

COMMUNITY STRUCTURE OF THE TINTINNIDS (CILIOPHORA: SPIROTRICHEA) IN THE REGION OF ABROLHOS (BAHIA, BRAZIL)

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ABSTRACT

The tintinnid community in the region of Abrolhos (Bahia, Brazil) was studied during February 2012. We hypothesized that the tintinnid community structure varies significantly over a short temporal scale (photoperiod), as well as spatially over a short scale (on and away from the reefs), and a broad scale (distance of the reef area from the coast). Three areas in Abrolhos were studied. Two sampling points were delimited in each area, where the tintinnids were collected by horizontal subsurface plankton net (20 μ m mesh-size) hauls. Sampling was undertaken every 6 hours, during 24 hours in each area. 24 species were found, all of which are of neritic, cosmopolitan, and of warm-water distribution. The only hypothesis that is not rejected is that related to variability on an extensive spatial scale. There are significant differences between the samples collected in the three areas studied (ANOVA $p = 0.017$). The clustering of the species highlights a continent-ocean gradient. There is one community typical of the internal arc, composed mainly of neritic agglutinated tintinnids, and another community typical of the external arc, composed mainly of hyaline warm-water and cosmopolitan tintinnids. The factor which exercises the greatest influence on the tintinnid community in the Abrolhos region is the distance from the coast.

RESUMO

A comunidade dos tintinídeos da região de Abrolhos (Bahia, Brasil) foi estudada durante o período de fevereiro de 2012. Nossas hipóteses são de que a estrutura da comunidade dos tintinídeos varia em uma escala temporal curta (fotoperíodo), além de variar espacialmente, tanto em curta escala (sobre o recife e distante dele) como em larga escala (distância da área recifal em relação à costa). Três áreas em Abrolhos foram estudadas. Em cada área foram delimitados dois pontos de amostragem, nos quais se coletou tintinídeos através de arrastos horizontais subsuperficiais de rede de plâncton (20 μ m abertura de malha), a cada 6 horas, ao longo de 24 horas. 24 espécies foram encontradas, sendo todas de distribuição nerítica, cosmopolita e de águas quentes. A única hipótese não rejeitada está relacionada com a variabilidade da comunidade em uma escala espacial extensa. Existem diferenças significativas entre as três áreas estudadas (ANOVA $p = 0,017$). Análises de agrupamento realizadas com as espécies revelaram um gradiente continente-oceano. Existe uma comunidade típica do arco interno, formada basicamente por espécies neríticas, além de uma comunidade típica do arco externo, formada basicamente por espécies hialinas cosmopolitas e de águas quentes. O grande fator influenciando a comunidade dos tintinídeos em Abrolhos é a distância da costa.

Descriptors: Protozooplankton, Ciliates, Coral reef ecosystems.

Descritores: Protozooplâncton, Ciliados, Ecossistemas Recifais.

INTRODUCTION

Coral reefs are very highly diverse ecosystems, being second only in diversity to tropical

forests (SOUTER and LINDÉN, 2000). Although these ecosystems occur in tropical regions, which are characterized by very low levels of dissolved nutrients, they present very high biomasses and

production rates of many classes of organisms (LEWIS, 1977).

Since the 1970s, the importance of the bacteria in nutrient regeneration within reef ecosystems has been observed not only through the activity of the picoplankton, which are distributed in the water column, but also through the activity of those bacteria living in association with the mucus-rich coral surface microlayer (SOROKIN, 1971; 1973; PAUL et al., 1986; FERRIER-PAGÈS and GATTUSO, 1998). The so-called microbial loop was described at the beginning of the 1980s (AZAM et al., 1983). According to this theory, picoplanktonic organisms constitute the main consumers of the dissolved organic carbon pool, using this material as an energy source for their growth. As they do so, part of this energy is reintroduced into the main food web through the feeding activity of protozooplanktonic organisms, mainly heterotrophic flagellates and ciliates (SHERR et al., 1989; BERNINGER and WICKHAM, 2005). These organisms serve as food sources for mesozooplanktonic and demersal organisms living in association with the coral reefs (STOECKER and CAPUZZO, 1990; FESSENDEN and COWLES, 1994; HEIDELBERG et al., 2004; CALBET and SAIZ, 2005). It is in this context that some microplanktonic protists, such as tintinnid ciliates, carry out a fundamental role within coral reef ecosystems. The tintinnids are a group of choreotrich ciliates that are characterized by the construction of a proteinaceous lorica (AGATHA and SIMON, 2012), inside which they dwell. The differences in lorica morphology are the main features used in tintinnid species identification. In addition to the importance of the tintinnids in connecting the microbial loop to the main food web, their intense feeding activity allows them to consume up to 70% of the daily primary production in some regions (BEERS and STEWART, 1971).

