Short communication

Abundance and diversity of tintinnids (planktonic ciliates) under contrasting levels of productivity in the Argentine Shelf and Drake Passage

Luciana F. Santoferrara [a,b,*], Viviana A. Alder [a,b,c]

[a] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, C1428EHA, Buenos Aires, Argentina
[b] Consejo Nacional de Investigaciones Científicas y Técnicas, Av. Rivadavia 1917, C1033AAJ, Buenos Aires, Argentina
[c] Instituto Antártico Argentino, Cerrito 1248, C1010AAZ, Buenos Aires, Argentina

ARTICLE INFO

ABSTRACT

The relationship between the abundance and diversity of tintinnids and the concentration of chlorophyll a (Chl$a$) was contrasted between neritic and oceanic waters of the SW Atlantic during autumn and summer. Chl$a$ and tintinnid abundance and biomass reached maximum values (17.53 µg L^{-1}, 2.76×10^3 ind. L^{-1}, and 6.29 µg C L^{-1}, respectively) in shelf waters during summer, and their mean values generally differed by one order of magnitude between environments. Peaks in species richness (13) and Shannon diversity index (2.12) were found in the shelf–ocean boundary, but both variables showed nonsignificant differences between areas. Species richness correlated significantly with both Chl$a$ and abundance. Such relationships, which followed a negative linear or quadratic function in the shelf and a positive linear function in oceanic waters, are thought to reflect either the competitive dominance of one species or a relatively wide spectrum of tintinnid size-classes, respectively.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Ciliates play a key role as trophic link between the smallest and the largest components of planktonic food webs in marine environments. Tintinnids are usually a minority group among ciliates, but are ubiquitous in the microzooplankton and can be important consumers of phytoplankton (Lynn, 2008). The lorica that characterizes tintinnids allows for species classification, and its opening width, the Lorica Oral Diameter (LOD), is linked to ecological features such as the maximum and preferred prey size (Dolan, 2010). In addition, tintinnid species display consistent patterns of diversity (Dolan et al., 2006b) and provide reliable indicators of hydrography and biogeography (Alder, 1999).

One of the main factors that explains tintinnid distribution and abundance is chlorophyll a concentration (Chl$a$), while the relationship between this variable and tintinnid diversity has been reported as weak or non-significant in either neritic (Dolan et al., 2006a; Sitran et al., 2007) or oceanic waters (Dolan et al., 2002, 2007; Thompson, 2004). Indeed, tintinnid diversity has been shown to be linked more closely with prey diversity than with food concentration (Dolan et al., 2002). In contrast, significant correlations are found between species richness and different measures of productivity (e.g.,

Chl$a$) for other pelagic organisms and benthic communities, although the type of relationship (linear or quadratic) depends on the taxonomic group and the scale of analysis (Gaston and Spicer, 2004; Witman et al., 2008).

We explored the relationship between Chl$a$ and both tintinnid abundance and species richness in two adjacent environments, the Argentine Shelf and the Drake Passage, during autumn and summer. These regions are influenced by multiple oceanographic processes and exhibit dissimilar current circulation patterns (Fig. 1A). While the oceanic waters of the Drake Passage show low, uniform Chl$a$, the mid-depth sector (50–100 m) of the Argentine Shelf is characterized by a strong seasonality in primary production (Rivas et al., 2006). These contrasting conditions are reflected in a significant decrease in the abundance and biomass of total ciliates from the shelf to oceanic waters (Santoferrara and Alder, 2009a). In the present study, we first analyzed the general trends of tintinnid abundance, diversity, species structure and LOD size-classes, and then we addressed the following questions: (1) Is Chl$a$ significantly related to tintinnid species richness? (2) If tintinnid abundance is linked to Chl$a$, is there a relationship between abundance and species richness? Knowing these relationships under heterogeneous Chl$a$ levels will help to understand productivity effects on marine microzooplankton diversity.

