JOURNAL OF PLANKTON RESEARCH | VOLUME 31 | NUMBER 8 | PAGES 837–851 | 2009

Abundance trends and ecology of planktonic ciliates of the south-western Atlantic (35–63°S): a comparison between neritic and oceanic environments

LUCIANA SANTOFERRARA[1,2]* AND VIVIANA ALDER[1,2,3]

[1]CONSEJO NACIONAL DE INVESTIGACIONES, CIENTÍFICAS Y TÉCNICAS, AV. RIVADAVIA 1917 C1033AAJ, BUENOS AIRES, ARGENTINA, [2]DEPARTAMENTO DE ECOLOGÍA, GENÉTICA Y EVOLUCIÓN, FACULTAD DE CIENCIAS EXACTAS Y NATURALES, UNIVERSIDAD DE BUENOS AIRES, C1428EHA BUENOS AIRES, ARGENTINA AND [3]INSTITUTO ANTÁRTICO ARGENTINO, CERRITO 1248, C1010AAZ BUENOS AIRES, ARGENTINA

*CORRESPONDING AUTHOR: lusantoferrara@ege.fcen.uba.ar

Received February 3, 2009; accepted in principle April 17, 2009; accepted for publication April 22, 2009; published online 19 May, 2009

Corresponding editor: John Dolan

Ciliates from sub-surface waters of the Argentine shelf and the Drake Passage under austral summer and autumn conditions were examined and compared for the first time. In both environments, the taxonomic structure of ciliates was related to temperature and salinity, and aloricate oligotrichs dominated in density (80%) over loricate oligotrichs, litostomatids and prostomatids, while the microplanktonic fraction prevailed in terms of biomass (90%) over the nanociliates. Myrionecta rubra was found all along the Argentine shelf only in autumn, but showed isolated peaks of abundance (10^3 ind. L^{-1}) during summer. Mean values of density and biomass of total ciliates decreased ca. 2-fold from the shelf-slope to oceanic waters, while potential maximum production of aloricate oligotrichs decreased 9-fold, in relation with the drop in chlorophyll a *concentration and the latitudinal decline of temperature, also reflected in maximum growth rates. Fifty percent of total ciliate abundance was represented by local increases (maximum: 20 000 ind. L^{-1} and 25 μg C L^{-1}), which were spatially superimposed with ranges of seawater temperature and chlorophyll* a *concentrations of 10–15°C and 0.6–6 μg L^{-1}, respectively, and were found in the nearby of fronts located on the shelf and the slope.*

INTRODUCTION

Ciliates play a key role in the transfer of nutrients and energy through planktonic food webs, acting as top-down regulators of pico- and nanoplankton, as primary producers in the case of autotrophic and mixotrophic species (*Myrionecta rubra* and some aloricate oligotrichs, respectively), and as a food source for micro- and mesozooplankton (Pierce and Turner, 1992). The spatial and seasonal distribution of their density and biomass usually follows the fluctuations of bacterial and phytoplankton production (Leakey *et al.*, 1996; Modigh, 2001; Chiang *et al.*, 2003; Kim *et al.*, 2007). The taxonomic and size structure of ciliates is usually shaped by the size composition of the food resources (Montagnes *et al.*, 1988; Setälä and Kivi, 2003; Johansson *et al.*, 2004). Temperature is also known to markedly affect ciliates, mainly by controlling their growth rates (Montagnes, 1996; Montagnes and Lessard, 1999). Finally, other factors, such as grazing (Nielsen and Kiørboe, 1994) as well as current circulation and frontal

doi:10.1093/plankt/fbp033, available online at www.plankt.oxfordjournals.org

processes (Montagnes *et al.*, 1999; Safi *et al.*, 2007; Zarauz *et al.*, 2008), are also known to have some bearing on the qualitative and/or quantitative attributes of a given ciliate community.