Because of their ecological importance in terms of nutrient regeneration, we studied the community structure of these ciliates in the region of Abrolhos. Three hypotheses were tested: i) the tintinnid community structure varies on a short temporal scale (photoperiod), since during the night period they may be exposed to a more intense predation rate as an effect of the feeding activity of mesozooplanktonic organisms (HEIDELBERG et al., 2004); ii) there is a significant difference between the community structure of the tintinnids on and away from the reefs, since the feeding activity specially of suspension-feeding benthonic organisms living in association with the reefs is responsible for a higher capture of planktonic organisms (GLYNN, 1973;

PRATAP et al., 1976; YAHIEL et al., 1998); iii) the tintinnid community structure is significantly different in reef areas closer to and further from the coast as the availability of mineral particles, much more readily available in shallow areas, may interfere in the lorica building process, leading to a limitation of the spatial distribution of several species (GOLD and MORALES, 1976).

MATERIAL AND METHODS

Study Area

Situated off the southern littoral of the State of Bahia (northeastern Brazil), the region of Abrolhos consists of a complex of coral reefs, volcanic islands, mangrove forests, and tidal channels. A considerable part of this region lies within the protected National Marine Park of the Abrolhos, which covers approximately 270 square nautical miles (IBAMA, 1991).

Brazil is the only country bordering the western South Atlantic Ocean in which it is possible to find coral reefs (CASTRO and PIRES, 1999). The Abrolhos reefs constitute the most extensive and richest reefs in Brazilian waters (LEÃO, 2002). They are located on a wider area of the Brazilian continental shelf and are divided into two arcs. These arcs lie parallel to the coast, the internal one located closer to it than the external one, which is less extensive (IBAMA, 1991). The internal arc is located approximately 20 km from the coast, and the waters between this arc and the coast are up to 15 m deep. The Parcel das Paredes reef area is located in this arc. There is a channel between the two arcs with depths as great as 30 m. The external arc is located approximately 70 km from the coast, and the depths are greater than 25 m (LEÃO, 2002). The Parcel dos Abrolhos reefs are located in this arc (see Fig. 1).

Sampling Strategy and Analysis of the Samples

The samples were collected in three different reef areas in the Abrolhos region: Parcel das Paredes (PP), Arquipélago de Abrolhos (AA), and Parcel dos Abrolhos (PA). In each area, two sampling sites were selected. One of them directly on the reef and identified as the reef site (R), while the other was located approximately 1 km from the reef and identified as the control site (C).

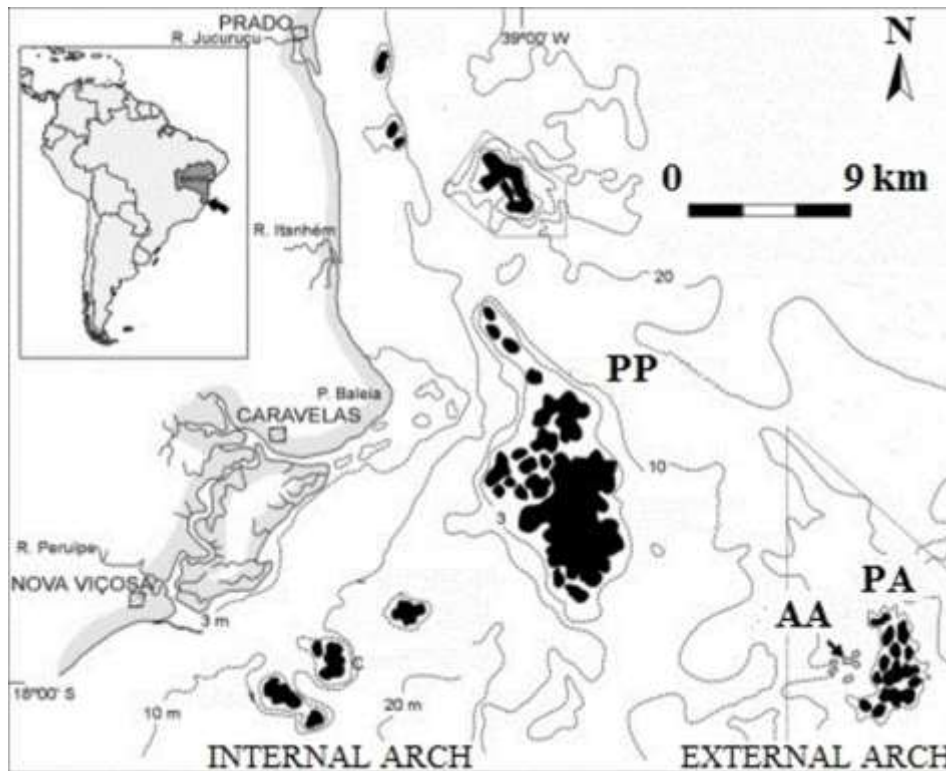


Fig. 1. Location of the Parcel das Paredes (PP), Arquipélago de Abrolhos (AA), and Parcel dos Abrolhos (PA) areas in the region of Abrolhos – BA, Brazil. Modified from LEÃO (2002).

Sampling was undertaken during a period of 24 hours in each area. The tintinnids were sampled by means of subsurface hauls with a plankton net (mesh width 20 μm , mouth diameter 30 cm, length 2 m). A flux meter was coupled to the mouth of the plankton net to assess the water volume filtered by the haul. The hauls were performed at 6-hour intervals at each site. A total of eight samplings were, thus, performed in each area, providing a total of 24 samples. All samples were fixed with borax-buffered formaldehyde at a final concentration of 4%. This fixative may cause some level of shrinkage and distortion to ciliate cells (MODIGH and CASTALDO, 2005), but it does not affect tintinnid identification or quantitative estimates since the loricae used in such analyses are resistant and have been used historically (BRANDT, 1906; JÖRGENSEN, 1924; KOFOID and CAMPBELL, 1929).

