

Tintinnid diversity trends in the southwestern Atlantic Ocean (29 to 60° S)

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ABSTRACT: A latitudinal profile of tintinnid specific richness and diversity in the southwestern Atlantic Ocean during spring was evaluated in relation to environmental parameters obtained during 4 oceanographic cruises (TABIA series). The area surveyed included different biogeographic zones and comprised waters of the Brazil-Malvinas Confluence zone, the Argentine shelf-slope, the Malvinas Current and the Antarctic Circumpolar Current. Parameters of tintinnid diversity decreased as latitude of the oceanic cruises increased (TABIA I to III). Latitude explained 53 to 60 and 28 to 60% of specific richness and diversity variation, respectively. Comparisons between cruises indicated that the rate of change in diversity parameters was constant with latitude, but diversity parameters did not change with latitude during TABIA V cruise over the shelf-break front. To explain this difference, environmental (physical and biological) factors that could affect and determine diversity parameters in the Confluence and Subantarctic Zones were analyzed. The conclusion drawn is that the determination and maintenance of tintinnid diversity were mainly caused by various biological factors (available food, predators, 'cooccurrence', resilience of dominant tintinnid species) and by particular physical and hydrological characteristics of each biogeographic zone (ingress and egress of water masses in the Confluence, oscillations in the flow of the Malvinas and Brazil Currents, and the presence of a large spatial and temporal scale event: the shelf-break front).

KEY WORDS: Specific diversity · Specific richness · Tintinnids · Southwestern Atlantic

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INTRODUCTION

Tintinnids are a group of planktonic ciliates that play an important role in marine pelagic food webs by acting as a link between the microbial fraction and larger grazers (Pierce & Turner 1994, Alder 1999). Field studies indicated that tintinnids can remove large portions of daily primary production and that they are efficiently exploited at higher trophic levels (Heinbokel & Beers 1979, Capriulo & Carpenter 1983, Verity 1985, Pierce & Turner 1992). Changes in the composition of tintinnid communities can be easily evaluated since species identification is based on lorica morphology. Many reports summarizing tintinnid species revealed some general biogeographic patterns, i.e. taxa association with cold, temperate and warm water masses or identification of cosmopolitan, neritic, boreal, austral

or warm water taxa (Souto 1981, Pierce & Turner 1993, Alder 1999). However, quantitative data on tintinnid diversity are scarce, and studies at large geographical scales are recent and almost exclusively related to the Mediterranean Sea (Dolan et al. 1999, 2002, Dolan 2000). On the basis of 17 reports from different authors and zones (open ocean, coastal waters and estuaries), Dolan & Gallegos (2001) proposed a latitudinal gradient (between 81° N and 75° S) of tintinnid specific richness, with number of species increasing as latitude decreases. The presence of such latitudinal gradient may reflect a difference between tintinnids and benthic ciliates, which are considered as cosmopolitan because of their global and local diversity (Finlay et al. 1996). Unfortunately, in Dolan & Gallegos' (2001) review, no explanation was provided for the underlying cause(s) of the latitudinal gradient of specific richness, and the

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influence of differences in classification criteria, sampling effort or sample volume analyses on gradient determination cannot be discarded.

The southwestern Atlantic is a highly dynamic area with an interesting and complex circulation pattern. Previous studies in this ocean revealed an important variety of tintinnid species (Balech 1971, Souto 1981, Fernandes 1998, Alder 1999, Thompson et al. 1999) and an apparent gradual decrease of tintinnid diversity in open waters between mid- and high latitudes (Thompson et al. 1999).

The southwestern Atlantic area surveyed included different biogeographic zones and comprised water masses of the Argentine shelf-slope, the open ocean and the Antarctic sector (Thompson et al. 1999, 2001). Hydrologically, the northern portion of the studied area is occupied by subtropical waters of the Brazil Current (29 to 34° S; Subtropical Zone, Fig. 1). To the south, these waters converge with the South Atlantic

Current waters and the Malvinas Current subantarctic waters forming the Brazil-Malvinas Confluence Zone. This zone is delimited to the north (~34° S) by the Brazil Current Front and to the south (48 to 50° S) by the Subtropical Front (Fig. 1). The oceanic subantarctic waters of the Malvinas Current are located to the south and west of the Brazil-Malvinas Confluence (oceanic sector), while shelf waters of the Patagonian Current are present west of the Malvinas Current and over the continental shelf (shelf-break sector, Fig. 1). Between parallels 36 and 50° S, both currents are separated by a rather well-defined shelf-break front (Carreto et al. 1995). The oceanic and shelf-break sectors constitute the Subantarctic Zone (Fig. 1). The Antarctic waters of the Antarctic Circumpolar Current are located in the southern section of the studied area and separated by the Polar Front (~55° S) (Antarctic Zone; Fig. 1).

Characterisation of the biogeographic zones was based on the studies of Provost et al. (1996), Podestá (1997), Brandini et al. (2000) and Thompson et al. (2001), as follows: (1) Subtropical Zone, seawater temperature over 20°C and concentration of chlorophyll *a* below 0.2 $\mu\text{g l}^{-1}$; (2) Confluence Zone, seawater temperature between 21 and 10°C and chlorophyll *a* values below 1 $\mu\text{g l}^{-1}$ with frequent subsurface peak concentrations up to 3.6 $\mu\text{g l}^{-1}$; (3) oceanic sector of Subantarctic Zone, seawater temperature between 10 and 4°C and chlorophyll *a* up to 2.6 $\mu\text{g l}^{-1}$, and shelf-break sector of Subantarctic Zone, seawater temperature between 12 and 5°C and chlorophyll *a* up to 5 $\mu\text{g l}^{-1}$; (4) Antarctic waters, seawater temperature below 1.5°C and chlorophyll *a* less than 0.4 $\mu\text{g l}^{-1}$ except for patches in subsurface layers with concentrations up to 2.2 $\mu\text{g l}^{-1}$.

