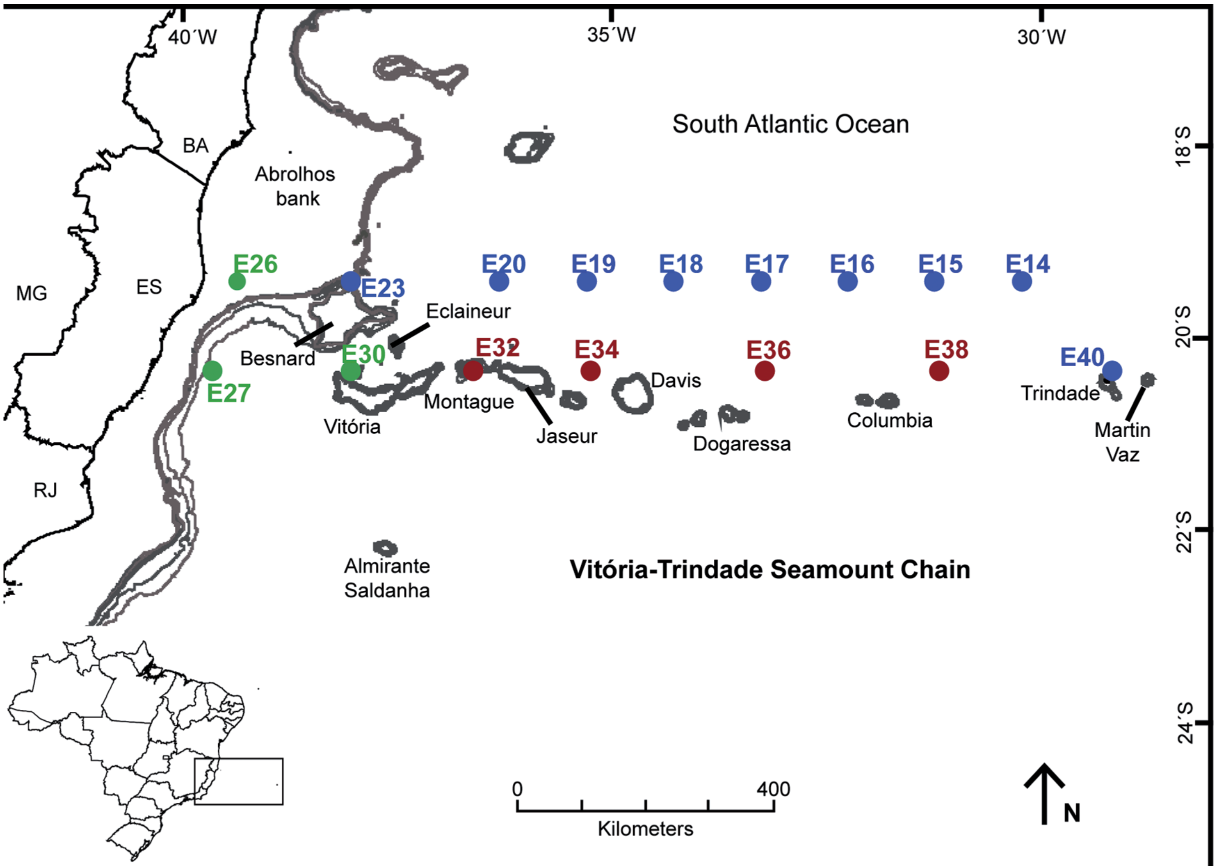

Figure 1. Map of the study area and sampling station sites. The colors of the stations are in accordance with Figure 5. Green stations are neritic, red, those closer to the Vitória-Trindade Seamount Chain, and bluethose located over deep offshore oceanic waters. The grey lines are isobaths (100- 2000 deep meters).

Results

The 175 identified infrageneric taxa of the micro and meso-phytoplankton identified were distributed among four phyla, viz., Bacillariophyta L.S.Dillon, Cyanobacteria Stanier ex Cavalier-Smith, Dinophyta F.E.Round and Ochrophyta Cavalier-Smith in Cavalier-Smiith & E.E.Chao (Table 1). The number of species registered per sample varied between 29 and 90 (average 54 ± 15.59).

The least represented phylum was Ochrophyta with only one species (0.57%) of Dictyochophyceae P.C.Silva, *Dictyocha fibula* Ehrenberg, followed by Cyanobacteria, with two species of *Trichodesmium* Ehrenberg ex Gomont (1.14%), Bacillariophyta, with 21 genera and 36 species (20.57%), and finally, Dinophyta, the most numerous, with 24 genera and 131 infrageneric taxa (74.85%) (Figure 2).

The family Rhizosoleniaceae De Toni contributed most to species diversity among the diatoms (9 species, 5.14%). Chaetocerotaceae Ralfs in Pritchard came next (5, 2.86%), followed by Coscinodiscaceae Kützing (4, 2.3%), and finally, Asterolampraceae H.L.Smith (4, 2.3%).

The order Gonyaulacales F.J.R.Taylor presented the highest number of identified taxa among all taxa (62, 35%), while its family Ceratiaceae Kofoid was the most diverse, due to the large number of *Tripos* Bory de St.-Vincent (45, 25.7%). The second, as regards orders and families, were Dinophysiales Kofoid (40 taxa, 22.52%) and Dinophysaceae Bütschli (30 taxa, 17.14%). In the Dinophysaceae, *Dinophysis* Ehrenberg and *Histioneis* Stein were the most representative, comprising 11 (6.3%) and 10 (5.7%) species, respectively.

According to frequency of occurrence, 17 taxa (9%) were very common, having been reported in more than 70% of the stations (Table 2 and Figure 3). All were dinoflagellates, ten of which *Tripos* (58.8%). *Ceratocorys horrida* Stein and *Tripos contrarius* (Gourret) F.Gómez were observed in all the stations. The common category consisted of 55 (31%) infrageneric taxa, two of which Cyanobacteria, five Bacillariophyta, and 48 Dinophyta, whereas the uncommon, 51 (29%), was comprised of one Ochrophyta, 17 Bacillariophyta, and 33 Dinophyta. Among rare taxa, 50 (28.5%) were recorded. Once again, dinoflagellates were the most diverse (31 species), followed by diatoms (19 species).