Species identification was performed using classical and recent works on the taxonomy of the group (BRANDT, 1906; JÖRGENSEN, 1924; KOFOID AND CAMPBELL, 1929; HADA, 1937; CAMPBELL, 1942; BALECH, 1948; 1971; 1975; MARSHALL, 1969; FERNANDES, 2004a; 2004b; NOGUEIRA, 2002; 2005). The validity of the species' names was checked using the WoRMS digital data

base (World Register of Marine Species: www.marinespecies.org). The quantitative analyses were performed using Sedgewick-Rafter chambers and common optical microscopy. During the procedure, a subsample (1 ml) of the sample was taken to the Sedgewick-Rafter chamber, and all tintinnids contained in the subsample were identified and quantified. At least 100 individuals were counted in each subsample. The process was repeated three times for each sample, and the mean result of the three subsamples calculated. The mean values were used to calculate the tintinnid density (ind.m^{-3}). The tintinnid biomass was calculated using the density values and biovolume of the loricae in accordance with the method proposed by HILLEBRAND et al. (1999). Mathematical equations were used to calculate the biovolume of the loricae (μm^3). The biovolume values were converted into biomass values (pgC.cell^{-1}) using a carbon to lorical biovolume ratio:

$$\text{pgC.cell}^{-1} = \text{lorical biovolume} \times 0.053 + 444.5$$

(VERITY and LANGDON, 1984)

A cluster analysis was undertaken to determine the main species assemblages. The Ward method was used (ROMESBURG, 1984), using a

similarity matrix produced by the determination of the Pearson linear correlation. Multidimensional scaling (MDS) was performed to visualize which samples were more closely related to each other.

A normality test was performed with the data to determine whether the results had a normal or non-normal distribution. It was necessary to evaluate whether there were significant differences between samples collected in different time periods (diurnal or nocturnal), between different points within the same area, or between different areas of the Abrolhos region, with the appropriate statistical tests. When the normality test pointed to a non-normal distribution of the results, non-parametric tests such as the Kruskal-Wallis and Mann-Whitney tests were used to compare the results. When the normality test indicated a normal distribution of the results, parametric tests such as ANOVA and the *t*-test were used to compare the results.

RESULTS

Frequency of Occurrence, Relative Abundances, Quantitative and Biomass Results

The most conspicuous species were *Codonellopsis schabii* KOFOID and CAMPBELL (1929), *Epiplocytilis brandti* KOFOID and CAMPBELL (1929), *Tintinnopsis nana* LOHMANN (1908), and *T. beroidea* STEIN (1867). The first two species were found to occur in 95% of the samples, while the latter two occurred in 73% (as shown in Table 1). Although these species presented high occurrence frequencies, they were more abundant in certain areas. *C. schabii*, for example, was more abundant in relation to the other species in the PP and AA areas. It represented 30% and 70%, respectively, of the tintinnids found in these areas. In the PA area the relative abundance of the same species was only 2% (as shown in Table 1).

Table 1. Frequency of occurrence (FO), relative abundance (RA), mean density (MD), and mean biomass (MB) of the tintinnid species found in the PP, AA, and PA areas during February, 2012. The values of tintinnid mean density (Mean D.), tintinnid maximum density (Max. D.), tintinnid minimum density (Min. D.), tintinnid mean biomass (Mean B.), tintinnid maximum biomass (Max. B.), tintinnid minimum biomass (Min. B.), and standard deviation (SD) for each area during the diurnal and nocturnal periods, are also presented. Density values are presented in ind.m^{-3} , and biomass values are presented in $\mu\text{gC.m}^{-3}$. The classification of the geographical distribution of each species is presented according to DOLAN and PIERCE (2013).