2. Material and methods

Sixty-six oceanographic stations were sampled on two latitudinal transects on board the icebreaker *Almirante Irizar* during austral

* Corresponding author at: EGE, FCEN, UBA, Intendente Güiraldes 2160, Ciudad Universitaria, 4° Piso, Pabellón II, Lab. 87. Buenos Aires (1428), Argentina. Tel.: +54 11 4576 3300; fax: +54 11 4576 3384.
E-mail address: lusantoferrara@yahoo.com.ar (LF. Santoferrara).
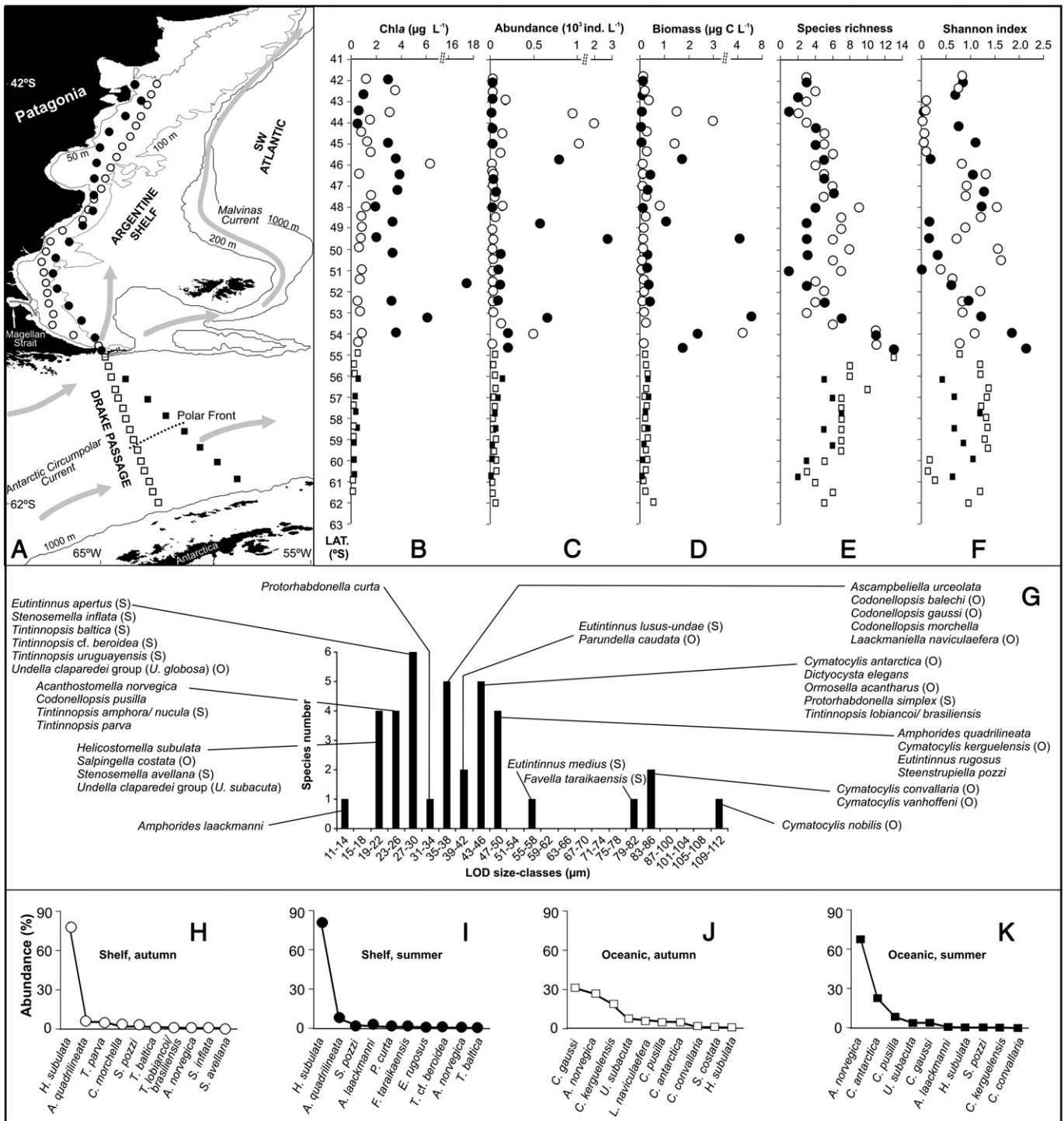
Fig. 1. Main features of the region under study and tintinnid assemblages. A Stations analyzed; current circulation after Matano et al. (2010). B Chlorophyll *a* concentration. C Tintinnid abundance. D Biomass. E Species richness. F Shannon diversity index. G Species distribution into size-classes based on the mean oral diameter of the lorica (LOD). Species found exclusively in the shelf (S) or oceanic waters (O) are indicated. H–K Rank/abundance plots based on the ten species with higher contribution to total tintinnids. From A to F, symbols represent stations from the shelf (circles) and oceanic waters (squares) during autumn (white) and summer (black).