Thirty five new records of micro-and mesophytoplankton infrageneric taxa were found in the Vitória-Trindade Seamount Chain and continental shelf of Espírito Santo State, this including 12 new reports for Brazil (Table 3 and Figure 4). At a depth of 100 meters, and among stations, there was no significant change in environmental variables. Salinity varied between 37.39 and 37.055 (average 37.25) and temperatures 25.55 and 24.01°C (average 24.7ºC), thereby showing the predominance of tropical water in surface layers. Average dissolved oxygen was 4.64mg/l, this varing from 4.95 to 4.32mg/l.

Table 1. Taxa occurrence frequency throughout the sampled stations

Taxa	Taxa Frequency Occurrence																	
	Sampling stations																	
	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40	Number of occurrences	% of occurrences
Cyanobacteria																		
Cyanophyceae																		
Oscillatoriales																		
Microcoleaceae																		
Trichodesmium thiebautii Gomont ex Gomont 1890		X		X					X		X	X				X	6	37.5
Trichodesmium erythraeum Ehrenberg ex Gomont 1892		X						X	X	X	X	X	X			X	8	50
Ochrophyta																		
Dictyochophyceae																		
Dictyochales																		
Dictyochaceae																		
Dictyocha fibula Ehrenberg 1839				X							X	X				X	4	25
Bacillariophyta																		
Bacillariophyceae																		
Bacillariales																		
Bacillariaceae																		
										X	X						2	12.5
Bacillariales sp. 1											X			X	X		3	18.75
Bacillariales sp. 2									X								1	6.25
Bacillariales sp. 3													X				1	6.25
Bacillariales sp. 4		X															1	6.25
Fragilariales																		
Fragilariaceae																		
Ceratoneis closterium Ehrenberg 1839										X							1	6.25
Naviculales																		
Pleurosigmataceae																		
Pleurosigma sp.1											X						1	6.25

Continued Table 1.

	Taxa Frequency Occurrence																	
	Sampling stations																	
Taxa	**E14**	**E15**	**E16**	**E17**	**E18**	**E19**	**E20**	**E23**	**E26**	**E27**	**E30**	**E32**	**E34**	**E36**	**E38**	**E40**	**Number of occurrences**	**% of occurrences**
Coscinodiscophyceae																		
Asterolamprales																		
Asterolampraceae																		
Asterolampra marylandica Ehrenberg 1844	X	X	X	X			X						X	X	X	X	9	56.25
**Asteromphalus flabellatus* (Brébisson) Greville 1859		X															1	6.25
Asteromphalus heptactis (Brébisson) Ralfs in Pritchard 1861	X	X	X	X		X	X							X	X	X	9	56.25
***Asteromphalus stellatus* (Greville) J.J.Ralfs	X	X											X	X			4	25
Biddulphiales																		
Biddulphiaceae																		
Isthmia enervis Ehrenberg 1838											X	X	X				3	18.75
**Trigonium formosum* (Brightwell) Cleve 1867																X	1	6.25
Triceratilaes																		
Triceratiaceae																		
**Lampriscus shadboltianum* (Greville) Peragallo & Peragallo 1902											X						1	6.25
Chaetocerotales																		
Chaetocerotaceae																		
Bacteriastrum cf. *hyalinum* Lauder 1864									X								1	6.25
Chaetoceros cf. *coarctatus* Lauder 1864					X		X					X	X		X		5	31.25
**Chaetoceros* cf. *concavicornis* Mangin 1917		X															1	6.25
**Chaetoceros mitra* (Bailey) Cleve 1896		X													X		2	12.5
Chaetoceros peruvianus Brightwell 1856		X											X		X		3	18.75
Coscinodiscales																		
Coscinodiscaceae																		
Coscinodiscus cf. *centralis* Ehrenberg 1844						X					X		X				3	18.75
Coscinodiscus granii Gough 1905														X		X	2	12.5
Coscinodiscus sp.1							X			X			X		X		4	25
Coscinodiscus sp.2									X								1	6.25

Continued Table 1.

Taxa Frequency Occurrence																		
	Sampling stations																	
Taxa	**E14**	**E15**	**E16**	**E17**	**E18**	**E19**	**E20**	**E23**	**E26**	**E27**	**E30**	**E32**	**E34**	**E36**	**E38**	**E40**	**Number of occurrences**	**% of occurrences**
Hemidiscaceae																		
Hemidiscus cuneiformis Wallich 1860															X		1	6.25
Hemiaulales																		
Hemiaulaceae																		
Cerataulina pelagica (Cleve) Hendey 1937									X								1	6.25
Hemiaulus hauckii Grunow ex Van Heurck 1882		X		X									X	X	X		5	31.25
Hemiaulus membranaceus Cleve									X								1	6.25
Leptocylindrales																		
Leptocylindraceae																		
Leptocylindrus danicus Cleve 1889									X								1	6.25
Paraliales																		
Paraliaceae																		
Paralia sulcata (Ehrenberg) Cleve 1873									X								1	6.25
Rhizosoleniales																		
Rhizosoleniaceae																		
Guinardia delicatula (Cleve) Hasle in Hasle & Syvertsen 1997											X						1	6.25
Guinardia flaccida (Castracane) H.Peragallo 1892										X	X						2	12.5
Neocalyptrella robusta (G.Norman ex Ralfs) Hernández-Becerril & Meave del Castillo 1997									X	X							2	12.5
Proboscia alata (Brightwell) Sundström 1986										X		X	X				3	18.75
**Rhizosolenia castracanei* H.Peragallo 1888		X								X				X	X		4	25
Rhizosolenia hebetata Bailey 1856				X			X			X		X	X	X	X		7	43.75
Rhizosolenia imbricata Brightwell 1858		X								X							2	12.5
Rhizosolenia setigera Brightwell 1858										X							1	6.25
Rhizosolenia styliformis T.Brightwell 1858				X						X					X		3	18.75
Thalassiosirales																		
Thalassiosiraceae																		
**Thalassiosira leptopus* (Grunow ex Van Heurck) Hasle & G.Fryxell 1977					X											X	2	12.5

Continued Table 1.