In this work, we evaluated factors affecting tintinnid specific richness and diversity in the southwestern Atlantic Ocean during 4 oceanographic cruises in spring. Tintinnid specific richness and diversity were analyzed in relation to latitude, seawater temperature, depth, water masses, tintinnid food resource distribution, abundance of predators such as foraminifers and crustacean larvae, and interannual change in environmental conditions.

MATERIALS AND METHODS

Samples were collected during 4 oceanographic cruises during spring. The sampling area comprised oceanic waters of the southwestern Atlantic Ocean between 29 and 60° S (Cruises TABIA I to III), and the shelf-break sector between 40 and 56° S (TABIA V). Information on each cruise and the geographic locations of the sampling stations are shown in Table 1 and Fig. 2. During the TABIA I, II and V cruises, tintinnids

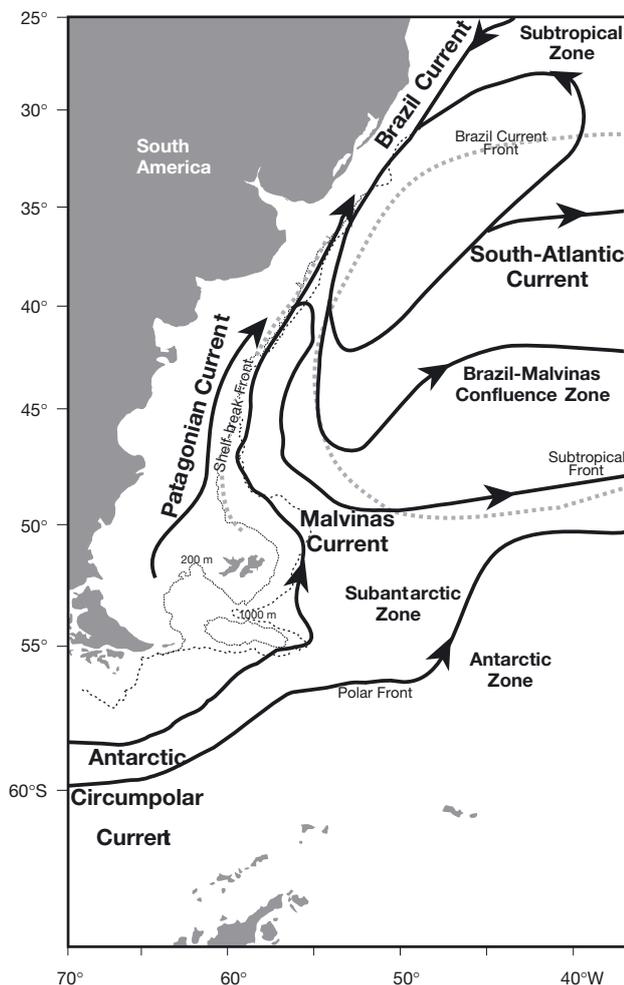


Fig. 1. General circulation pattern, hydrological fronts and biogeographic zones in study area

Table 1. Sampling data for each TABIA cruise

| Parameter | TABIA I | TABIA II | TABIA III | TABIA V |
|---|-------------------------------|------------------------------------|---------------|------------------------------------|
| Date (d/mo/yr) | 6–21/11/1993 | 8–16/11/1994 | 14–21/11/1995 | 13–18/11/1996 |
| No. of stations | 20 | 22 | 15 | 16 |
| No. of samples | 61 | 57 | 38 | 76 |
| Seawater sample (l) | 260–2800 | 200–3000 | 18 | 200–4000 |
| Sampling depth (m) | 5–15; 15–30; 30–50; 50–100 | 0–5; 5–15; 15–30; 30–50; 50–100 | 5; 10; 25; 50 | 0–5; 5–15; 15–30; 30–50; 50–100 |
| Total no. of tintinnids collected | 14 490 | 21 851 | 19 560 | 29 587 |
| Tintinnid density (ind. l ⁻¹) | 0.01–31.59 | 0.16–59.22 | 0–500 | 0.04–269.42 |

were collected with flowmetered 35 μm mesh nets, and during TABIA III cruise with Niskin bottles and reverse-filtering through 10 μm mesh nets. All samples were preserved in 3% formaldehyde; 3 aliquots of each microzooplankton sample were settled in sedimentation chambers (10 to 100 ml) and the tintinnids

were examined with an inverted microscope at a magnification of 200 \times to 400 \times . Samples were diluted prior to counting if materials were too concentrated in the original sample, and in this case a larger number of aliquots was examined (up to 6 subsamples). Tintinnid species were identified using the classification system proposed by Alder (1999), which is based on lorical morphology and information on the cytology and ultra-structure of ciliates in Laval-Peuto (1994). An average of 380 specimens per sample were found (Table 1). Tintinnid diversity was estimated by counting the number of species per sample (specific richness) and using the Shannon-Wiener diversity index (Shannon & Weaver 1949; ln-based expression), herein referred to as specific diversity.

The relationship between diversity parameters and latitude was estimated for each cruise using Model I regression analysis (log- and square-transformation of specific richness and diversity data, respectively). The significance of each regression was tested by analysis of variance and by computing the coefficient of determination (r^2). In addition, the equality of all slopes was tested by analysis of covariance (Zar 1999).

Data on the seawater temperature, concentration of chlorophyll *a*, and abundance of tintinnids, foraminifers and crustacean larvae registered during the 4 TABIA cruises have already been published (Thompson et al. 1999, 2001, Brandini et al. 2000, Thompson 2001). Tintinnid diversity parameters were correlated with the above-mentioned variables using the non-parametric Spearman rank order correlation test.