	Species	Parcel das Paredes				Arq. de Abrolhos			Parcel Abrolhos			
		FO (%)	RA (%)	MD	MB	RA (%)	MD	MB	RA (%)	MD	MB	
Neritic	<i>Tintinnopsis fimbriata</i>	36	1.10	519	1.85	0.07	287	0.92	-	-	-	
	<i>Tintinnopsis gracilis</i>	36	6.94	2864	13.64	-	-	-	-	-	-	
	<i>Tintinnopsis beroidea</i>	73	0.61	672	0.91	37.12	19144	33.81	26.83	4004	8.34	
	<i>Tintinnopsis nana</i>	73	25.41	10481	11.67	1.71	1009	1.77	0.09	66	0.11	
	<i>Tintinnopsis tocaninensis</i>	9	0.04	64	0.08	-	-	-	-	-	-	
	<i>Tintinnopsis nucula</i>	5	0.02	56	0.22	-	-	-	-	-	-	
	<i>Favella cf. azorica</i>	14	0.10	112	1.77	-	-	-	-	-	-	
	<i>Leprotintinus nordqvisti</i>	41	9.54	3938	37.97	0.02	96	0.65	-	-	-	
	<i>Metacylis mereschkowskii</i>	23	0.44	289	0.44	-	-	-	-	-	-	
	Cosmopolitan	<i>Codonellopsis schabii</i>	95	30.27	12489	55.14	36.80	18978	76.56	2.10	313	1.11
<i>Codonellopsis ecaudata</i>		14	-	-	-	0.25	344	0.97	-	-	-	
<i>Dadayiella ganymedes</i>		27	0.05	84	0.11	0.10	140	0.17	0.02	16	0.02	
<i>Eutintinnus tubulosus</i>		64	13.66	7516	24.09	5.64	4651	13.30	25.39	6316	22.65	
<i>Eutintinnus apertus</i>		36	5.83	6412	38.21	0.43	595	2.45	2.05	763	2.88	
<i>Eutintinnus cf. pinguis</i>		23	-	-	-	1.03	2131	9.63	20.99	5221	26.09	
<i>Ormosella</i> sp.		27	0.53	1761	ND	0.84	1156	ND	6.74	2516	-	
Warm-water		<i>Undella globosa</i>	45	-	-	-	1.50	1032	25.89	0.63	117	1.86
		<i>Undella</i> sp.	64	0.32	210	2.92	1.64	846	11.75	0.09	66	0.92
		<i>Rhabdonella elegans</i>	9	0.06	205	1.38	-	-	-	0.09	66	0.18
	<i>Rhabdonella</i> sp.	5	-	-	-	0.07	305	0.73	-	-	-	
	<i>Ascampbelliella aperta</i>	5	-	-	-	-	-	-	0.19	138	0.61	
	<i>Epiplocytilis brandti</i>	95	5.07	2093	10.38	12.14	6263	32.31	14.29	2132	11.53	
	<i>Epiplocytilis cf. acuminata</i>	18	-	-	-	0.14	192	0.87	0.23	173	0.81	
	<i>Epiplocyloides reticulata</i>	41	-	-	-	0.48	332	1.29	0.29	72	0.26	
		Max. D.	Min. D.	Mean D.	SD	Max. B.	Min. B.	Mean B.	SD			
	PP Diurnal	160559	5614	54388	71530	666.87	12.83	222.08	301.24			
	PP Nocturnal	32278	17714	28124	8100	148.52	84.06	110.25	29.38			
	AA Diurnal	81498	5229	46112	33040	321.52	13.83	170.76	129.17			
	AA Nocturnal	77021	34042	57034	18277	260.61	140.83	207.32	59.29			
	PA Diurnal	10392	257	3080	4893	39.98	2.39	12.29	18.47			
	PA Nocturnal	35108	27202	31155	5590	126.1	93.59	109.85	22.99			

The tintinnid density and biomass values were higher in the samples collected in the PP and AA areas than in the PA area (as shown in Table 1). In the first two areas, the tintinnids reached densities as high as 160,500 and 81,500 ind.m⁻³. Their highest biomass values in the PP and AA areas were 666.87 and 321.52 µgC.m⁻³, respectively. In the PA area the highest density was 35,100 ind.m⁻³, while the highest biomass was 126.1 µgC.m⁻³. The individual density values for each species in each sample are shown in Table 2, while the individual biomass values are shown in Table 3.

Temporal (Diurnal and Nocturnal Samples) and Spatial Variations

There was no significant difference between the quantitative results for the diurnal and nocturnal samples collected in the PP and AA areas ($p > 0.05$). In the PA area, the diurnal and nocturnal samples were significantly different (t -test $p = 0.002$). The total density values were lower in the diurnal samples. There was no difference between the results of the samples collected at different points within the same area ($p > 0.05$). However, when the results obtained from the analysis of the samples collected in the three different areas were compared, the ANOVA indicated significant differences ($p = 0.017$).

Cluster Analysis and MDS

The cluster analysis provided two main groups of species association (see Fig. 2A). Group A consisted mainly of neritic species, whose distribution

was limited to the PP area. Group B was further divided into two subgroups, one of which contained the widespread species, while the other contained the rare species. Both groups, however, contained mainly warm-water and cosmopolitan species (as shown in Table 1).

The multidimensional scaling (MDS) provided two main groups of samples, one containing the samples collected in the PP area (close to the coast), and other containing the samples collected in the PA and AA areas, thus highlighting a significantly different spatial distribution (Fig. 2B).

DISCUSSION

Geographical Distribution and Biodiversity

PIERCE and TURNER (1993) described six different patterns of tintinnid global distribution using tintinnid occurrence data from more than 1,400 different locations worldwide. These distribution patterns were identified as cosmopolitan, neritic, warm-water, boreal, austral, and tropical Pacific. DOLAN and PIERCE (2013) updated these global distributions, increasing the number of sampled locations to more than 1,800. The study excluded the tropical Pacific distribution, and some genera were moved from one distributional pattern to another. According to DOLAN and PIERCE (2013), the genera identified are classified as being of neritic, cosmopolitan and warm-water distributions (as shown in Table 1).