Marked changes in practically all of the above biotic and abiotic factors are well exemplified by the sharp neritic-to-oceanic transition observed for the sector extending from the Argentine shelf to the proximity of the Antarctic Peninsula (Fig. 1), which is accompanied by the latitudinal decrease in temperature. Although previous studies suggest that planktonic ciliates generally show abundance levels at least one order of magnitude higher in neritic than in oceanic waters (Pierce and Turner, 1992), there is little information on the contrast of ciliate abundance and structure in both environments.

The Argentine shelf is one of the most productive (Behrenfeld and Falkowsky, 1997) and largest in the World Ocean, with a width up to 800 km and an area of ca. 1×10^6 km^2 (Acha *et al.*, 2004). It encompasses temperate to cold waters and is characterized by a strong seasonality, a latitudinal delay of phytoplankton spring blooms (Rivas *et al.*, 2006; Romero *et al.*, 2006), and several thermohaline and/or tidal fronts often linked to high concentrations of chlorophyll, picoplankton, phytoplankton, mesozooplankton and other organisms, including species of ecological and commercial relevance (Acha *et al.*, 2004; Alder and Franzosi, 2004; Sabatini *et al.*, 2004; Almandoz *et al.*, 2007). Its main hydrological inputs are those of the diluted waters derived from continental run-off and from the Pacific Ocean via the Cape Horn Current and through the Magellan Strait, and those of the cold, saline, nutrient-enriched subantarctic waters of the Malvinas Current, a branch of the Antarctic Circumpolar Current (Piola and Rivas, 1997). At ca. 55°S, the shelf ends in the oceanic Drake Passage, a complex and dynamic oceanographic sector which includes waters of subantarctic and antarctic origin and is characterized by strong eddy activity and at least three permanent oceanographic fronts (Orsi *et al.*, 1995), often associated with relative increases in chlorophyll *a* (Moore and Abbott, 2002).

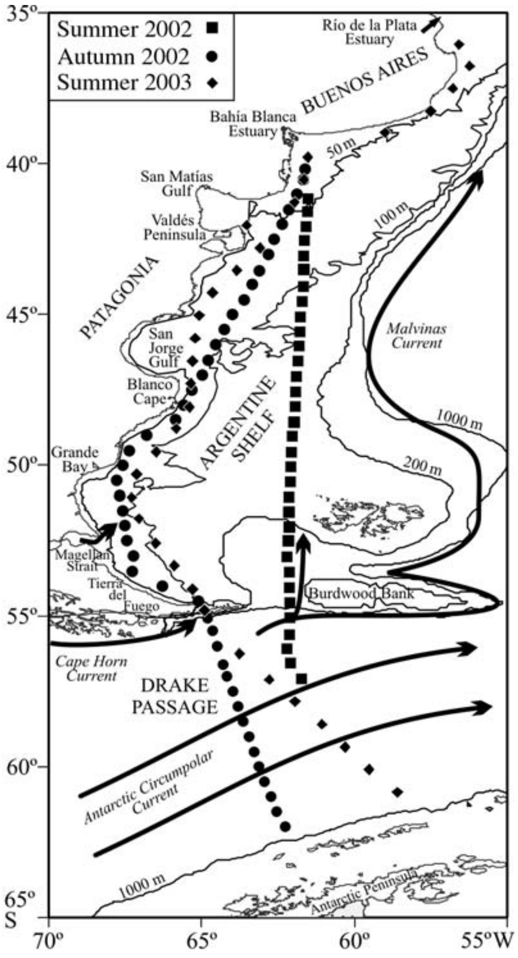

Fig. 1. Geographical position of oceanographic stations.

Although the Argentine shelf and the Drake Passage provide an ideal scenario to analyse variations in biological communities along a bathymetric and thermal gradient, planktonic ciliates have never been studied in this region. The information available on these organisms is restricted to estuaries (Barría de Cao *et al.*, 2003; Kogan, 2005) and adjacent oceanic waters of the south-western Atlantic (Fernandes and Brandini, 1999). Consequently, the aim of the present work was to examine, for the first time, the major ecological trends related to ciliates inhabiting sub-surface waters of those neritic and oceanic waters under austral summer and autumn conditions. The abundance and cell size of major taxonomic classes, as well as potential metabolic rates, were estimated in relation to bathymetry, temperature, salinity and chlorophyll *a* concentration. In this context, we hypothesized that the taxonomic and size structure of ciliates and their levels of abundance are clearly different between both environments, as a response to the environmental conditions and food availability.