RESULTS

A total of 76 species of tintinnids were recorded during the 4 cruises (Table 2). Specific richness was below 28 species per sample, while specific diversity oscillated between 0.04 and 2.57. Both parameters reached a maximum in waters of the Brazil-Malvinas Confluence Zone (although some of the lowest specific diver-

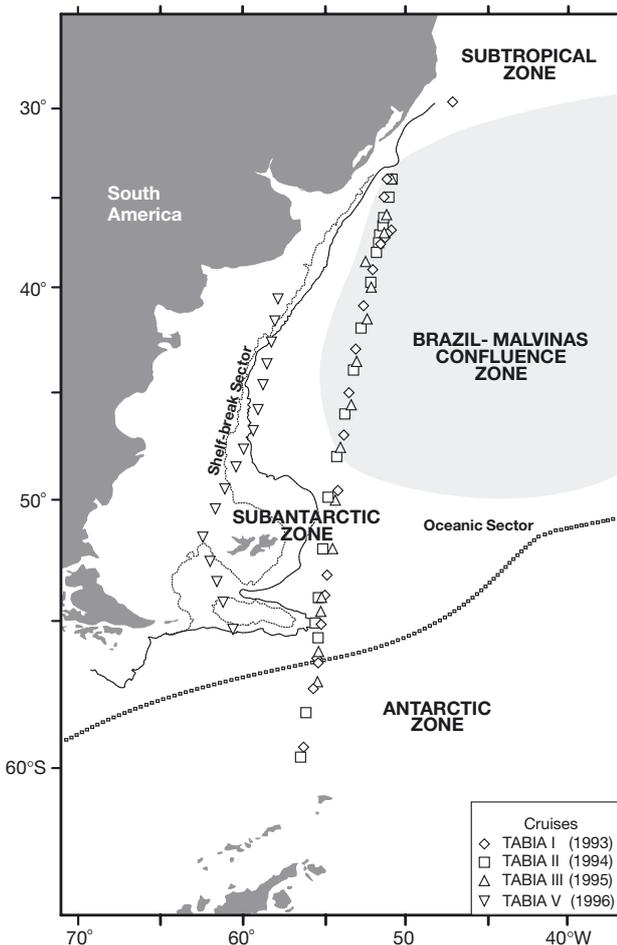


Fig. 2. Locations stations on the 4 TABIA cruises in relation to biogeographic zones of Thompson et al. (1999)

Table 2. Tintinnid species recorded on each TABIA cruise. Presence denoted by biogeographic zones. A: Antarctic; ST: Subtropical; C: Brazil-Malvinas Confluence; SA: Subantarctic. *: most abundant species in that zone

| Species | TABIA cruise | | | | Species | TABIA cruise | | | |
|------------------------------------|--------------|---------|--------|-----|-------------------------------------|--------------|-------|------|-----|
| | I | II | III | V | | I | II | III | V |
| <i>Acanthostomella norvegica</i> | ST/C/SA*/A | C/SA*/A | C*/SA* | SA* | <i>Eutintinnus medius</i> | ST*/C | C | C | |
| <i>Amphorellopsis quinquealata</i> | A | | | | <i>Eutintinnus rugosus</i> | | | | SA |
| <i>Amphorides amphora</i> | C | C | C | | <i>Favella serrata</i> | C | | | |
| <i>Amphorides quadrilineata</i> | C | C/SA | C/SA | SA* | <i>Helicostomella subulata</i> | | | C | SA |
| <i>Ascampbelliella acuta</i> | | C/SA | | | <i>Laackmanniella naviculaefera</i> | A | SA/A | A | |
| <i>Ascampbelliella armilla</i> | C | C | C | | <i>Ormosella acantharus</i> | | | C/SA | SA |
| <i>Ascampbelliella protuberans</i> | C | C | C | | <i>Ormosella bresslaueri</i> | C | | | |
| <i>Ascampbelliella urceolata</i> | | C | C | | <i>Parundella caudata</i> | ST/C | C/SA | C/SA | SA |
| <i>Brandtiella palliata</i> | | C | | | <i>Parundella messinensis</i> | C | C | | |
| <i>Canthariella</i> sp. | | | C | | <i>Petalotricha ampulla</i> | ST/C | C | | |
| <i>Climacocylis scalaria</i> | C | | | | <i>Poroecus apiculatus</i> | ST/C | C | | |
| <i>Climacocylis scalaroides</i> | ST/C | C* | C | | <i>Poroecus curtus</i> | ST/C | | | |
| <i>Codonella amphorella</i> | C | C | | | <i>Protorhabdonella curta</i> | ST/C | C*/SA | C* | SA |
| <i>Codonella aspera</i> | ST/C | C | C | | <i>Protorhabdonella simplex</i> | ST/C*/SA | C* | C | |
| <i>Codonella galea</i> | ST/C | C | | | <i>Rhabdonella amor</i> | ST/C* | C/SA | C | |
| <i>Codonella perforata</i> | | C | | | <i>Rhabdonella apophysata</i> | ST*/C | C | | |
| <i>Codonellopsis balechi</i> | | | SA | SA* | <i>Rhabdonella cornucopia</i> | ST* | C | C | |
| <i>Codonellopsis gaussi</i> | SA/A* | SA/A* | SA/A* | | <i>Rhabdonella spiralis</i> | | C*/SA | C | |
| <i>Codonellopsis morchella</i> | C | C | | | <i>Salpingella acuminata</i> | C/A | C | C | |
| <i>Codonellopsis orthoceras</i> | | C | | | <i>Salpingella acuminatoides</i> | C | C | C | |
| <i>Codonellopsis pusilla</i> | C/SA/A | C/SA | C/SA | SA* | <i>Salpingella subconica</i> | A | | | |
| <i>Cymatocylis antarctica</i> | SA*/A | C/SA*/A | C/SA* | SA* | <i>Steenstrupiella pozzii</i> | C/SA | C/SA | C/SA | SA* |
| <i>Cymatocylis calyciformis</i> | A | A | A | | <i>Steenstrupiella steenstrupii</i> | ST/C | C | C | |
| <i>Cymatocylis convallaria</i> | A | A | A | | <i>Tintinnopsis brasiliensis</i> | | | C | |
| <i>Cymatocylis cristallina</i> | | A | | | <i>Tintinnopsis parva</i> | C | | C | SA |
| <i>Cymatocylis drygalskii</i> | A | A* | | | <i>Tintinnopsis</i> sp. (A) | | | | SA |
| <i>Cymatocylis nobilis</i> | | A* | | | <i>Tintinnopsis</i> sp. (B) | C | | C | |
| <i>Cymatocylis vanhoeffeni</i> | A | C/A* | A | | <i>Undella claparedei</i> | ST/C | C | C | SA |
| <i>Cyrtarocylis cassis</i> | C | C | | | <i>Undella globosa</i> | C/SA | C/SA | C | SA |
| <i>Dadayiella ganymedes</i> | ST*/C | C/SA/A | C/SA | | <i>Undella hyalina</i> | ST | | | |
| <i>Dictyocysta californiensis</i> | | | | SA | <i>Undella ostenfeldi</i> | C | | | |
| <i>Dictyocysta elegans</i> | ST/C*/SA/A | C/SA | C | SA | <i>Undella subacuta</i> | C | C | C | |
| <i>Dictyocysta mitra</i> | ST/C*/SA/A | C*/SA | C | SA | <i>Undella subcaudata</i> | C | C/SA | C | SA |
| <i>Epiplocyliis acuminata</i> | ST/C/SA | C*/SA | C | | <i>Xystonella lanceolata</i> | | C | | |
| <i>Epiplocyliis undella</i> | | C | | | <i>Xystonella longicauda</i> | ST*/C | C* | C | |
| <i>Eutintinnus apertus</i> | ST/C | C | C | | <i>Xystonella treforti</i> | ST*/C | C* | | |
| <i>Eutintinnus birictus</i> | ST | | | | <i>Xystonellopsis cymatica</i> | ST/C | C | | |