autumn (April 2002) and summer (February 2003) (Table 1). For plankton samples, 100 to 200 L of sub-surface (9 m) seawater were collected by a centrifugal pump, concentrated through a sieve (20 μm pore size) and preserved with Bouin's Solution (10% final). In addition, 2 to 4 L of seawater from 52 of the stations were concentrated on GF/F filters and frozen until spectrophotometric quantification of Chl*a* (Strickland and Parsons, 1972).

For each plankton sample, two sub-samples equivalent to a mean volume of 10 L of seawater were settled and analyzed under an

inverted microscope (Uthermöhl, 1958). A total of 26,000 tintinnid individuals were classified into species according to Alder (1999). The absolute abundance of each species, the species richness, and the Shannon diversity index (ln-based; Magurran, 2004) were estimated for each station. Both empty loricae and those containing cells were considered, because cells may be lost during sampling and lorica contents cannot be differentiated for species with densely agglomerated loricae (Alder, 1999). Whenever possible, at least 30 loricae (up to 400) per species were measured. Each species was then

Table 1

General data on stations and variables analyzed in the Argentine Shelf and Drake Passage waters. The range and (average) of each variable are included.

	Argentine Shelf		Drake Passage	
	Autumn	Summer	Autumn	Summer
Number of stations	26	18	15	7
Bottom depth (m)	47–112	41–103	3000–4250	2460–5000
Latitude (°S)	42.00–54.50	42.00–54.73	55.00–62.00	56.17–60.75
Longitude (°W)	62.38–67.82	63.08–67.28	62.28–64.85	58.58–63.75
Temperature (°C)[a]	8.13–17.49 (11.63)	9.70–18.75 (13.17)	0.30–8.20 (3.58)	3.32–6.96 (4.94)
Salinity (ssu)[a]	32.54–34.16 (33.19)	32.58–34.07 (33.14)	33.04–34.01 (33.78)	33.59–33.93 (33.75)
Chl$a$ (µg L^{-1})	0.47–6.30 (1.36)	0.47–17.53 (3.71)	0.04–0.48 (0.15)	0.05–0.39 (0.23)
Total ciliate abundance (10^3 ind.L^{-1})[b]	0.39–4.95 (1.44)	0.04–19.74 (2.63)	0.20–1.00 (0.57)	0.38–3.09 (0.88)
Total ciliate biomass (µg C L^{-1})[b]	0.27–13.65 (3.12)	0.01–25.05 (3.87)	0.28–2.30 (1.15)	0.52–6.87 (1.79)
Tintinnid abundance (10^3 ind.L^{-1})	<0.01–1.87 (0.20)	<0.01–2.76 (0.31)	<0.01–0.05 (0.04)	<0.01–0.12 (0.04)
Tintinnid biomass (µg C L^{-1})	0.01–4.65 (0.49)	<0.01–6.29 (1.04)	0.04–0.45 (0.14)	0.01–0.19 (0.09)
Tintinnid abundance: total ciliate abundance (%)	<1–49 (9)	<1–48 (11)	3–23(8)	<1–13 (5)
Tintinnid biomass: total ciliate biomass (%)	1–86 (11)	1–89 (24)	4–27 (14)	1–30 (9)
Tintinnid species richness	2–11 (6)	1–13 (5)	3–13 (7)	2–7 (5)
Tintinnid Shannon diversity index	0.01–1.61 (0.73)	0.01–2.12 (0.80)	0.11–1.38 (1.00)	0.42–1.19 (0.78)