METHOD

Three latitudinal transects were performed on the Argentine shelf and the Drake Passage (Fig. 1) during austral summer (January–February 2002 and 2003) and autumn (April 2002) on board the icebreaker Almirante Irizar, where sub-surface (9 m) seawater was continuously provided by a centrifugal pump specially designed to preserve fragile microorganisms. The transects carried out during autumn 2002 and summer 2003 covered

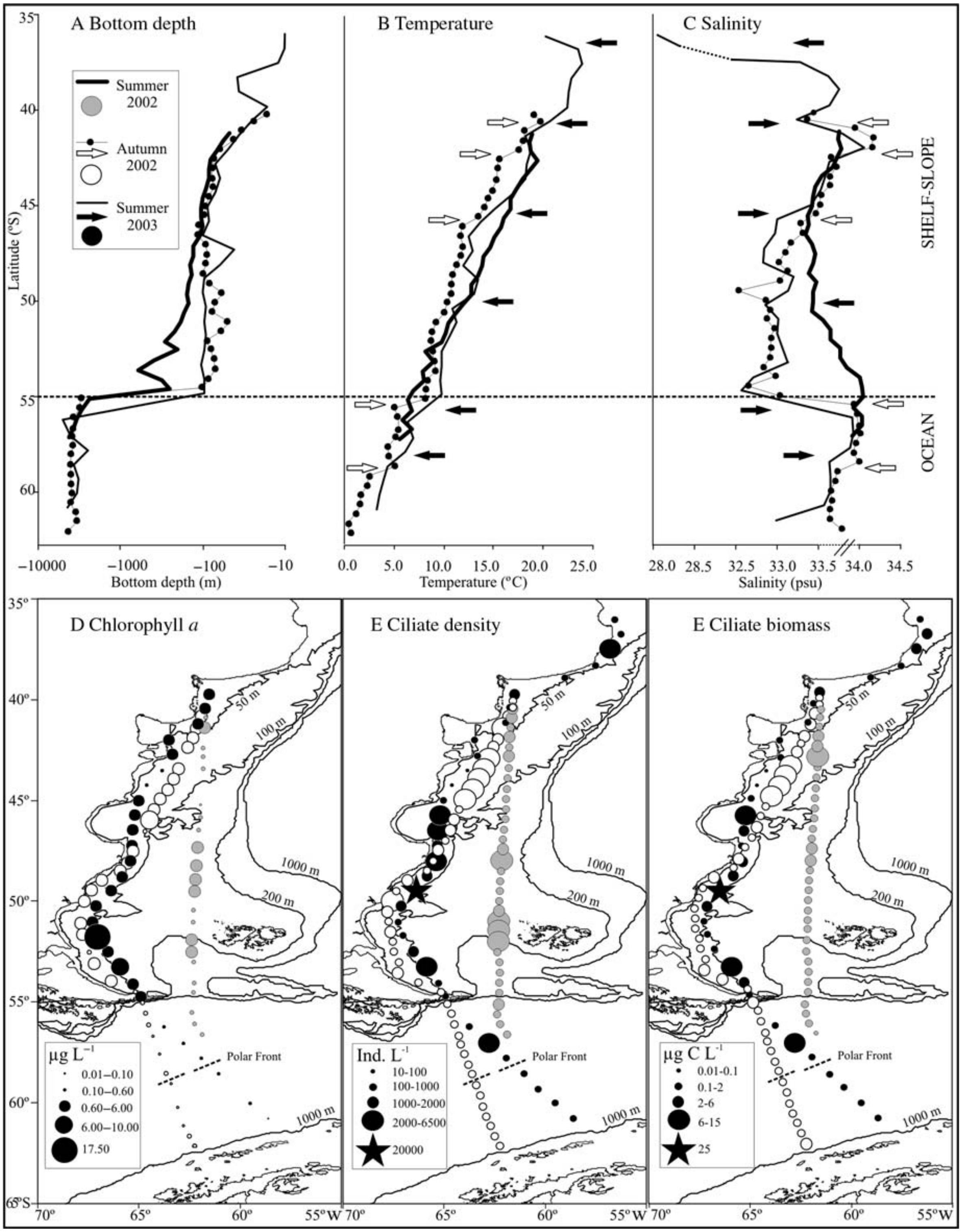

Fig. 2. Environmental parameters (**A**–**D**), density (**E**) and biomass (**F**) of ciliates on the Argentine shelf and Drake Passage waters under summer and autumn conditions. Arrows indicate decreases of temperature (B) and salinity (C). Bottom depth was plotted on a logarithmic scale.

both inner (<50 m) and middle (50–100 m) shelf waters, and are characterized by a sharp transition to the oceanic subantarctic–antarctic environment (Fig. 2A). In summer 2002, only waters from the subantarctic regime were surveyed, covering the outer shelf (100–200 m), the slope (200–600 m) and the oceanic domain.

Temperature and salinity were measured by a continuous automated system (ARGAU Project: http://dataipsl.ipsl.jussieu.fr/ARGAU/argau.htm), while bathymetric information and plankton samples were obtained at 111 oceanographic stations with a spatial resolution of 0.5–0.8° of latitude. Both filtered (100–200 L; 20 μm mesh size) and non-filtered (0.5 L) samples were preserved with Bouin's solution 10 and 5% (f.c.) to study loricate and aloricate ciliates, respectively. In addition, at 83 stations, 2–4 L of water were concentrated on GF/F filters and frozen until spectrophotometric quantification of chlorophyll *a* (Strickland and Parsons, 1972).