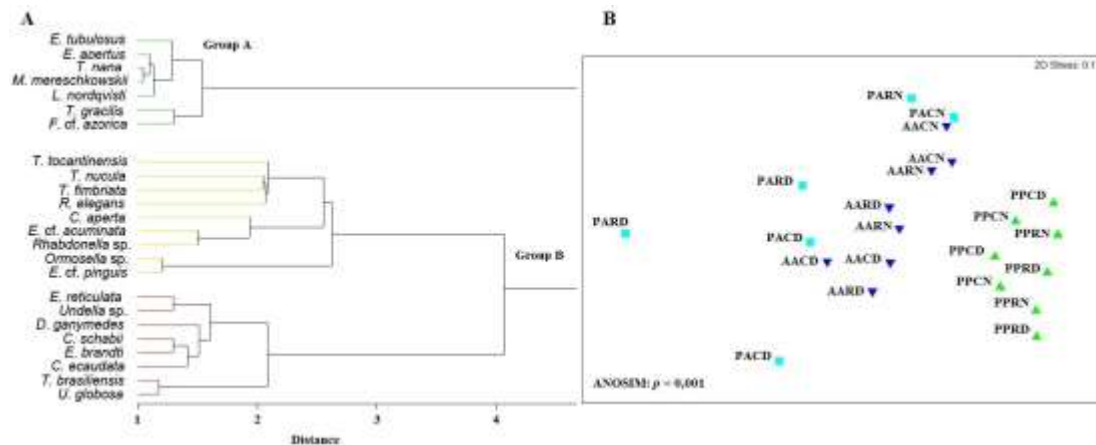


Fig. 2. Cluster analysis determining the most common species assemblages in the PP, AA, and PA areas during February, 2012. 2B – Multidimensional scaling (MDS) of the samples collected in the PP, AA, and PA areas during February, 2012. The AA and PA areas are more closely related to each other than to the PP area because they are located in the external reef arch. PP – Parcel das Paredes; AA – Arquipélago de Abrolhos; PA – Parcel dos Abrolhos; R – reef point; C – control point; D – diurnal period; N – nocturnal period.

Table 2. Individual density values of each species in all the samples analyzed. All the samples were collected during February, 2012 in the Abrolhos region (Bahia, Brazil). The times at which the sampling was performed are indicated on the samples. Density values are presented in ind.m⁻³. PP – Parcel das Paredes; AA – Arquipélago de Abrolhos; PA – Parcel dos Abrolhos; R – Reef site; C – Control site.

Density values at ind.m ³	06.11	06.20	12.06	18.16	01.13	07.16	12.56	18.02	18.13	00.33	06.48	12.03	19.12	01.35	07.03	13.29	12.19	18.52	06.31	13.22	19.10	06.50	
	PPR	PPR	PPR	PPR	PPC	PPC	PPC	PPC	AAR	AAR	AAR	AAR	AAC	AAC	AAC	PAR	PAR	PAR	PAC	PAC	PAC	PAC	
<i>Tritonopsis fimbriata</i>	-	74	55	3177	56	135	33	103	-	286,7	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. gracilis</i>	3411	4308	2666	3177	1070	5284	163	1335	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. barodea</i>	-	-	-	-	897	-	196	924	11758	11753	37225	4140	8488	23167	32684	23028	-	5483	5559	157	7998	945	-
<i>T. nana</i>	5593	4398	5252	13273	3898	42003	3656	4829	1447	2222	542	218	763	209	1866	-	-	-	-	-	-	66	-
<i>T. locantianalis</i>	-	74	55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. nucula</i>	-	-	-	-	56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Codonellopsis schradi</i>	3477	15376	7988	9108	6446	36177	480	20647	38259	8600	23672	545	29182	24488	20714	5367	-	289	483	18,56	529	248	-
<i>C. ecaudata</i>	-	-	-	-	-	-	-	289	-	381	-	-	381	-	-	-	-	-	-	-	-	-	-
<i>Epitrypa brandi</i>	1312	1253	711	1059	1121	8943	588	1746	7813	3708	15360	54	6103	9450	4060	3466	86	3539	3753	157	3107	-	-
<i>E. cf. acuminata</i>	-	-	-	-	-	-	-	-	193	181	-	-	-	203	-	-	-	-	-	173	-	-	-
<i>Epitrypa reticulata</i>	-	-	-	-	-	-	-	-	985	215	181	-	95	203	-	335	-	48	35	-	132	-	-
<i>Metacyclops maroccanus</i>	197	74	219	141	-	813	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Favella cf. azonica</i>	131	-	-	71	-	130	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eubranchius tubulosus</i>	7282	-	711	-	56	31434	65	5545	-	4658	181	-	5913	12295	206	-	-	10004	-	18,56	8928	-	-
<i>E. apertus</i>	328	-	-	-	-	18292	-	515	-	287	-	-	381	1118	-	-	-	337	-	-	1190	-	-
<i>E. pinguis</i>	-	-	-	-	-	-	-	-	502	-	-	-	-	3790	-	-	-	5050	35	-	10579	-	-
<i>Leprotolimus nordqvisti</i>	4395	5274	1850	71	3644	14904	326	1027	96	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Undella globosa</i>	-	-	-	-	-	-	-	-	482	502	1526	109	-	-	1457	2013	171	-	207	74,23	-	18	-
<i>Undella sp.</i>	262	-	109	71	-	542	65	-	2026	573	1688	163	95	102	1041	783	-	-	-	-	66	-	-
<i>Rhabdonella elegans</i>	-	-	-	-	-	-	-	205	-	-	-	-	-	-	-	-	-	-	-	-	58	-	-
<i>Rhabdonella sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	385	-	-	-	-	-	-	-	-	-
<i>Dedyrella parymedes</i>	-	-	-	-	-	135	33	-	96	143	181	-	-	-	-	-	-	-	-	-	-	18	-
<i>cf. Ormoeella sp.</i>	-	-	-	-	-	1761	-	-	502	-	-	-	1240	1727	-	-	-	2453	-	-	2579	-	-
<i>Ascaropelella aperta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	138	-	-	-	-
Total Density	27356	30753	20526	30147	17714	180598	5614	37278	64404	34042	81498	5229	52641	77621	61829	35882	257	27202	90392	445	35908	1224	-