[a] http://dataipsl.ipsl.jussieu.fr/ARGAU/argau.htm ARGAU.
[b] Santoferrara and Alder (2009a).

assigned to a discrete 4-µm size-class according to its mean LOD. Biomass estimations were based on lorica dimensions and the regression formula proposed for carbon content in tintinnids (Verity and Langdon, 1984).

The relationships between Chl$a$ and abundance, biomass or species richness, as well as between abundance and species richness, were analyzed by means of linear (first order) regressions. When similar trends were found for autumn and summer, data from both periods were pooled for the shelf and oceanic waters to test for significance of regressions. All variables were log$_{10}$-transformed. Normality and homogeneity of variances were verified using the tests of Kolmogorov–Smirnov and Levene, respectively. In cases where non-significant linear regressions were obtained, the significance of polynomial (quadratic) regressions was tested by F tests (Zar, 1999). Species richness and the Shannon index were contrasted between environments and seasons by the non-parametric test of Kruskal–Wallis.

3. Results and discussion

3.1. General trends

The data analyzed in this study are summarized in Table 1. Chl$a$ reached maximum values up to 6.30 and 17.53 µg L^{-1} in the shelf during autumn (46.0°S) and summer (51.7°S), respectively (Fig. 1B). In oceanic waters, Chl$a$ was below 0.60 µg L^{-1} regardless of the season. Tintinnid abundance and biomass showed similar spatial trends in autumn and summer, with values below 0.25×10^3 ind.L^{-1} and 1 µg C L^{-1}, respectively, in almost all stations (Fig. 1C–D). Higher values were found only in shelf waters, and maximum values were detected in summer (2.76×10^3 ind.L^{-1} and 6.29 µg C L^{-1} at 49.5°S and 53.3°S, respectively). Mean values of abundance and biomass were from three- to twelve-fold higher in the shelf than in oceanic waters (Table 1), in agreement with the general trend reported for total ciliates (Santoferrara and Alder, 2009a). The mean contribution of tintinnids to total ciliate abundance and biomass was relatively low (5–11% and 9–24%, respectively) under the four conditions analyzed. The highest contributions (ca. 50% for abundance and ca. 90% for biomass) were found in shelf waters, but such proportions never exceeded 30% in oceanic waters. Both the constant relative abundance of tintinnids and their tendency to sporadically dominate the ciliate community in neritic waters (but not in oceanic ones) is a general finding for several environments (McManus and Santoferrara, in press).

Tintinnids were classified into 20 genera and 37 species. The total number of species found in the Argentine Shelf (25) and Drake Passage waters (26) corresponded to ca. 90% and 80%, respectively, of the species reported in these areas (Alder, 1999). Species richness showed values between 1 and 7 in almost all stations (Fig. 1E); values between 8 and 13 were detected only in two stations at 48°S and 50°S (in autumn), and in the boundary between neritic and oceanic waters (53.5–56.5°S, in both seasons). The trend of the Shannon diversity index was similar to that of species richness, except for a peak (1.85–2.12) that was evident only at 54–55°S in summer (Fig. 1F). Given the homogeneous ranges and averages of species richness and Shannon diversity index (Table 1), the values of both variables did not differ significantly among the four conditions analyzed (test of Kruskal–Wallis, p > 0.05). In addition, such values were comparable to those previously reported in the adjacent shelf-break and oceanic waters (species richness range: 3–13; Shannon index range ~0–1.80; 48–60°S) by Thompson (2004), and in the Drake Passage (mean Shannon index: 0.73–1.00) by Alder and Thompson (2000).