Over 15 000 individual ciliates were examined under upright and/or inverted microscopes (250×–1000×) and classified at the class level (Lynn and Small, 2002). *Myrionecta rubra* was classified up to the specific level due to its unique trophic mode. Density was estimated under an inverted microscope (Utermöhl, 1958), counting at least 100 individuals per sample and reaching a standard error <30%. Biomass was assessed first by measuring 40 specimens per station to calculate their volume, and then by applying the regression formula (0.053 lorica volume+444.5) or the conversion factor (0.19 pg C μm^{-3}) proposed for estimating the content of organic carbon in loricate ciliates (Verity and Langdon, 1984) and aloricate ciliates fixed with acid Lugol's solution 2% (Putt and Stoecker, 1989), respectively. Since Bouin's solution 5% can cause cell shrinkage, on average, 7% higher than acid Lugol's solution 2% (Stoecker *et al.*, 1994), our biomass values for aloricate ciliates may be slightly underestimated. The contribution to density and biomass according to size was evaluated by differentiating between nanociliates (<20 μm) and microciliates (20–200 μm).

Potential maximum values of growth rate (Müller and Geller, 1993) and ingestion rate (Hansen *et al.*, 1997) of aloricate oligotrichs at each station were calculated using the following equations:

$$\ln \mu = 1.52 \ln T - 0.27 \ln V - 1.44$$
$$\log \mathrm{IR} = 0.10 - 0.20 \log V$$

where μ is the maximum growth rate (day^{-1}), IR the maximum ingestion rate (h^{-1}), T the temperature (°C) and V the cell volume (μm^3). Subsequently, the biomass was multiplied by either IR or μ to estimate potential maximum values (in $\mu g\ C\ L^{-1}\ \mathrm{day}^{-1}$) of consumption (Verity *et al.*, 1996) and production (Montagnes *et al.*, 1988), respectively.