sity values were also recorded here), with a southward sharp decrease (from 34° S to ~48/50° S; Fig. 3). In the oceanic sector of the Subantarctic Zone (from ~48/50° S to 55° S) the values of diversity parameters remained relatively constant (specific richness: 5 to 8; specific diversity: 0.8 to 1.4), and were similar to those registered in most of the samples of the shelf-break sector (TABIA V cruise). Specific richness values in the Antarctic Zone (55 to 60° S) were similar to those in the Subantarctic Zone, while specific diversity values were similar to slightly higher.

Changes in specific richness and diversity with depth (0 to 100 m) did not show a clear trend: these parameters increased with depth on the TABIA I and II cruises, but decreased during TABIA III. However, differences in the values of these variables with depth during the 3 cruises were not significant (Table 3). On

the TABIA V cruise, diversity parameters did not change with depth (Table 3). The influence of vertical stability of the water column (based only on temperature profiles) on specific richness and diversity did not show a uniform pattern: the slight increase in specific diversity in antarctic waters during TABIA II could be attributable to a high vertical stability of the water column. In contrast, vertical stability occurred almost along the whole transect (40 to 52° S) in the shelf-break sector (TABIA V), although diversity values were not higher than those obtained from the turbulent subantarctic waters of the oceanic sector (TABIA I to III).

Significant linear relationships between tintinnid diversity parameters (specific richness and diversity) and latitude were obtained during the 4 surveys (Fig. 3). During the oceanic cruises (TABIA I to III), these parameters decreased as latitude increased, and