A total of 13 LOD size-classes were found (Fig. 1G). Minimum and maximum LOD ranged from 11 to 111 µm and were represented by *Amphorides laackmanni* and *Cymatocylis nobilis*, respectively. Most of the species fell within 8 size-classes between 19 and 50 µm, thus suggesting a grazing impact on nanoplankton cells between 4 and 10 µm, if we assume that the preferred prey size of tintinnids is 20% of LOD (Dolan, 2010). Larger species found only in oceanic waters (*Cymatocylis* spp. ≥ 83 µm) may graze even on microdiatoms. Species abundance distribution was more variable between environments than between periods (Fig. 1H–K; Supplementary Table 1). In shelf waters, one species, *Helicostomella subulata*, represented ca. 80% of tintinnid abundance both in autumn and summer. In oceanic waters, *Codonellopsis gaussi*, *Acanthostomella norvegica* and *Cymatocylis kerguelensis* presented maximum relative abundances during autumn (20–30%), while *A. norvegica* and *Cymatocylis antarctica* prevailed in summer (70 and 22%, respectively). In all cases, the remaining species showed relative abundances lower than 15%.

3.2. Relationship between Chla, tintinnid abundance and species richness

Fig. 2 shows that relationships between log-transformed variables were significant in almost all cases, both in the shelf and oceanic waters (see also the Supplementary Table 2). We found a positive linear relationship between Chl$a$ and either abundance or biomass (p < 0.05, except a non-significant result for biomass in oceanic waters; Fig. 2A–D), thus confirming the known influence of food concentration on tintinnid
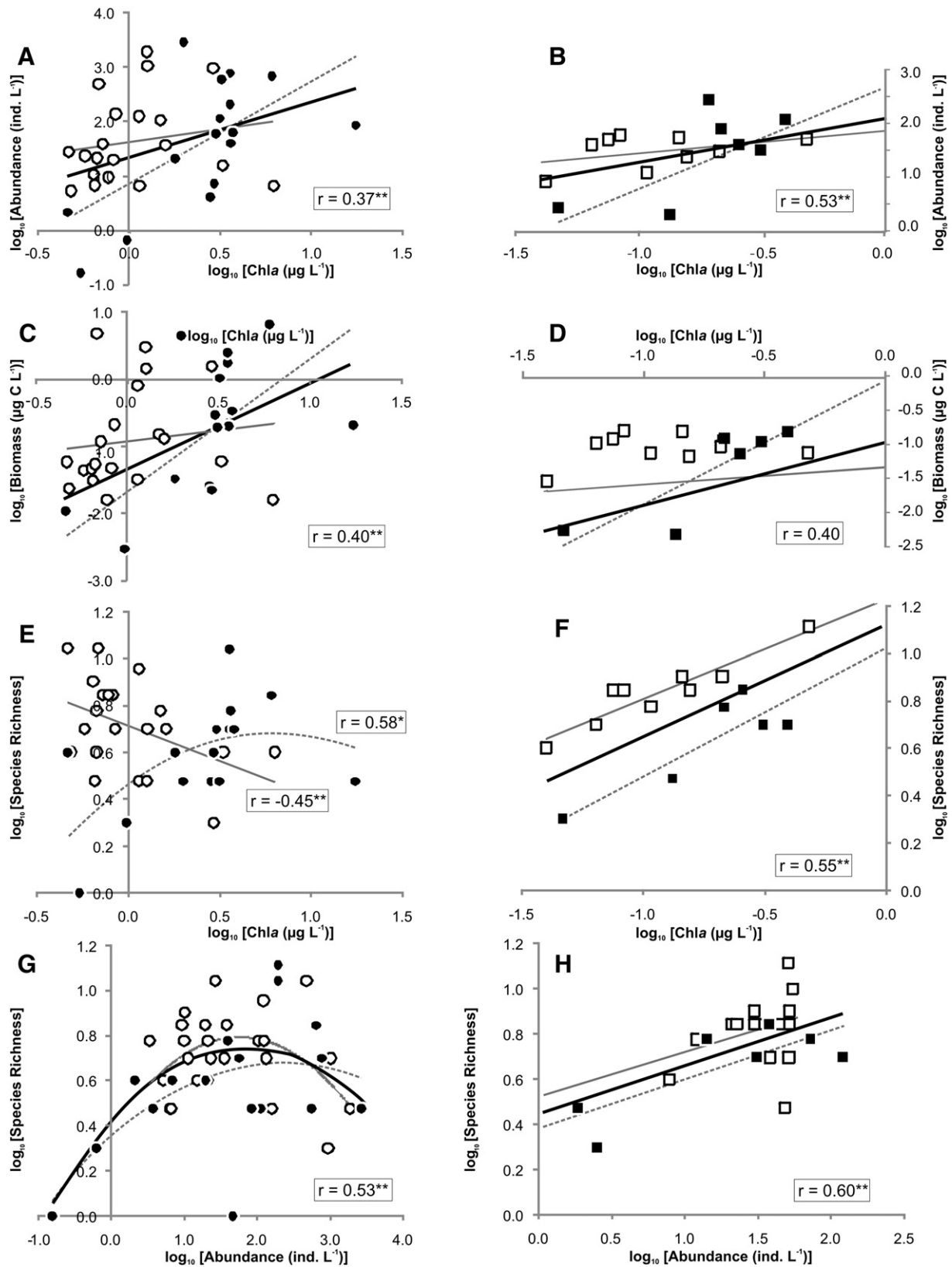
Fig. 2. Regressions between chlorophyll *a* concentration and tintinnid variables in the Argentine shelf (A–C–E–G) and Drake Passage waters (B–D–F–H). Correlation coefficients (r), significance levels (**p<0.05; *p<0.10), and regression lines (thick complete lines) are shown for each environment. Regression lines are shown also for autumn (thin complete lines, white symbols) and summer (thin incomplete lines, black symbols). Coefficients for each period are shown only in E.