The data were statistically analysed by: (i) the non-parametric Spearman's coefficient (R), to evaluate the correlation between bottom depth, latitude, temperature, salinity and chlorophyll *a* with the density and biomass of total ciliates, the potential production of aloricate oligotrichs, the proportion of each class and size fraction and the absolute abundance of *M. rubra*. Correlations in oceanic waters were omitted for some taxonomic classes which were recorded only at a few stations. (ii) Non-parametric, one-way ANOVA (Mann–Whitney's test and Kruskal–Wallis' test for two or more means, respectively), to compare ciliate abundance between different groups of stations (Zar, 1999). (iii) Non-metric multi-dimensional scaling (MDS) (Field *et al.*, 1982) using a Bray–Curtis dissimilarity matrix based either on the relative density or biomass of ciliates according to taxonomic classes and size fractions, to analyse their spatio-temporal trend.

RESULTS

Environmental variables and ciliate abundance

For the three transects analysed, temperature ranged from 0.3°C (autumn 2002, 61.5°S) to 23.9°C (summer 2003, 37.5°S) (Fig. 2B). Considering the same latitudinal range (41–57°S) for the three periods, the mean temperature was found to decrease from 13°C in summer to 11°C in autumn. Salinity varied between ca. 28 psu at the northernmost sector (36–36.7°S) and ca. 34 psu at 41–42°S and in the Drake Passage (Fig. 2C). Simultaneous drops of temperature (2–3°C) and salinity (0.2–5.0 psu) were only detected in autumn 2002 and summer 2003 (Fig. 2B and C). The lowest mean chlorophyll *a* concentrations (Fig. 2D) were detected in oceanic (0.21 $\mu g\ L^{-1}$) and outer shelf waters (0.65 $\mu g\ L^{-1}$), while maximum figures corresponded to inner and middle shelf waters, where the value recorded for summer (2.79 $\mu g\ L^{-1}$) doubled that of autumn (1.34 $\mu g\ L^{-1}$).

Spatial and temporal variations in ciliate abundance are summarized in Fig. 2E and F and Table I. During summer 2002, the highest values of density and biomass were found in outer shelf-slope and middle shelf waters, respectively, whereas in autumn of the same year, these two parameters peaked in the middle shelf. The lowest values during 2002 were detected in oceanic waters. In contrast, both maximum and minimum abundances during summer 2003 were found in middle shelf waters. When considering all stations pooled together, abundance ranges were found to be wider for shelf-slope (38–19 739 ind. L^{-1} and 0.01–25.05 $\mu g\ C\ L^{-1}$) when compared with oceanic waters (196–1102 ind. L^{-1} and 0.07–2.30 $\mu g\ C\ L^{-1}$,

Table I: Ciliate abundance in each period and bathymetric zone examined

Area		Season	n	Density (ind. L^{-1}) Mean	Density (ind. L^{-1}) Range	Biomass (μg C L^{-1}) Mean	Biomass (μg C L^{-1}) Range
Shelf-slope	Inner shelf	Summer 2002	1	1766	–	1.28	–
		Autumn 2002	4	1283	573–2280	2.51	0.62–4.09
		Summer 2003	9	826	171–2496	1.87	0.43–3.97
	Middle shelf	Summer 2002	6	1076	434–1667	3.22	0.62–7.59
		Autumn 2002	26	1435	392–4949	3.12	0.27–13.65
		Summer 2003	17	2777	38–19 739	4.07	0.01–25.05
	Outer shelf	Summer 2002	15	1056	126–5371	0.96	0.09–3.75
	Slope	Summer 2002	6	1113	282–2880	0.57	0.33–0.82
	Total		84	1520	38–19 739	2.60	0.01–25.05
Ocean	Subantarctic	Summer 2002	5	529	199–1102	0.46	0.07–1.01
		Autumn 2002	8	557	196–944	1.22	0.53–2.30
		Summer 2003	3	1456	384–3086	2.67	0.52–6.87
	Antarctic	Autumn 2002	7	575	192–1000	1.08	0.28–2.16
		Summer 2003	4	563	376–999	1.17	0.63–2.00
	Total		27	640	196–3086	1.20	0.07–6.87

n, number of stations.