Taxa	Taxa Frequency Occurrence																	
	Sampling stations																	
	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40	Number of occurrences	% of occurrences
Thalassiosira sp.1												X	X	X	X		4	25
Thalassiosira sp.2							X										1	6.25
Dinophyta																		
Dinophyceae																		
Dinophysiales																		
Amphisoleniaceae																		
Amphisolenia bidentata Schröder 1900	X	X										X			X	X	5	31.25
**Amphisolenia bifurcata* Murray & Whitting 1899	X		X	X												X	4	25
Amphisolenia globifera Stein 1883		X				X									X	X	4	25
**Amphisolenia schauinslandii* Lemmermann 1899	X	X	X				X	X			X	X				X	8	50
***Amphisolenia schroederi* Kofoid 1907							X										1	6.25
Dinophysaceae																		
Citharistes apsteinii F.Schütt 1895	X	X				X										X	4	25
**Citharistes regius* Stein 1883				X		X											2	12.5
Dinophysis acuminata Claparède & Lachmann 1859											X						1	6.25
Dinophysis argus (Stein) Abé		X	X				X									X	4	25
**Dinophysis caudata* Saville-Kent 1881									X								1	6.25
**Dinophysis fortii* Pavillard 1923									X								1	6.25
Dinophysis hastata Stein 1883	X					X	X					X			X		5	31.25
Dinophysis cf. *operculoides* (Schütt) Balech 1967		X		X		X	X	X	X		X	X	X	X	X	X	12	75
**Dinophysis pusilla* Jørgensen 1923	X	X		X								X		X	X		6	37.5
Dinophysis schuettii Murray & Whitting 1899	X	X	X	X		X	X	X			X	X	X	X	X	X	13	81.25
Dinophysis sp. 1									X								1	6.25
Dinophysis sp. 2							X					X					2	12.5
Dinophysis sp. 3		X															1	6.25
Histioneis cymbalaria Stein 1883	X	X	X	X												X	5	31.25
Histioneis elongata Kofoid & Michener 1911						X											1	6.25
***Histioneis garrettii* Kofoid & Michener 1907		X				X											2	12.5
Histioneis highleyi Murray & Whitting 1899												X					1	6.25
Histioneis inclinata Kofoid & Michener 1911													X				1	6.25
***Histioneis joergensenii* Schiller 1928						X											1	6.25

Continued Table 1.

Taxa	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40	Number of occurrences	% of occurrences
	Taxa Frequency Occurrence																	
	Sampling stations																	
Histioneis megalocopa Stein 1883	X	X	X				X	X				X	X	X	X	X	10	62.5
Histioneis milneri Murray & Whitting 1899														X	X		2	12.5
Histioneis panaria Kofoid & Skogsberg 1928	X		X														2	12.5
Histioneis para Murray & Whitting 1899	X	X	X	X										X		X	6	37.5
***Metaphalacroma skogsbergii* L.-S.Tai in L.-S.Tai & Skogsberg 1934		X															1	6.25
***Ornithocercus cristatus* Matzenauer 1933		X		X													2	12.5
Ornithocercus heteroporus Kofoid 1907	X	X		X		X					X	X		X	X	X	9	56.25
Ornithocercus magnificus Stein 1883	X	X	X	X		X	X	X		X	X	X	X		X	X	13	81.25
Ornithocercus quadratus Schütt 1900	X	X		X		X											4	25
Ornithocercus steinii Schütt 1900	X	X	X	X	X	X	X	X		X			X	X	X	X	13	81.25
Ornithocercus thumii (Schmidt) Kofoid & Skogsberg 1928				X			X						X	X		X	5	31.25
Oxyphysiaceae																		
Phalacroma cf. *doryphorum* Stein 1883	X					X										X	3	18.75
Phalacroma circumcinctum Kofoid & Michener 1911		X	X														2	12.5
Phalacroma cuneus F.Schütt 1895	X	X	X	X		X	X			X			X		X	X	10	62.5
Phalacroma hindmarchii Murray & Whitting 1899		X				X								X			3	18.75
Phalacroma rapa Jørgensen 1923		X							X			X		X			4	25
Gonyaulacales																		
Ceratiaceae																		
Tripos arietinus (Cleve) F.Gómez 2013											X	X				X	3	18.75
Tripos azoricus (Cleve) F.Gómez 2013	X	X		X	X	X	X	X	X				X	X	X	X	12	75
Tripos candelabrus (Ehrenberg) F.Gómez 2013		X			X	X	X	X		X	X	X	X		X	X	11	68.75
Tripos carriensis (Gourret) F.Gómez 2013	X			X		X	X					X	X	X	X	X	9	56.25
**Tripos cephalotus* (Lemmermann) F.Gómez 2013	X	X		X	X		X			X					X	X	8	50
Tripos concilians (Jørgenen) F.Gómez 2013	X									X		X	X		X		5	31.25
Tripos contortus (Gourret) F.Gómez 2013	X	X		X	X	X	X	X	X				X	X	X		11	68.75
Tripos contrarius (Gourret) F.Gómez 2013	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16	100
Tripos declinatus (Karsten) F.Gómez 2013	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	15	93.75
Tripos digitatus (Schütt) F.Gómez 2013				X			X										2	12.5
Tripos euarcuatus (Jörgenen) F.Gómez 2013	X	X	X		X	X				X		X	X	X	X	X	11	68.75

Continued Table 1.