Table 3. Individual biomass values for each species in all the samples analyzed. All the samples were collected during February, 2012 in the Abrolhos region (Bahia, Brazil). The times at which the sampling was performed are indicated on the samples. Biomass values are presented in µgC.m⁻³. PP – Parcel das Paredes; AA – Arquipélago de Abrolhos; PA – Parcel dos Abrolhos; R – Reef site; C – Control site.

Biomass in µgC.m ⁻³	06.11	06.20	12.06	18.16	01.13	07.16	12.56	18.02	18.13	00.33	06.48	12.03	19.12	01.35	07.03	13.29	12.19	18.52	06.31	13.22	19.10	06.50	
Species	PPR	PPR	PPR	PPR	PPC	PPC	PPC	PPC	AAR	AAR	AAR	AAR	AAC	AAC	AAC	PAR	PAR	PAR	PAC	PAC	PAC	PAC	
<i>Tritonopsis fimbriata</i>	-	0.17	0.22	11.29	0.20	0.53	0.13	0.40	-	0.92	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. gracilis</i>	14.85	21.91	15.18	18.77	8.12	22.53	0.77	8.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. barodea</i>	-	-	-	-	1.19	-	0.20	1.33	19.22	21.13	57.75	7.79	14.96	40.21	58.82	40.55	-	11.91	10.31	0.32	17.10	2.05	-
<i>T. nana</i>	7.52	3.07	5.23	11.84	5.15	49.67	3.64	7.10	2.49	3.83	0.90	0.36	1.53	0.36	2.87	-	-	-	-	-	0.11	-	-
<i>T. locantianalis</i>	-	0.10	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>T. nucula</i>	-	-	-	-	0.22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Codonellopsis schradi</i>	14.45	69.20	25.58	40.01	28.89	166.80	1.87	84.19	158.10	38.42	100.96	2.32	100.80	113.53	78.87	19.48	0.00	1.23	2.02	0.86	2.26	1.06	-
<i>C. ecaudata</i>	-	-	-	-	-	-	-	-	0.59	-	1.08	-	1.14	-	-	-	-	-	-	-	-	-	-
<i>Epitrypa brandi</i>	8.96	5.72	3.34	5.77	5.80	43.97	2.75	8.73	34.87	18.37	91.10	0.27	31.17	45.53	18.26	19.53	0.38	17.89	22.83	0.84	15.71	-	-
<i>E. cf. acuminata</i>	-	-	-	-	-	-	-	-	0.82	-	0.77	-	-	1.02	-	-	-	-	-	0.61	-	-	-
<i>Epitrypa reticulata</i>	-	-	-	-	-	-	-	-	3.54	0.83	0.98	-	0.38	0.75	-	1.24	-	0.18	0.13	-	0.48	-	-
<i>Metacyclops maroccanus</i>	0.29	0.11	0.32	0.21	-	1.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Favella cf. azonica</i>	2.07	-	-	1.11	-	2.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eubranchius tubulosus</i>	23.34	-	2.28	-	0.18	106.78	0.21	17.78	-	14.42	0.56	-	21.20	29.80	0.50	-	-	35.87	-	0.07	32.01	-	-
<i>E. apertus</i>	1.95	-	-	-	-	108.02	-	3.57	-	1.71	-	-	1.44	4.21	-	-	-	1.27	-	-	4.49	-	-
<i>E. pinguis</i>	-	-	-	-	-	-	-	-	2.51	-	-	-	-	16.75	-	-	-	25.23	0.17	-	52.89	-	-
<i>Leprotolimus nordqvisti</i>	42.53	41.87	12.64	0.71	34.30	162.44	2.22	8.86	0.95	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Undella globosa</i>	-	-	-	-	-	-	-	-	12.17	30.57	29.55	0.80	-	-	36.66	45.59	3.05	-	3.10	1.08	-	0.22	-
<i>Undella sp.</i>	3.94	-	1.52	0.98	-	7.53	0.91	-	28.13	7.96	27.60	2.26	1.32	1.42	14.45	10.87	-	-	-	-	0.92	-	-
<i>Rhabdonella elegans</i>	-	-	-	-	-	-	-	1.38	-	-	-	-	-	-	-	-	-	-	-	-	0.18	-	-
<i>Rhabdonella sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.73	-	-	-	-	-	-	-	-	-
<i>Dedyrella parymedes</i>	-	-	-	-	-	0.17	0.04	-	0.12	0.17	0.23	-	-	-	-	-	-	-	-	-	-	0.02	-
<i>cf. Ormoeella sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ascaropelella aperta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.61	-	-	-	-
Total Biomass	117.72	142.24	66.37	90.70	84.06	666.87	12.83	148.52	260.61	140.83	321.52	13.83	173.94	253.91	210.43	137.26	3.43	93.59	38.96	2.38	126.10	3.36	-