stocks (e.g., Dolan et al., 2006a, 2007). While the ratio of total ciliate biomass to Chl*a* has been reported to increase in one order of magnitude from neritic to oceanic environments (Dolan and Marrasé, 1995), we found that the ratio of tintinnid biomass to Chl*a* differed in a factor lower than two between the Argentine Shelf and Drake Passage (0.47 and 0.83, respectively).

The type of function between Chl*a* and species richness varied between environments, whereas differences between seasons were found only in the shelf (Fig. 2E–F). Both the variability in species richness explained by Chl*a* (20–34%) and the significance level of the relationships (Supplementary Table 2) are comparable to those reported for other marine communities (e.g., benthos of Arctic and Subarctic ecosystems; Witman et al., 2008). In shelf waters, a significant negative linear relationship was found in autumn ($p < 0.05$), while a marginally significant hump-shaped quadratic function was obtained for summer ($p < 0.1$). In oceanic waters, a significant positive linear relationship was found during both periods ($p < 0.05$).

The different kinds of relationships observed between Chl*a* and species richness might be explained by the relative abundance of species and the variety of LOD size-classes. On the one hand, the negative relationship found in the shelf during autumn may be due to the fact that species richness can decrease with productivity if a single species uses most of the food resources and outcompetes other species (Rosenzweig and Abramsky, 1993). Similarly, although the hump-shaped model observed for this environment during summer suggests a positive effect of intermediate Chl*a* levels on species richness, the descending part of the curve may also be explained by competitive dominance at high food levels. The LOD of the species that clearly prevailed in both periods (*H. subulata*, 19–22 µm) suggests a food preference for the phytoplankton size-fraction that dominated during the same sampling cruises (flagellates ≤ 5 µm; Schloss et al., 2007), and thus the available prey may have favored the proliferation of this species (Santoferrara and Alder, 2009b). On the other hand, a positive relationship between Chl*a* and species richness as we detected in oceanic waters may be explained by the fact that species richness can increase with productivity if higher productivity is linked to higher diversity of producers (Rosenzweig and Abramsky, 1993). This agrees with reports for the Drake Passage, where higher Chl*a* values are linked to higher diatom species richness (Olguín and Alder, 2011). In addition, the relatively equitable tintinnid assemblages found in oceanic waters in terms of species and size-classes may reflect a diverse, wide size-spectrum of prey (e.g., nanoflagellates and microdiatoms, see above).