Taxa	Taxa Frequency Occurrence																	
	Sampling stations																Number of occurrences	% of occurrences
	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40		
Tripos extensus (Gourret) F.Gómez 2013	X	X	X		X	X	X	X			X	X	X	X		X	12	75
Tripos furca (Ehrenberg) F.Gómez 2013									X								1	6.25
Tripos fusus (Ehrenberg) F.Gómez 2013	X	X	X		X		X	X		X		X	X	X	X	X	12	75
Tripos geniculatus (Lemmermann) F.Gómez 2013							X					X					2	12.5
Tripos gibberus (Gourret) F.Gómez 1883	X	X	X		X	X				X			X	X	X	X	10	62.5
Tripos gravidus (Gourret) F.Gómez 2013	X	X		X		X							X		X		6	37.5
Tripos hexacanthus (Gourret) F.Gómez 2013	X			X		X	X	X		X	X		X	X	X	X	11	68.75
Tripos horridus (Cleve) F.Gómez 2013	X	X	X		X		X	X		X							7	43.75
**Tripos horridus molle* (Kofoid) F. Gómez 2013									X	X							2	12.5
Tripos inflatus (Karsten) F.Gómez 2013		X															1	6.25
Tripos karstenii (Pavillard) F.Gómez 2013	X	X	X	X		X	X	X					X			X	9	56.25
Tripos limulus (Pouchet) F.Gómez 2013	X	X														X	3	18.75
Tripos lineatus (Ehrenberg) F.Gómez 2013		X															1	6.25
***Tripos longinus* (Karsten) F.Gómez 2013	X	X					X	X		X	X	X		X	X	X	10	62.5
Tripos longirostrus (Gourret 1883) F. Gómez 2013	X		X			X			X		X	X	X		X		8	50
Tripos lunula (Schimper ex Karsten) F.Gómez 2013	X		X	X	X	X				X			X	X	X		9	56.25
**Tripos macroceros* var. *gallicum* (Kofoid) F.Gómez 2013										X			X	X			3	18.75
Tripos macroceros (Ehrenberg) F.Gómez 2013	X	X	X	X		X	X	X	X	X	X		X	X	X	X	14	87.5
**Tripos massiliensis* var. *armatum* (Karsten) F. Gómez									X					X			2	12.5
Tripos massiliensis (Gourret) F.Gómez 2013	X	X	X	X		X	X		X	X	X		X	X	X	X	13	81.25
Tripos muelleri Bory de Saint-Vincent in J.V.Lamouroux et al. 1824	X		X	X					X	X	X		X			X	8	50
Tripos pentagonus (Gourret) F.Gómez 2013	X	X	X	X		X		X	X	X	X	X		X	X	X	13	81.25
Tripos praelongus (Lemmermann) Gómez 2013				X			X									X	3	18.75
Tripos pulchellus (Schröder) F.Gómez 2013	X	X	X	X	X	X	X	X				X	X	X	X		12	75
***Tripos pulchellus* f. *tripodioides* (Jørgensen) F. Gómez 2013	X	X	X			X	X		X	X	X	X	X	X	X	X	13	81.25
**Tripos ranipes* (Cleve) F.Gómez 2013	X	X		X	X	X	X		X				X			X	9	56.25
Tripos reflexus (Cleve) F.Gómez 2013		X	X	X		X										X	5	31.25
Tripos setaceum (Jörgensen) F. Gómez 2013					X												1	6.25
Tripos sumatranus (Karsten) F.Gómez 2013	X	X				X	X		X	X			X	X		X	9	56.25
**Tripos symmetricus* (Pavillard) F.Gómez 2013	X		X		X		X	X								X	6	37.5
Tripos teres (Kofoid) F. Gómez 2013	X	X	X	X	X	X	X	X			X	X	X	X	X	X	14	87.5

Continued Table 1.

Taxa	Taxa Frequency Occurrence																	
	Sampling stations																	
	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40	Number of occurrences	% of occurrences
Tripos trichoceros (Ehrenberg) Gómez 2013									X	X							2	12.5
Tripos vultur (Cleve) F.Gómez 2013																X	1	6.25
**Tripos vultur* var. *japonicum* (Schröder) F. Gómez 2013	X			X	X	X				X		X	X	X	X	X	10	62.5
Cladopyxidaceae																		
Cladopyxis brachiolata Stein 1883	X	X	X	X		X	X					X	X	X	X	X	11	68.75
***Cladopyxis hemibrachiata* Balech 1964	X	X	X	X	X		X							X	X	X	9	56.25
Goniodomataceae																		
Triadinium polyedricum (Pouchet) Dodge 1981		X	X	X	X	X	X	X		X	X	X	X	X	X	X	14	87.5
Goniodoma sp.		X	X					X					X	X		X	6	37.5
Gonyaulacaceae																		
Gonyaulax birostris Stein 1883	X	X					X					X	X	X	X	X	8	50
***Gonyaulax milneri* (Murray & Whitting) Kofoid 1911g)		X															1	6.25
Gonyaulax polygramma Stein 1883	X	X					X			X	X	X	X	X	X	X	10	62.5
Gonyaulax sp.													X				1	6.25
**Spiraulax kofoidii* H.W.Graham 1942	X		X													X	3	18.75
Heterodiniaceae																		
***Heterodinium dispar* Kofoid & Adamson 1933		X												X	X		3	18.75
Heterodinium sp.1	X	X					X					X				X	5	31.25
Heterodinium sp.2		X															1	6.25
Protoceratiaceae																		
Ceratocorys gourretii Paulsen 1931	X	X	X			X		X				X		X	X	X	9	56.25
Ceratocorys horrida Stein 1883	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16	100
Ceratocorys armata (Schütt) Kofoid 1910														X			1	6.25
Protoceratium cf. *aculeatum* (Stein) Schiller 1937		X	X				X							X			4	25
Protoceratium spinulosum (Murray & Whitting) Schiller 1937		X															1	6.25

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Continued Table 1.

Taxa	Taxa Frequency Occurrence																	
	Sampling stations																	
	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40	Number of occurrences	% of occurrences
Gymnodiniales																		
Gymnodiniaceae																		
Gymnodinium sp.														X			1	6.25
Noctilucales																		
Kofoidiniaceae																		
***Kofoidinium velleloides* Pavillard 1929												X					1	6.25
Peridiniales																		
Oxytoxaceae																		
Oxytoxum milneri Murray & Whitting 1899	X	X	X	X	X	X	X				X	X	X	X	X	X	13	81.25
Oxytoxum scolopax Stein 1883		X	X		X	X	X					X	X		X	X	9	56.25
Peridiniales inc. sed.																		
Corythodinium tesselatum (Stein) Loeblich Jr. & Loeblich III 1966		X															1	6.25
Corythodinium constrictum (Stein) F.J.R.Taylor 1976				X									X				2	12.5
Corythodinium sp. 1				X													1	6.25
Podolampaceae																		
Podolampas bipes Stein 1883	X	X		X		X	X	X	X			X	X	X		X	11	68.75
Podolampas elegans Schütt 1895	X	X	X	X	X	X			X				X		X		9	56.25
Podolampas palmipes Stein 1883	X	X										X	X	X		X	6	37.5
Podolampas spinifera Okamura 1912		X			X				X			X	X	X	X	X	8	50
Protoperidiniaceae																		
**Protoperidinium oceanicum* (Vanhöffen) Balech 1974									X								1	6.25
**Protoperidinium elegans* (Cleve) Balech 1974	X	X	X	X	X	X							X		X	X	9	56.25
Protoperidinium ovatum Pouchet 1883													X	X			2	12.5
**Protoperidinium pentagonum* (Gran) Balech 1974													X				1	6.25
Protoperidinium sp.1		X															2	12.5
Protoperidinium sp.2	X					X						X	X			X	5	31.25
Protoperidinium sp.3		X								X	X	X			X		5	31.25
Protoperidinium sp.4			X														1	6.25

Continued Table 1.