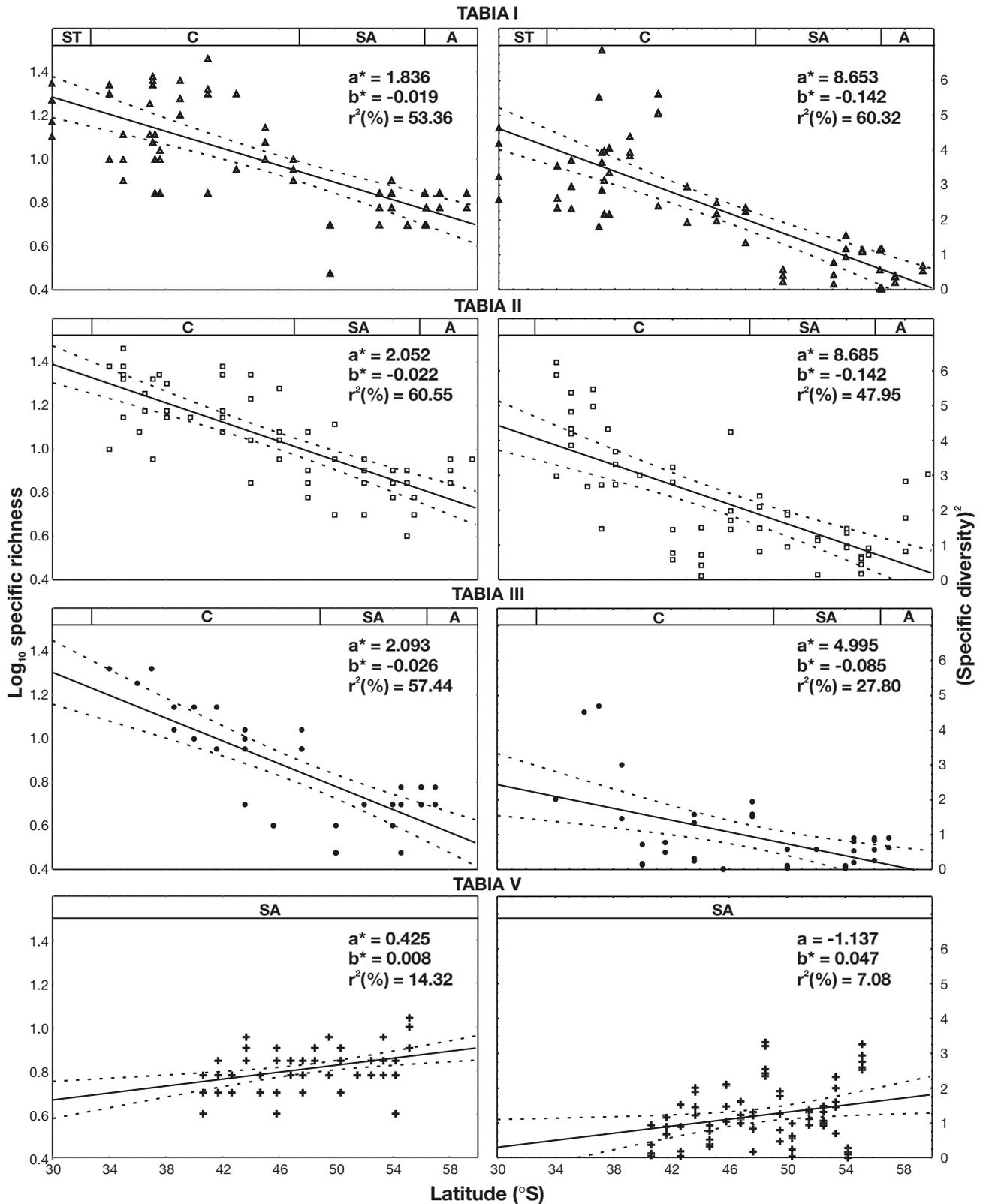


Fig. 3. Regression line ($\pm 95\%$ confidence intervals) between latitude and specific richness (log_{10} -transformed data) and specific diversity (square-transformed data) for each TABIA cruise. Biogeographic zones are delimited (ST: Subtropical; C: Confluence; SA: Subantarctic; A: Antarctic). Regression parameters are shown. a: y-intercept; b: slope; r^2 : coefficient of determination.

*Significance at probability level of 0.001

Table 3. Spearman rank correlations among tintinnid diversity parameters (Div. par.) and depth and seawater temperature for each cruise. SR: tintinnid specific richness; SD: tintinnid specific diversity; N: number of samples; r_s : correlation coefficient

| Div. par. | Depth | | | Seawater temperature | | |
|------------------|-------|-------|---------|----------------------|--------|---------|
| | N | r_s | p | N | r_s | p |
| TABIA I | | | | | | |
| SR | 61 | 0.23 | (0.072) | 59 | 0.798 | (0.000) |
| SD | | 0.19 | (0.144) | | 0.797 | (0.000) |
| TABIA II | | | | | | |
| SR | 57 | 0.14 | (0.292) | 57 | 0.729 | (0.000) |
| SD | | 0.02 | (0.897) | | 0.587 | (0.000) |
| TABIA III | | | | | | |
| SR | 38 | -0.29 | (0.066) | 25 | 0.859 | (0.000) |
| SD | | -0.10 | (0.557) | | 0.232 | (0.310) |
| TABIA V | | | | | | |
| SR | 76 | 0.08 | (0.512) | 76 | -0.138 | (0.234) |
| SD | | -0.03 | (0.815) | | 0.061 | (0.597) |

latitude accounted for 53 to 60 and 28 to 60% of species richness and diversity variation, respectively (see coefficient of determination in Fig. 3). In contrast, in the shelf-break sector (TABIA V cruise), diversity parameters showed a slight increase with increasing latitude (Fig. 3), which only explained 14 and 7% of the variation in specific richness and diversity, respectively (Fig. 3). Because there were no differences among the slopes of the trend lines estimated in the oceanic cruises (ANCOVA results; $F_{0.05(1), 2, 149} = 1.56$; $p = 0.213$ and $F_{0.05(1), 2, 149} = 1.33$; $p = 0.267$ for specific richness and diversity, respectively), a common slope was estimated (values of -0.021 and -0.132 for specific richness and diversity, respectively). These results indicated that the rate of change of specific richness and diversity values with latitude (slope) was constant in the southwestern Atlantic Ocean, at least during

spring, and suggested that the methodological differences (seawater volume analyzed and planktonic fractions registered) between TABIA cruises (TABIA I/II vs TABIA III), had a minor effect on the values estimated for diversity parameters.

On the TABIA I and II cruises, diversity was positively and significantly correlated with seawater temperature (Table 3), one of the environmental factors that changes consistently with latitude (Fig. 4). During TABIA III, only specific richness was correlated with temperature, while during TABIA V neither specific richness nor specific diversity were correlated with this environmental variable (Table 3).

In most cases, diversity parameters were not significantly correlated with density of phytoplankton (chlorophyll *a*), or with density of 2 tintinnid predators (crustacean larvae, foraminifers). Tintinnid diversity parameters were negatively correlated with density of phytoplankton in TABIA II and with density of predators in TABIA I and III (Table 4). In contrast, a positive correlation was found between tintinnid specific diversity and foraminifer abundance during TABIA V (Table 4).

On the other hand, some of the lowest specific diversity values detected in the oceanic waters of the Confluence and Subantarctic Zones were related to highest tintinnid density (negative trend), although almost no significant correlation was found between tintinnid abundance and diversity parameters (Table 4).

DISCUSSION

Around 60% of the tintinnid species described up to now for the South Atlantic and Antarctic Ocean (129 species, cf. Alder 1999), were recorded in this study (Table 2). The remaining species occur in tropical and neritic zones. Comparing similar latitudinal ranges, the numbers recorded in this work were larger than those reported in previous studies, which mainly covered neritic waters of Argentina, Uruguay and Brazil (Table 5).

In spite of the methodological and geographical differences involved, the comparison between the present data and previous information indicates that species richness in oceanic waters is higher than that in neritic waters. For example, for the interval 40 to 55°S, a total of 50 species were identified in oceanic waters (TABIA surveys), while less than 40 species are cited in the available literature concerning neritic waters of the shelf