The neritic genus showed the highest number of species (9 species), despite the elevated number of warm-water genera (5 genera, as shown in Table 1). All species in the genera *Tintinnopsis* STEIN (1867) and *Leprotintinnus* JÖRGENSEN (1899) are known to incorporate mineral particles in their loricae. This could be a limiting factor to their distribution, restricting their occurrence to shallow water environments where such particles are readily available (PIERCE and TURNER, 1993). In environments where the availability of these particles is limited, the loricae produced by these agglutinated species are weaker (GOLD and MORALES, 1976). Interestingly, some tintinnid species may select specific types of particles (WASIK et al., 1996; GOLD and MORALES, 1976). These authors argue that some species are specific in their use of quartz, while others may select particles of biogenic origin, such as fragments of diatom frustules, protozoan shells and coccoliths. The study of the origin, shape, and size of the adhered particles may thus reveal information about the ecosystem in which the lorica was produced (RASSOULZADEGAN, 1980). The specificity in the selection of particles makes the agglutinated tintinnids an important means of mineral particle accumulation and transport to higher trophic levels in the food web (GOLD and MORALES, 1976).

Three of the four most conspicuous species in the study region are agglutinated tintinnids (*C. schabii*, *T. nana* and *T. beroidea*). This finding arises from the fact that, although some of the areas studied are located far from the coast (because the AA and PA areas are situated in the external reef arc), these areas are characterized by shallow waters, which makes the ideal formation of agglutinated loricae possible. Thus, it is possible for agglutinated species to be part of the tintinnid community. In addition, the AA area is composed of five islands and fringe reefs (LEÃO, 2002). These islands may contribute the necessary particles for the ideal construction of agglutinated loricae. Even so, most of the agglutinated species occur exclusively or almost exclusively in the samples collected in the PP area, which is located in the internal arc, closer to the coast. These species are *Tintinnopsis fimbriata* MEUNIER (1919), *T. gracilis* KOFOID and CAMPBELL (1929), *T. tocantinensis* KOFOID and CAMPBELL (1929), *T. nucula* FOL (1884) and *L. nordqvisti*. Species of these genera are commonly found in coastal regions worldwide (BAKKER and PHAFF, 1976; PIERCE and TURNER, 1993; GODHANTARAMAN, 2002; DOLAN ET al., 2002; BOJANIC et al., 2012; DOLAN and GALLEGOS, 2001). Although they were quantitatively less abundant, some of these species, such as *T. gracilis* and *L. nordqvisti*, showed higher mean density values in the PP area than *T. nana*, which showed high mean density and was

considered a conspicuous species in this area (as shown in Table 1).

The greater distance of the external arc from the coast influences the structure of the tintinnid community in the region. One of the most conspicuous species, *E. brandti*, in addition to 15 other species, builds hyaline loricae.

There are few studies on reef areas in Brazilian waters that mention the occurrence of tintinnids. MAYAL et al. (2009), NEUMANN-LEITÃO et al. (2009) and MELO et al. (2002) found eight tintinnid species while studying the plankton of the Maracajaú reefs in the State of Rio Grande do Norte in the northeastern region of Brazil. Seven of these species had agglutinated loricae. The proximity of these reefs to the coastal region is the factor which most influences the dominance of species with agglutinated loricae in the community. SASSI and MELO (1982) studied the hyaline tintinnids on the Ponta do Seixas reefs in the State of Paraíba, also located in the northeastern region of Brazil. They collected samples weekly for two years and found only seven hyaline species. In addition, only two of these species presented a considerable occurrence frequency. Quantitative and biomass data are not presented in their study.

Temporal-Spatial Variability

Three hypotheses related to the temporal-spatial variability in the tintinnid community were tested. The first hypothesis is related to the small-scale spatial variability. The hypothesis is the following: in each area of the study region, the tintinnid community found at the sites actually on the reefs is not the same as that found at sites further from them (control sites). This distribution may occur in response to the higher capture rate of planktonic organisms on the reefs, mainly by benthonic organisms living in association with the reefs, as has already been observed by several authors (GLYNN, 1973; PRATAP et al., 1976; YAHIEL et al., 1998). This hypothesis was rejected. The community on the reefs is the same as that found at the control sites 1 km away from them. It is possible that the area under the influence of the reefs extends to these limits because no significant variations in quantitative terms, such as would support the limitation of the reef's influence, were observed.