Taxa	Taxa Frequency Occurrence																	
	Sampling stations																	
	E14	E15	E16	E17	E18	E19	E20	E23	E26	E27	E30	E32	E34	E36	E38	E40	Number of occurrences	% of occurrences
Prorocentrales																		
Prorocentraceae																		
Prorocentrum compressum (Bailey) Abé ex J.D.Dodge 1975		X				X											2	12.5
Prorocentrum gracile Schütt 1895				X	X												2	12.5
Prorocentrum balticum (Lohmann) Loeblich 1970			X				X		X				X			X	5	31.25
Pyrocystales																		
Pyrocystaceae																		
Pyrocystis fusiformis C.W.Thomson in J.Murray 1876	X	X		X		X		X	X					X		X	8	50
***Pyrocystis hamulus* var. *semicircularis* Schröder 1900					X												1	6.25
Pyrocystis pseudonoctiluca Wyville-Thompson in Murray 1876		X								X		X	X	X	X		6	37.5
Pyrocystis robusta Kofoid 1907		X	X	X	X	X			X	X		X	X	X	X	X	12	75
Dinophyceae not identified																		
Dinophyceae sp.1											X						1	6.25
Dinophyceae sp.2					X						X						2	12.5
Dinophyceae sp.3			X														1	6.25

** New occurence for Brazil; * New occurence for the state of Espírito Santo.

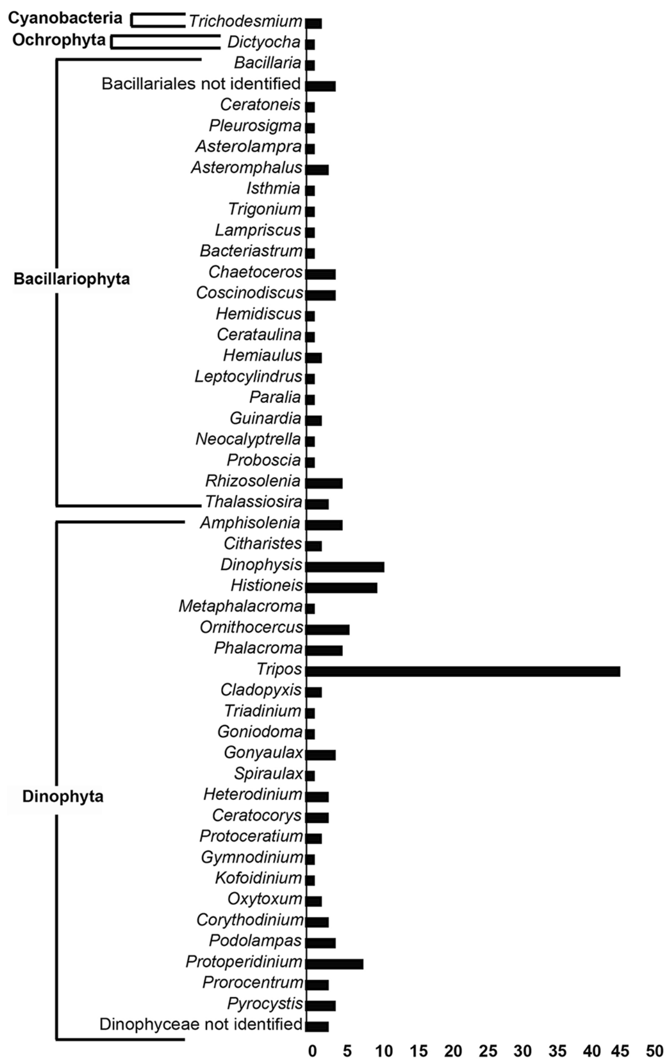

Figure 2. Genera biodiversity in the proximity of the Vitória-Trindade Seamount Chain. Four different phyla were identified. The number of species found for each genus is represented by bars.

Cluster analysis, by revealing differences in taxonomic composition among the various stations (Figure 5), facilitated their division into three main groups (Figure 1 and 5). The first, marked in green, and located closer to the continental shelf, were the most distant (71% AU value), the second, in red, were near the Vitória-Trindade Seamount Chain (81% AU), and the third, in blue, were in deep offshore areas (81% AU).

Discussion

The high infrageneric diversity among the micro and mesophytoplankton observed corroborates previous findings for tropical oligotrophic regions (Hallegraeff & Jeffrey 1984, Balech 1988). The high diversity of dinoflagellates collected in this area seems to be correlated with its preference for warm oligotrophic oceanic zones (Taylor et al 2007). Recently, the marine species of the genus *Ceratium* F.Schrank were renamed *Tripos* (Gómez et al. 2010, Gómez 2013) marine species of Ceratium (Dinophyceae, Alveolata. This presents, by far, the highest number of infrageneric taxa. Incidentally, it was the most common genus in the samples collected. Furthermore, besides being more specious in tropical regions (Dodge 1993, Dodge & Marshall 1994, Okolodkov & Dodge 1996, Tunin-Ley & Lemée 2013), it is usually the most diverse of the dinoflagellates (Taylor et al. 2007).

Table 2. Very common taxa in the stations (≥70% of occurrence).