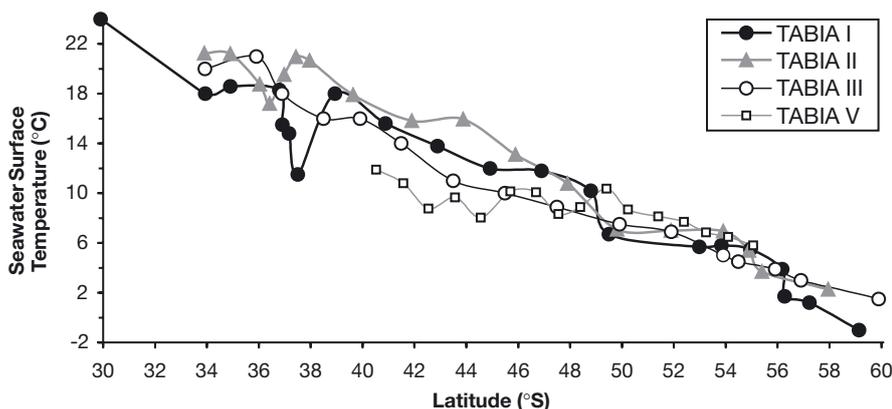


Fig. 4. Comparison of latitudinal profile of seawater surface temperature among TABIA cruises. Based on Brandini et al. (2000) and Thompson et al. (2001)

Table 4. Spearman rank correlations among tintinnid diversity parameters (Div. par.) and concentration of chlorophyll *a*, foraminifers, crustacean larvae and tintinnids for each cruise. Further details as in Table 3 legend

| Div. par. | Chlorophyll <i>a</i> | | | Foraminifers | | | Crustacean larvae | | | Tintinnids | | |
|------------------|----------------------|-------|---------|--------------|-------|---------|-------------------|-------|---------|------------|-------|---------|
| | N | r_s | p | N | r_s | p | N | r_s | p | N | r_s | p |
| TABIA I | | | | | | | | | | | | |
| SR | 58 | 0.17 | (0.187) | 60 | -0.44 | (0.000) | 60 | -0.06 | (0.660) | 60 | -0.21 | (0.097) |
| SD | | 0.22 | (0.097) | | -0.58 | (0.000) | | -0.42 | (0.001) | | -0.46 | (0.000) |
| TABIA II | | | | | | | | | | | | |
| SR | 55 | -0.46 | (0.000) | 56 | 0.12 | (0.358) | 56 | 0.15 | (0.276) | 56 | 0.23 | (0.085) |
| SD | | -0.55 | (0.000) | | 0.04 | (0.771) | | 0.09 | (0.494) | | -0.35 | (0.797) |
| TABIA III | | | | | | | | | | | | |
| SR | 37 | -0.01 | (0.943) | 38 | 0.12 | (0.437) | 38 | -0.04 | (0.785) | 38 | 0.53 | (0.000) |
| SD | | -0.30 | (0.066) | | -0.28 | (0.092) | | -0.35 | (0.029) | | -0.02 | (0.899) |
| TABIA V | | | | | | | | | | | | |
| SR | 76 | -0.08 | (0.457) | 73 | 0.22 | (0.061) | 73 | -0.16 | (0.174) | 73 | 0.01 | (0.909) |
| SD | | 0.06 | (0.575) | | 0.28 | (0.015) | | -0.04 | (0.741) | | -0.18 | (0.132) |

(see Table 5). In addition, specific inventories of both areas barely overlap; only occasionally were some of the species reported for oceanic waters found in neritic environments (e.g. *Cymatocylis antarctica*, *Rhabdonella amor* and *Acanthostomella norvegica*; Souto 1979, Alder 1999). In addition, most of the taxa frequently recorded in neritic environments of the southwestern Atlantic Ocean were absent or rare in oceanic waters (i.e. *Stylicauda platensis*, *Favella taraikaensis*, *Stenosemella avellana*, and more than 20 species of the genus *Tintinnopsis*; Balech 1971, Souto 1979, Balech & Souto 1980, 1981, Alder 1999).

During the oceanic cruises (TABIA I to III), both specific richness and diversity showed a significant decrease from mid- to high latitudes, in agreement with previous findings for most terrestrial and marine animals (Clarke 1990, McGowan & Walker 1993, Angel 1994, Rosenzweig 1995, Briggs 1996), including tintinnids (Dolan & Gallegos 2001). The latter authors suggested that specific richness is possibly determined by a dominant factor associated with latitude. In this sense, it is worthy to mention a lack of change in tintinnid diversity parameters with latitude within the 15° range surveyed during the TABIA V cruise. An explanation of this difference was attempted based on the analyses of the environmental (physical and biological) factors that could affect and determine diversity parameters in the Confluence and Subantarctic Zones.

Hydrological conditions of the Brazil-Malvinas Confluence differed remarkably from the other water masses surveyed. Several inflows of water from different biogeographical provinces with distinct physical and chemical properties and particular flora and fauna meet in this area, mix and interleave horizontally and vertically. This

results in strong gradients and singular environments (such as restricted areas of enhanced chlorophyll build-up, upwelling cells, cyclonic and anticyclonic eddies and tongues of warm or cold water), with seasonal and interannual changes (Bianchi et al. 1993). In this context, tintinnid assemblages of the Confluence are almost entirely constituted by allochthonous populations of warm water, cold water and neritic species (Thompson et al. 1999, Thompson 2001), and this is reflected in the highest values of tintinnid diversity (Fig. 3). Tintinnid assemblages were also affected by annual changes in hydrology, since a shift in species dominance was detected among the 3 cruises, with species with a relatively high mean abundance in one

Table 5. Comparison between tintinnid species recorded during TABIA cruises and previous recordings in the Southwestern Atlantic. *: only data from same latitudinal range were considered. E: estuarine stations; N: neritic stations; SB: shelf-break stations; O: oceanic stations

| Latitude | No. of species recorded | |
|---------------------|--|-------|
| | Previous studies | TABIA |
| 35° S (E) | 18 (Balech 1948) | 38 |
| 35° S (E) | 4 (Souto 1973) | 38 |
| 39° S (E) | 19 (Barría de Cao 1992) | 29 |
| 39° S (N) | 15 (Balech 1945) | 29 |
| 55° S (N) | 4 (Balech 1942) | 14 |
| 55° S (N) | 9 (Balech 1944) | 14 |
| 31–35° S (N) | 41 (Souto 1970) | 47 |
| 32–41° S (N) | 25 (Balech 1959) | 59 |
| 36–60° S (N) | 40* (Balech 1971) | 71 |
| 37–56° S (N) | 43 (Balech & Souto 1980, 1981) | 64 |
| 42–57° S (N) | 13 (Souto 1972) | 52 |
| 41–60° S (N, O) | 15 (Balech 1962) | 60 |
| 29–60° S (N, SB, O) | 41* (Fernandes 1998) | 75 |
| 55–60° S (O) | 14* (Alder 1995 – Irizar 86/87 cruise) | 27 |
| 57–60° S (O) | 9* (Alder 1995 – EPOS cruise) | 15 |

cruise being rare in others (for detailed information see Thompson 2001). All these factors suggest a significant contribution of large-scale advection events (input or egress of water masses resulting in immigration or emigration processes) to the maintenance of high diversity values in the Confluence.