Species richness and abundance showed a hump-shaped relationship in the shelf ($p < 0.05$), and a positive linear correlation in oceanic waters ($p < 0.05$) (Fig. 2G–H). The latter result (Fig. 2H) may derive from the similar functions found between each of these variables and Chl*a* (Fig. 2B and F), while the relationship found in the shelf (Fig. 2G) may be explained again by competition, and also by prey quality and predator abundance. Shelf sites with low species richness (≤3) coincided with either peaks of *H. subulata* (ca. $2–3 \times 10^3$ ind.L^{-1}) or minimum tintinnid abundances (<100 ind. L^{-1}) (Fig. 1C and E). Such minimum values were found, for example, at 51–52°S (summer) and 53°S (autumn), where blooms of diatoms >10 µm (Schloss et al., 2007) and high abundances of mesozooplankton (Sabatini et al., 2004), respectively, have been reported, thus suggesting the influence of inadequate food resources and predation on tintinnid abundance and species richness.

3.3. Conclusions

The main ecological trends of tintinnids were contrasted between the Argentine Shelf and Drake Passage for the first time. In terms of mean values, heterogeneous Chl*a* levels were reflected in tintinnid abundance and biomass, while species richness and diversity did not differ between the shelf and oceanic waters. Differences between environments in both LOD size-classes and the ratio of tintinnid biomass to Chl*a* are thought to indicate dissimilarities in the type and concentration of food available. Species richness showed significant relationships with both abundance and Chl*a*, and different kinds of functions between these variables suggested the influence of competition and prey diversity on tintinnid assemblages. However, Chl*a*

alone is far from explaining all the variability in species richness, and thus other factors and processes (e.g., temperature, random dispersal) should be explored as additional causes in future studies.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2012.04.002.

References

Alder, V.A., 1999. Tintinnoinea. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp. 321–384.

Alder, V.A., Thompson, G.A., 2000. Spatial and temporal distribution of tintinnids (Protozoa, Ciliata) in relation to frontal systems and the general hydrologic dynamics of the Southern Ocean (SW Atlantic Sector; 50°–64°S, 65°–49°W). In: Davidson, W., Howard-Williams, C., Broady, P. (Eds.), Antarctic Ecosystems: Models for Wider Ecological Understanding. SCAR, Christchurch, pp. 203–214.

Dolan, J.R., 2010. Morphology and ecology in tintinnid ciliates of the marine plankton: correlates of lorica dimensions. Acta Protozoologica 49, 235–344.

Dolan, J.R., Marrasé, C., 1995. Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993. Deep Sea Research Part I: Oceanographic Research Papers 42, 1965–1987.

Dolan, J.R., Claustre, H., Carlotti, F., Plounevez, S., Moutin, T., 2002. Microzooplankton diversity: relationship of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean. Deep Sea Research Part I: Oceanographic Research Papers 49, 1217–1232.

Dolan, J.R., Jacqet, S., Torréton, P.-P., 2006a. Comparing taxonomic and morphological biodiversity of tintinnids (planktonic ciliates) of New Caledonia. Limnology and Oceanography 51, 950–958.

Dolan, J.R., Lemée, R., Gasparini, S., Mousseau, L., Heyndrickx, C., 2006b. Probing diversity in the plankton: using patterns in tintinnids (planktonic marine ciliates) to identify mechanisms. Hydrobiologia 555, 143–157.