Taxa	number occurrence	% occurrence
Ceratocorys horrida Stein 1883	16	100
Tripos contrarius (Gourret) F.Gómez 2013	16	100
Tripos declinatus (Karsten) F.Gómez 2013	15	93.75
Triadinium polyedricum (Pouchet) Dodge 1981	14	87.5
Tripos macroceros (Ehrenberg) F.Gómez 2013	14	87.5
Tripos teres (Kofoid) F. Gómez 2013	14	87.5
Dinophysis schuettii Murray & Whitting 1899	13	81.25
Ornithocercus magnificus Stein 1883	13	81.25
Ornithocercus steinii Schütt 1900	13	81.25
Oxytoxum milneri Murray & Whitting 1899	13	81.25
Tripos massiliensis (Gourret) F.Gómez 2013	13	81.25
Tripos pentagonus (Gourret) F.Gómez 2013	13	81.25
Tripos pulchellus f. *tripodioides* (Jørgensen) F. Gómez 2013	13	81.25
Dinophysis cf. *operculoides* (Schütt) Balech 1967	12	75
Tripos azoricus (Cleve) F.Gómez 2013	12	75
Tripos extensus (Gourret) F.Gómez 2013	12	75
Tripos fusus (Ehrenberg) F.Gómez 2013	12	75

In an environment with low nutrient availability, nitrogen fixation is an important feature for ensuring fitness. Hence, the prevalence of the Cyanobacteria *Trichodesmium* can be understood. It is a diazotrophic organism that has been well documented both in the marine waters of Brazil (Satô et al. 1963, Brandini et al. 1997, Carvalho et al. 2008, Proença et al. 2009, Monteiro et al. 2010) and worldwide (Sellner 1997, Janson et al. 1999).

Several micro- and mesophytoplankton organisms accompany cyanobacteria nitrogen fixers. *Richelia intracellularis* J.Schmidt in Ostenfeld & Schmidt is a diazotrophic cyanobacteria found in symbiotic relationship with certain diatoms, such as *Rhizosolenia* Brightwell (Padmakumaret al. 2010), *Hemiaulus* Heiberg (Kimor et al. 1978, Villareal 1994) and *Chaetoceros* Ehrenberg (Gómez et al. 2005). Furthermore, some oceanic dinoflagellates abide in symbiosis with unicellular diazotrophic bacteria, commonly found in certain genera of the non-photosynthetic Dinophysiales order, such as *Histioneis*, *Ornithocercus* Stein and *Amphisolenia* Stein (Foster et al. 2006, Farnelid et al. 2010). This corroborates our results on the high diversity of the above cited genera in the region of the Vitória-Trindade Seamount Chain.

When considering the lack of research on phytoplankton assemblages in Brazilian offshore waters, novel reports on infrageneric taxa can be expected. Other propitious factors could be (*i*) the fluctuation of phytoplankton composition due to environmental changes, such as

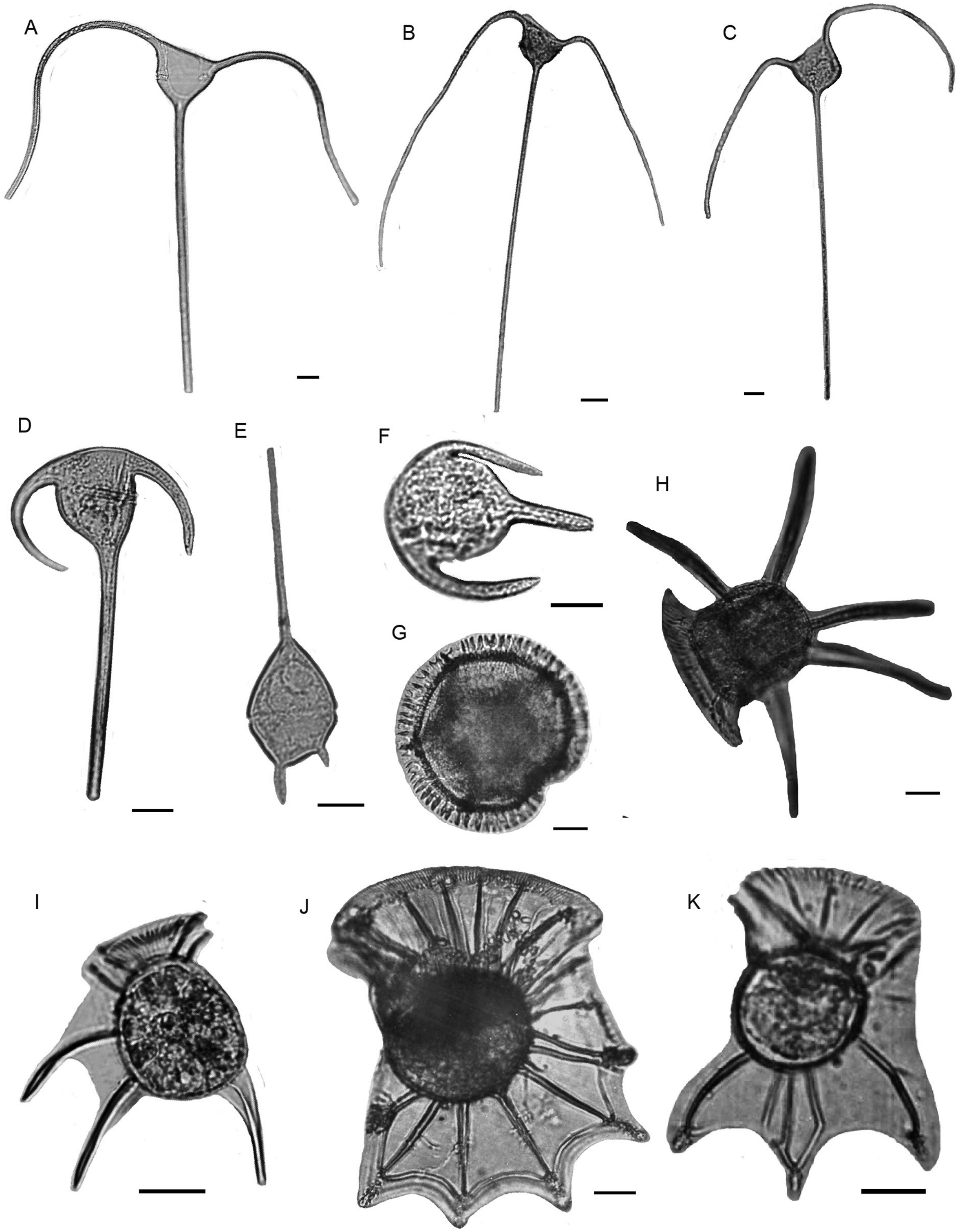

Figure 3. Very common taxa (≥70% of occurrence). Scale bar sizes are between brackets. (A) *Tripos contrarius* (20µm); (B) *Tripos massiliensis* (50 µm); (C) *Tripos macroceros* (20 µm); (D) *Tripos declinatus* (20µm); (E) *Tripos teres* (scale bar20µm); (F) *Tripos azoricus* (20µm); (G) *Triadinium polyedricum* (20µm); (H) *Ceratocorys horrida* (20 µm); (I) *Dinophysis schuettii* (20µm); (J) *Ornithocercus steinii* (20 µm); (K) *Ornithocercus magnificus* (20µm).