On the other hand, *in situ* processes such as growth and mortality rates of tintinnids were important at a local scale; the rapid turnover rates displayed by tintinnids (Pierce & Turner 1992) allow opportunistic species to react swiftly to enhanced feeding conditions in the Confluence (like short-term phytoplankton patches; Thompson et al. 1999), leading to a local decrease in diversity parameters, in particular specific richness. Many of these local declines were detected (Fig. 3) inside patches of high (over $1 \mu\text{g l}^{-1}$) chlorophyll concentrations (between 36 and 38° S: TABIA I; 43 and 46° S: TABIA II; 40 and 48° S: TABIA III; Brandini et al. 2000).

In brief, tintinnid diversity in the Confluence Zone is likely to be maintained by physical (advection) events at a large scale, and by biological processes at a local scale.

In the Subantarctic Zone, tintinnid assemblages differed from those of the Confluence Zone. In the former, they were mostly characterized by autochthonous populations of cold-water (subantarctic) species of the Malvinas and Patagonian Currents. Moreover, 70% of tintinnid species were found both in the shelf-break and the oceanic sectors (Table 2). The lack of latitudinal change in tintinnid diversity parameters from the shelf-break sector could be partially explained by analyzing the distribution of surface isotherms. These are parallel to the main axis of the Malvinas Current flow, having a north-south orientation rather than the east-west direction reported for the open ocean (Brandhorst & Castello 1971, Provost et al. 1996). This situation suggested that advective longshore processes, which are enhanced by the deformation of associated temperature fields, might favour the north-

ward dispersion of subantarctic species (Boltovskoy et al. 1999). In turn, this dispersion could explain similarities in the composition of tintinnid assemblages among TABIA V samples. In agreement with this environmental setting, in the TABIA cruise along the shelf-break sector, sea-surface temperature correlated significantly with latitude ($p < 0.001$), but this correlation was substantially lower than those observed in oceanic waters in the same latitudinal range (from 41 to 56° S; $r = -0.49$ for TABIA V and $r \approx -0.95$ for TABIA I to III). Therefore, although tintinnid diversity parameters were expected to be correlated with temperature rather than with latitude in the shelf-break sector, this did not occur (Table 3), and water temperature alone could not explain the lack of change in diversity parameters. In this sector, a thermohaline front along the shelf-break (between 36 and 50° S; Fig. 1) is the most important large-spatial scale physical process. This front is a south-north oriented dynamic structure with a seasonal variation in geographic location and degree of development, and where primary production is enhanced due to active vertical water mixture and the upwelling of deep waters (Carreto et al. 1995, Podestá 1997). Contrary to results obtained in the Confluence, the moderate high concentrations of chlorophyll *a* in the shelf-break sector (over $3 \mu\text{g l}^{-1}$ between 40 to 42° S and 48 to 54° S; Thompson et al. 2001) did not result in a local decrease of tintinnid specific richness (Fig. 3). This seems to be related to a long-term persistence of such levels of chlorophyll *a* along the entire shelf-break front (Podestá 1997). This unusually large (temporal and spatial)-scale phenomenon in the global ocean suggests that the continuous supply of available food resources for tintinnid assemblages may favour the maintenance of moderate diversity values along the whole latitudinal range covered. In addition, the almost constant tintinnid diversity in all cruises from subantarctic waters could be attributable to 2 biological factors ('cooccurrence' and constancy of the dominant species), which might be influencing both the shelf-break and oceanic sectors.

The dominant tintinnids *Cymatocyclus antarctica* and *Acanthostomella norvegica* in the oceanic sector and the species shown in Table 6 for the shelf-break sector were present in almost all subantarctic samples, but 'separated horizontally' (Thompson 2001, Thompson et al. 2001). This indicated that each of these species was capable of outcompeting its neighbours without excluding them from the system, and thus not leading to a reduction in diversity. It seems that at any given place one species was at a

Table 6. Comparison of latitudinal range of dominance (Thompson et al. 2001) and oral diameter for dominant species in shelf-break sector (TABIA V cruise). *: lorica oral diameters for specimens from oceanic sector were similar to those obtained for the shelf-break sector by Thompson (2001)

| Species | Dominance range (° S) | Lorica oral diameter Mean \pm SD (μm) | N |
|----------------------------------|-----------------------|--|-----|
| <i>Acanthostomella norvegica</i> | 44–45; 50–51; 53–54 | 26 \pm 2* | 460 |
| <i>Amphorides quadrilineata</i> | 41–42; 52–53 | 54 \pm 3 | 487 |
| <i>Codonellopsis balechi</i> | 54–56 | 36 \pm 3 | 80 |
| <i>Codonellopsis pusilla</i> | 42–44; 46–48 | 21 \pm 3 | 235 |
| <i>Cymatocyclus antarctica</i> | 48–50 | 47 \pm 3* | 200 |
| <i>Steenstrupiella pozzii</i> | 40–41 | 50 \pm 2 | 501 |