The second hypothesis is related to the variability of the community over a broader spatial scale. The hypothesis consists of the idea that the tintinnid community found in the PP area is different from that found in the AA and PA areas. This difference would result from the fact that the PP area is located on the internal reef arc, much closer to the coast than the other two areas, which are located on the external reef arc, more than 50 km from the coast.

This hypothesis was not rejected because significant differences were found between the results of the samples collected in the different areas (ANOVA $p = 0.017$). The nature of the tintinnid community found in the PP area fits well with the pattern found in the Maracajaú reefs by MAYAL et al. (2009), NEUMANN-LEITÃO et al. (2009), and MELO et al. (2002). Studies performed in other coastal tropical areas show the same pattern of tintinnid composition with many agglutinated species (GODHANTARAMAN, 2002; JYOTHIBABU et al., 2006). In the PP, a great number of agglutinated species were found, although a considerable number of hyaline species were also identified, similarly to the findings of SASSI and MELO (1982) on the Ponta do Seixas reefs. Farther from the coast, in the AA and PA areas, the number of agglutinated species decreased, whereas the number of hyaline species increased. This continent-ocean gradient is highlighted by multidimensional scaling (MDS). It is possible to clearly visualize how the samples collected in the internal arc, in the PP area, assembled separately from the samples collected in the external reef arc, in the AA and PA areas (see Figure 2B). The species assemblages are also a result of the continent-ocean gradient (see Figure 2A).

The third hypothesis tested is related to possible variations in the tintinnid community between the diurnal and nocturnal periods. The hypothesis is that the total tintinnid density and biomass are significantly different as between the diurnal and nocturnal periods, mainly due to differential predation as the nocturnal feeding activity of mesozooplanktonic demersal organisms could lead to a decrease in the density of microplanktonic organisms (HEIDELBERG et al., 2004). Statistical tests were performed separately for each area, and differences were only found in the PA area (t -test $p = 0.002$). The most plausible explanation is that this result is a misleading statistical artifact because the nocturnal values, although higher than the diurnal values in this area, are lower than the mean density values found in other areas during both the diurnal and nocturnal periods (as shown in Table 1). ZEITSCHERL (1969) argued that there was no variation in the vertical distribution of tintinnids between the diurnal and nocturnal periods. NOGUEIRA and SASSI (2011) studied the nycthemeral variation of the tintinnid community in the region of the Atol das Rocas in the northeastern region of Brazil. They found higher values of tintinnid densities during the nocturnal period but interpreted this result as a spurious observation.

Density and Biomass

Although MELO et al. (2002), MAYAL et al. (2009), and NEUMANN-LEITÃO et al. (2009)

present no specific quantitative data for tintinnid ciliates, they do present quantitative data for the entire microzooplankton community, which varied between 1,917 and 47,620 ind.m⁻³. The total density values for the tintinnid community in the Abrolhos region varied between 257 and 160,559 ind.m⁻³ (as shown in Table 1), which highlights the importance of these ciliates in the ecosystem. The tintinnids alone reached very high density values in some samples, and their mean density values in each area were close to the highest density values found in the Maracajaú reef system for the entire microzooplanktonic community. Although the tintinnid biomass values were lower than the microzooplanktonic biomass values found by other authors in reef systems (MELO ET AL., 2002; MAYAL et al., 2009; NEUMANN-LEITÃO et al., 2009), the tintinnids play a very important role in energy transfer within these ecosystems. They are characterized by intense feeding activity, being able to consume up to 70% of the daily primary production (BEERS and STEWART, 1971), and their feeding activity is sometimes similar to that of copepods (CAPRIULO and CARPENTER, 1980; CAPRIULO and CARPENTER, 1983). In addition, tintinnids serve as a direct food source for benthonic organisms living in association with coral reefs because they represent part of the microplanktonic community (GLYNN, 1973; PRATAP et al., 1976; YAHIEL et al., 1998; DUPUY et al., 1999; HEIDELBERG et al., 2004). Tintinnids may also serve as an indirect food source for benthic taxa because they constitute an important food item for mesozooplanktonic organisms (GIFFORD and DAGG, 1988; SANDERS and WICKHAM, 1993; DOLAN and GALLEGOS, 2001). In this way, the measurement of the biomass is a specific datum; the tintinnid biomass levels may remain low, even though they may present very high secondary production because their life cycle is much shorter than that of most other zooplanktonic organisms, with estimates of up to 1.2 generations per day (DOLAN, 2010).

In conclusion, there is no variation in the tintinnid community structure on a short spatial scale in the Abrolhos region, and this hypothesis is therefore rejected. In contrast, on a broader spatial scale, the existence of variation in the tintinnid community was not rejected. There is one community typical of the internal arc closer to the coast, composed mainly of agglutinated tintinnids of neritic distribution, and another community typical of the external arc, which is composed mainly of hyaline tintinnids of broader distribution (warm-water and cosmopolitan species). The continent-ocean gradient was also highlighted by the species' assemblages. The hypothesis of variation in the tintinnid community over a short timescale (diurnal and nocturnal periods) was also rejected. The factor which most influences the tintinnid community

structure in the Abrolhos region is the distance of the reefs from the coast.

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