Table 3. New infrageneric taxa reports. New records for Brazil. (*) New records for waters of the Espírito Santo continental shelf and near the Vitória-Trindade seamount chain.

Phylum	Species
Bacillariophyta	*Asteromphalus stellatus* (Greville) J.J.Ralfs
Dinophyta	*Amphisolenia schroederi* Kofoid 1907
Dinophyta	*Cladopyxis hemibrachiata* Balech 1964
Dinophyta	*Heterodinium dispar* Kofoid & Adamson 1933
Dinophyta	*Histioneis garrettii* Kofoid & Michener 1907
Dinophyta	*Histioneis joergensenii* Schiller 1928
Dinophyta	*Kofoidinium velleloides* Pavillard 1929
Dinophyta	*Metaphalacroma skogsbergii* L.-S.Tai in L.-S.Tai & Skogsberg 1934
Dinophyta	*Ornithocercus cristatus* Matzenauer 1933
Dinophyta	*Pyrocystis hamulus* var. *semicircularis* Schröder 1900
Dinophyta	*Tripos longinus* (Karsten) F.Gómez 2013
Dinophyta	*Tripos pulchellus* f. *tripodioides* (Jørgensen) F. Gómez 2013
Bacillariophyta	**Asteromphalus flabellatus* (Brébisson) Greville 1859
Bacillariophyta	**Chaetoceros* cf. *concavicornis* Mangin 1917
Bacillariophyta	**Chaetoceros mitra* (Bailey) Cleve 1896
Bacillariophyta	**Rhizosolenia castracanei* H.Peragallo 1888
Bacillariophyta	**Hemiaulus membranaceus* Cleve
Bacillariophyta	**Lampriscus shadboltianum* (Greville) Peragallo & Peragallo 1902
Bacillariophyta	**Thalassiosira leptopus* (Grunow ex Van Heurck) Hasle & G.Fryxell 1977
Bacillariophyta	**Trigonium formosum* (Brightwell) Cleve 1867
Dinophyta	**Amphisolenia bifurcata* Murray & Whitting 1899
Dinophyta	**Amphisolenia schauinslandii* Lemmermann 1899
Dinophyta	**Citharistes regius* Stein 1883
Dinophyta	**Dinophysis caudata* Saville-Kent 1881
Dinophyta	**Dinophysis fortii* Pavillard 1923
Dinophyta	**Dinophysis pusilla* Jørgensen 1923
Dinophyta	**Protoperidinium elegans* (Cleve) Balech 1974
Dinophyta	**Protoperidinium oceanicum* (Vanhöffen) Balech 1974
Dinophyta	**Protoperidinium pentagonum* (Gran) Balech 1974
Dinophyta	**Spiraulax kofoidii* H.W.Graham 1942
Dinophyta	**Tripos cephalotus* (Lemmermann) F.Gómez 2013
Dinophyta	**Tripos macroceros* var. *gallicum* (Kofoid) F.Gómez 2013
Dinophyta	**Tripos massiliense* var. *armatum* (Karsten) F. Gómez
Dinophyta	**Tripos symmetricus* (Pavillard) F.Gómez 2013
Dinophyta	**Tripos vultur* var. *japonicum* (Schröder) F. Gómez 2013

seasonality, (*ii*) misidentification of species, and (*iii*) very low density of some species, thereby precluding their perception in previous studies.

There was little variation in environmental data. In temperature, although the highest range, the values varied between 1.5°C. Considering the variables obtained, the conditions in the study area could be considered stable. Therefore, it was impossible to associate the differences in phytoplankton composition with the data obtained. Maybe, quantifying and qualifying nutrients could give a better indication for the findings.

Cluster analysis indicated how close the stations were in terms of taxonomic composition, and also that geographic distances between the stations were correlated with species composition: the closer the stations to one another, the more species they shared in common. The same association was found in a biogeographic study of *Tripos* (Dodge 1993). Furthermore, the grouping of stations into three different clusters could be justified by the high number of uncommon and rare taxa (101 taxa, 57.5%), thereby indicating that many species are not extensively disposed. It was noteworthy that the three clusters seemed to be correlated to continental closeness and seafloor bathymetry. This is in accordance with previous findings, whereby neritic species assemblage differs from the oceanic (Dodge 1993, Raine et al. 2002, Taylor et al. 2007), and seamounts can influence species composition and density (Genin & Boehlert 1985, Pitcher et al. 2007).

The high micro- and mesophytoplankton species diversity is apparently related to tropical oligotrophic oceanic zones. Several of the organisms identified were either mixotrophic, or maintained a symbiotic association with diazotrophic bacteria. The results are important in defining micro-and mesophytoplankton diversity, especially among the dinoflagellates. The numerous new infrageneric taxa reported for the marine waters off Espírito Santo State, and Brazil as a whole, indicate the importance of inventory surveys, and the lack of studies of phytoplankton assemblages. Bathymetric dissemblance in the area studied could be associated with differences in species composition. Neritic stations formed a distinct cluster from the oceanic and seamount. Furthermore, geographic distances between stations possibly exert an influence on species distribution. Further studies of phytoplankton should be extended to the area, especially those of other phytoplankton size-fractions, such as pico- and nanoplankton. The application of other methodologies, such as cultures, metabarcoding and metagenomics, would be useful for enhance the knowledge about the community.

Acknowledgements

We wish to thank FAPES (Fundação de Amparo à Pesquisa do Espírito Santo) for the scholarship ceded to Karoline Magalhães Ferreira Lubiana (44576170/2009), and also Caio C. M. Freire for helping with statistical analysis.