competitive advantage relative to others. This situation would resemble the niche-separation theory for diversity maintenance (Mc Gowan & Walker 1979, 1985), which postulates that each species tends to specialize on a fraction of the available resources. Unfortunately, there are no available data on phytoplankton composition and size to test this theory for TABIA cruises. However, Dolan et al. (2002) showed that the size of the prey most efficiently ingested by tintinnids is about 25% of their lorica oral diameter, thereby supporting the notion that values of lorica oral diameter would reflect the cell size of the phytoplankton community. Also, these authors found a high correlation between phytoplankton cell-size diversity and tintinnid diversity parameters, and they suggested that resource partition was the dominant mechanism accounting for tintinnid diversity in the Mediterranean Sea. Therefore, differences among lorica oral diameter values in the dominant species (Table 6), both for the oceanic and shelf-break sectors, could at least suggest the existence of a resource partition mechanism as a potential factor influencing tintinnid diversity. Further studies including phytoplankton cell-size diversity are needed to corroborate the actual occurrence of such mechanism in the southwestern Atlantic Ocean. In addition, the tintinnid population composition showed a remarkable resilience; in the subantarctic waters *C. antarctica* and *A. norvegica* remained as the dominant species for the 3 oceanic cruises (Thompson 2001), while in the shelf-break sector several studies carried out in different seasons and years, showed that the tintinnid species in Table 6 were the most abundant (Balech 1971, Souto 1972, Balech & Souto 1980, Fernandes 1998). Thompson et al. (2001) suggested that this resilience would be associated with abiotic factors at a mesoscale level. Modigh & Castaldo (2002) concluded that a particular area is likely to be characterized by a specific 'fingerprint' of dominant tintinnid species that persists in time despite environmental changes. Therefore, the 'fingerprint' concept was corroborated in the present study at a large-spatial scale (subantarctic waters).

It seems that large-scale physical processes (long-shore advection and thermohaline front) in the shelf-break sector and biological processes ('cooccurrence' and resilience of dominant species) in both sectors of the Subantarctic Zone contribute in a complex way to keep tintinnid diversity almost invariable.

Diversity values in the Antarctic Zone were similar to those registered in subantarctic waters, but species differed noticeably except for a few occasionally found on both sides of the Polar Front. The difference in specific inventories was due to the circumglobal circulation (ca. Antarctic Circumpolar Current), which characterizes the Southern Ocean and has its own endemic flora and fauna (McGowan & Walker 1993). Species found

both in antarctic and subantarctic waters belong to 2 cosmopolitan tintinnids (*Dictyocysta elegans*, *D. mitra*) and some specimens expatriated from one biogeographic domain to another (*Codonellopsis pusilla* and *Acanthostomella norvegica* from subantarctic waters, *C. gaussi* and *Laackmanniella naviculaefera* from antarctic waters; Table 2 and Alder & Thompson 2000)

Although predation pressure may also influence tintinnid diversity, in the present work its effect is ambiguous, in agreement with results of previous studies. Robertson (1983), Stoecker & Sanders (1985) and Dolan & Gallegos (2001) demonstrated that some copepod species prey selectively on certain tintinnid species. As a result, predation by copepods may have opposite effects on tintinnid diversity: if the preferred tintinnid species dominates the assemblage, predation may increase diversity by reducing dominance of the dominant species; in contrast, if the preferred species does not dominate the assemblage, it will be eliminated from the assemblage and diversity will decline. Dolan & Gallegos (2001) experimentally demonstrated these contrasting effects. Nevertheless, significant correlations between predators and tintinnid diversity parameters are not evidence of direct trophic relationships. Tintinnids, foraminifers and crustacean larvae could share food resources, since these groups are all consumers of phytoplankton (Capriulo & Carpenter 1980, Capriulo & Ninivaggi 1982, Capriulo 1990).

Temporal changes in diversity parameters can also shed some light on the mechanisms involved in determining tintinnid diversity. The latitudinal rate of change in diversity parameters for the 3 oceanic cruises showed a similar trend, but the shift observed in the trend lines suggested that changes in large-scale environmental conditions influenced diversity parameters. Diversity values were comparatively higher during the TABIA II cruise than during the TABIA I and III cruises (Fig. 3). This coincided with the seawater surface temperature (SST) profile, particularly in the Confluence Zone, where values of SST were higher in TABIA II and lower in TABIA III (Fig. 4). White & Peterson (1996) demonstrated that different perturbations (atmospheric pressure, wind, ice cover and seawater temperature) in the Antarctic Circumpolar Current caused changes in the intensity of oceanic circulation in the Southern Ocean (up to 30° S), with a 4 yr cycle. Therefore, the interannual change in SST would be related to variations in the flow of the Malvinas and Brazil Currents. In addition, Witter & Gordon (1999) registered a gradual decrease in the strength of the Malvinas Current between late 1993 and early 1995, followed by an increase through early 1997. In other words, the flow of the Brazil Current was higher in November 1994 than in November 1993 and 1995. The number of species in subtropical waters of

the Brazil Current is larger than that in subantarctic waters of the Malvinas Current for several planktonic groups (i.e. Foraminifera, Pteropoda, Salpida, Appendicularia; Boltovskoy 1986). This suggests the influence of warm waters further southwards during 1994, resulting in a larger number of tintinnid species and a subsequent increase in diversity parameters (and seawater temperature) compared to 1993 and 1995. Although changes in diversity with seawater temperature have been established for several groups (planktonic foraminifers: Rutheford et al. 1999; corals: Fraser & Currie 1996; mollusks: Roy et al. 1998, 2000), to my knowledge these have never been established for tintinnids. I do not assume that seawater temperature is the cause of tintinnid diversity. In fact, no relation between SST and diversity parameters could be established in the shelf-break sector. Seawater temperature is easily measured, and correctly reflects a complex hydrological system fluctuating at a large spatial-temporal scale such as the southwestern Atlantic Ocean. The conclusion drawn is that determination and maintenance of tintinnid diversity in the Southwestern Atlantic Ocean are possibly caused by various biological factors (available food, predators, 'cooccurrence', resilience of dominant tintinnid species) and by particular physical and hydrological characteristics of each biogeographic zone (ingress and egress of water masses in the Confluence, oscillations in the flow of the Malvinas and Brazil Currents, and the presence of a large spatial-temporal scale event: the shelf-break front).

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