Dolan, J.R., Ritchie, M.E., Ras, J., 2007. The "neutral" community structure of planktonic herbivores, tintinnid ciliates of the microzooplankton, across the SE Tropical Pacific Ocean. Biogeosciences 4, 297–310.

Gaston, K.J., Spicer, J.I., 2004. Biodiversity: An Introduction, second ed. Blackwell Publishing, Oxford.

Lynn, D.H., 2008. The Ciliated Protozoa. Characterization, Classification, and Guide to the Literature. Springer Verlag, Dordrecht.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford.

Matano, R.P., Palma, E.D., Piola, A.R., 2010. The influence of the Brazil and Malvinas Currents on the southwestern Atlantic shelf circulation. Ocean Science 6, 983–995.

McManus, G., Santoferrara, L., in press. Tintinnids in microzooplankton communities, in: Dolan, J.R., Agatha, S., Coats, D.W.C., Montagnes, D.J.S., Stoecker, D.K. (Eds.), Biology and Ecology of Tintinnid Ciliates: Models for Marine Plankton. Wiley/Blackwell, Oxford.

Olguín, H.F., Alder, V.A., 2011. Species composition and biogeography of diatoms in antarctic and subantarctic (Argentine shelf) waters (37–76°S). Deep Sea Research Part II: Topical Studies in Oceanography 58, 139–152.

Rivas, A., Dogliotti, A., Gagliardini, D., 2006. Seasonal variability in the satellite-measured surface chlorophyll in the Patagonian Shelf. Continental Shelf Research 26, 703–720.

Rosenzweig, M.L., Abramsky, Z., 1993. How are diversity and productivity related? In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago.

Sabatini, M., Reta, R., Matano, R., 2004. Circulation and zooplankton biomass distribution over the southern Patagonian shelf during late summer. Continental Shelf Research 24, 1359–1373.

Santoferrara, L.F., Alder, V.A., 2009a. Abundance trends and ecology of planktonic ciliates of the south-western Atlantic (35–63° S): a comparison between neritic and oceanic environments. Journal of Plankton Research 31, 837–851.

Santoferrara, L.F., Alder, V.A., 2009b. Morphological variability, spatial distribution and abundance of Helicostomella species (Ciliophora, Tintinnina) in relation to environmental factors (Argentine shelf; 40–55°S). Scientia Marina 73, 701–716.

Schloss, I., Ferreyra, G., Ferrario, M., Almandoz, G., Codina, R., Bianchi, A., Balestrini, C., Ochoa, H., Ruiz Pino, D., 2007. Role of plankton communities in sea–air variations in pCO2 in the SW Atlantic Ocean. Marine Ecology Progress Series 332, 93–106.

Sitran, R., Bergamasco, A., Decembrini, F., Guglielmo, L., 2007. Temporal succession of tintinnids in the northern Ionian Sea, Central Mediterranean. Journal of Plankton Research 29, 495–508.

Strickland, J., Parsons, T., 1972. A practical handbook of sea-water analysis. Journal of the Fisheries Research Board of Canada 167, 1–311.

Thompson, G.A., 2004. Tintinnid diversity trends in the southwestern Atlantic Ocean (29 to 60° S). Aquatic Microbial Ecology 35, 93–103.

Uthermöhl, H., 1958. Zur Vervollkommung der quantitativen phytoplankton-metodik. Mitteilung Internationale Vereinigung fuer Theoretische unde Amgewandte Limnologie 9, 1–38.

Verity, P., Langdon, C., 1984. Relationship between lorica volume, carbon, nitorgen, and ATP content of tintinnids in Narragansett Bay. Journal of Plankton Research 6, 859–868.

Witman, J.D., Cusson, M., Archambault, P., Pershing, A.J., Mieszkowskan, N., 2008. The relation between productivity and species diversity in temperate-arctic marine ecosystems. Ecology 89, S66–S80.

Zar, J., 1999. Biostatistical Analysis, fourth ed. Prentice-Hall Inc., New Jersey.