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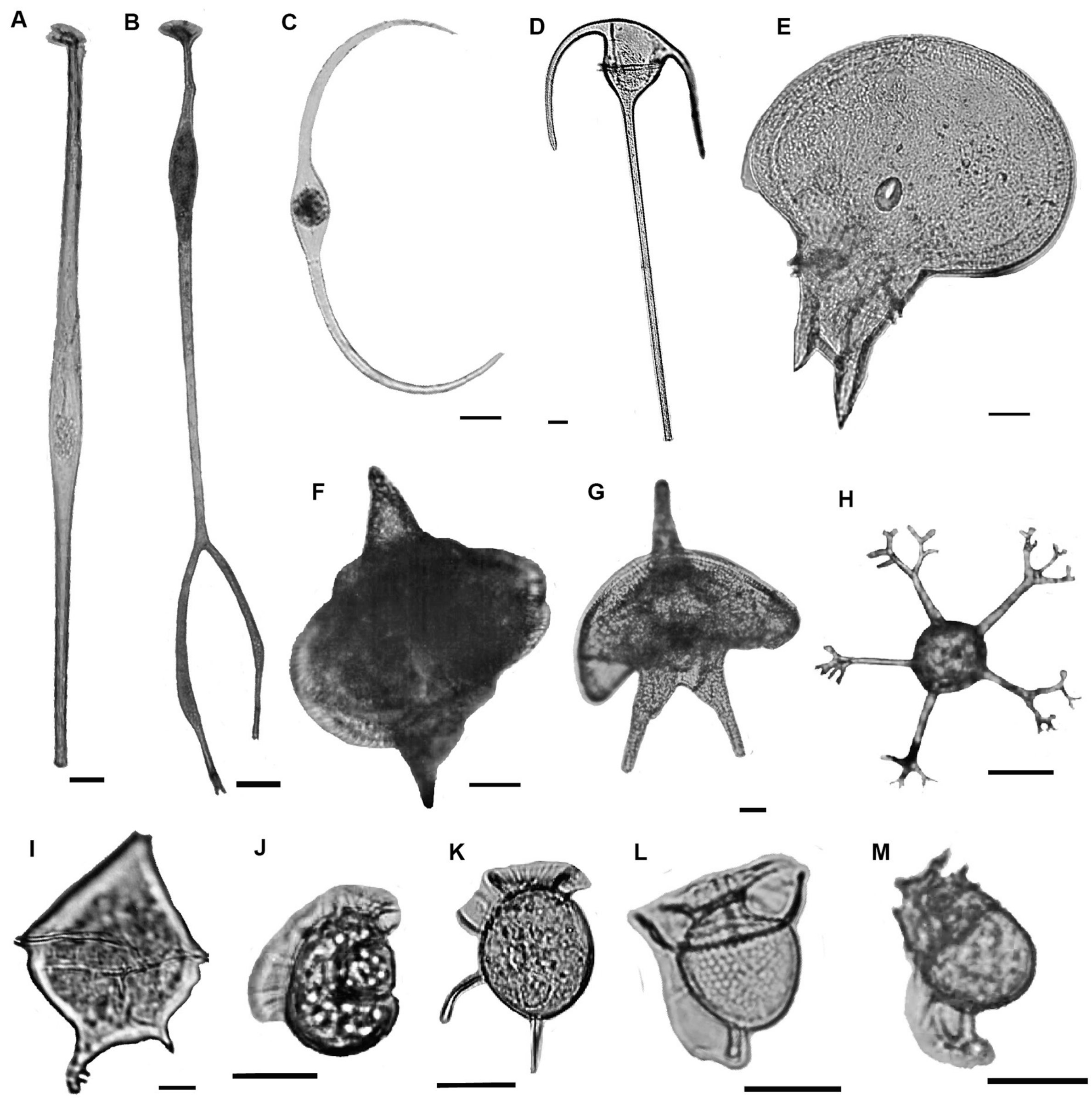

Figure 4. Some of the new records for marine waters of Brazil and Espírito Santo State (*). Scale bar sizes are between brackets. (A) **Amphisolenia schauinslandii* (20 µm); (B) **Amphisolenia bifurcata* (10µm); (C) *Pyrocystis hamulus* var. *semicircularis* (50 µm); (D) *Tripos pulchellus* f. *tripodioides* (20µm); (E) **Tripos cephalotus* (20µm); (F) **Spiraulax kofoidii* (20µm); (G) **Protoperidinium elegans* (20µm); (H) *Cladopyxis hemibrachiata* (20µm); (I) *Heterodinium dispar* (10µm); (J) **Citharistes regius* (20µm); (K) **Dinophysis pusilla* (20µm); (L) *Histioneis garrettii* (20µm); (M) *Histioneis joergensenii* (20µm)

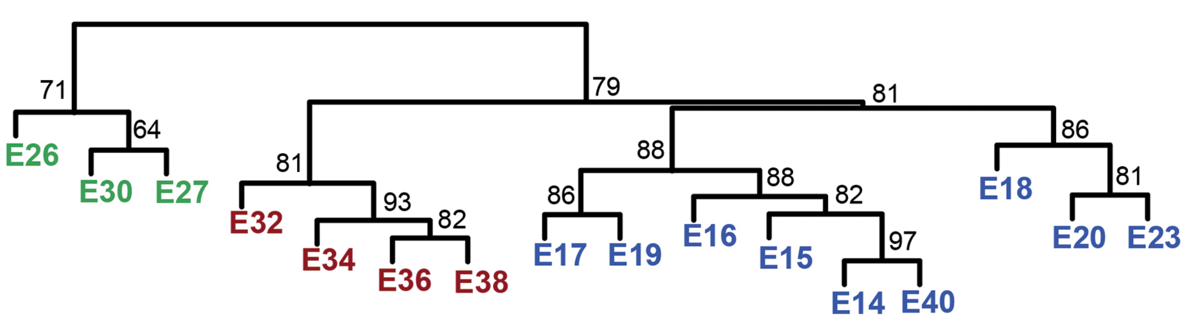

Figure 5. Hierarchical cluster dendrogram representing binary distances between stations according to phytoplankton species composition. Green represents the neritic group, red those closer to the seamounts, and blue those in deep offshore areas.

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Received: 27/01/2016
Revised: 01/08/2016
Accepted: 05/08/2016