Table II: Contrast of ciliate abundance between periods and bathymetric zones by means of non-parametric ANOVA (Mann–Whitney's and Kruskal-Wallis' tests; statistics=U and H, respectively)

Contrast	Density	Biomass
Shelf-slope versus ocean	**$U = 629$** **$P = 0.00$**	**$U = 776$** **$P = 0.03$**
Shelf-slope: all bathymetric bands, all periods	$H = 8.34$ $P = 0.30$	$H = 13.4$ $P = 0.06$
Shelf-slope: all bathymetric bands, summer 2002 and 2003	$H = 4.12$ $P = 0.53$	$H = 0.96$ $P = 0.06$
Shelf-slope: middle shelf, autumn 2002 and summer 2003	$U = 210$ $P = 0.80$	$U = 220$ $P = 0.99$
Ocean: subantarctic and antarctic waters, all periods	$H = 1.98$ $P = 0.74$	$H = 6.10$ $P = 0.19$

Significant results ($P < 0.05$) are shown in bold.
Averages, ranges and number of stations according to Table I.

excluding the exceptional values of 3086 ind. L^{-1} and 6.87 μg C L^{-1} found at 57°S–63°W during summer 2003). The transition from neritic to oceanic waters implied a significant decrease (Mann–Whitney's test, $P < 0.05$) in the mean values of density (58%) and biomass (54%) (Tables I and II). In contrast, spatial and temporal variations in abundance either within the shelf-slope region or within the Drake Passage were not significant (Mann–Whitney's and Kruskal–Wallis' tests, $P > 0.05$; Table II).

Total ciliate density showed a significant and positive correlation (Spearman's coefficient, $P < 0.05$) with temperature and chlorophyll *a* concentration, but covaried negatively with bottom depth, latitude and salinity (Table III). Biomass followed the same trend, except for salinity. When the stations carried out in shelf-slope and oceanic waters were considered independently, both density and biomass correlated significantly and positively only with chlorophyll *a* concentration.

Throughout the area and periods surveyed, we found three sectors and eight points where ciliates reached values of density >2000 ind. L^{-1} and/or biomass >6 μg C L^{-1} (Fig. 2E and F), including one station (49.5°S–66.5°W; summer 2003) with values one order of magnitude higher (10^4 ind. L^{-1}; 10^2 μg C L^{-1}) mainly caused by *Strombidium* spp. (60%) and *Helicostomella subulata* (15%). The plot of ciliate abundance per station in relation to environmental variables (Fig. 3) shows that almost all these stations were located in shelf and slope waters (12–280 m; except at 57°S–63°W in summer 2003), and were spatially overlapped with ranges of temperature of 10–15°C and chlorophyll *a* concentration of 0.6–6 μg L^{-1} (80 and 95% of the increases, respectively). The abundance of ciliates was significantly higher (Mann–Whitney's test, $P < 0.05$;

Table III: Spearman's correlations of density and biomass of total ciliates and potential maximum production of aloricate oligotrichs with environmental factors

	Bottom depth	Latitude	Temperature	Salinity	Chlorophyll *a*
All the area					
Density	**−0.27**	**−0.27**	**0.22**	**−0.23**	**0.49**
Biomass	**−0.26**	**−0.25**	**0.22**	−0.16	**0.46**
Production	**−0.49**	**−0.61**	**0.58**	−0.13	**0.46**
n	111	111	111	111	83
Shelf-slope					
Density	−0.06	−0.02	−0.05	−0.05	**0.33**
Biomass	−0.22	−0.18	0.13	−0.04	**0.41**
Production	**−0.35**	**−0.53**	**0.47**	0.18	**0.30**
n	84	84	84	84	62
Ocean					
Density	0.13	−0.31	0.03	0.04	**0.51**
Biomass	0.24	0.02	−0.01	−0.19	**0.41**
Production	0.00	−0.11	0.18	−0.17	0.38
n	27	27	27	27	21

Significant results ($P < 0.05$) are shown in bold. *n*, number of stations. Production was not estimated when temperature was out of the range of 4–23°C (Müller and Geller, 1993): 2 and 10 stations of shelf-slope and oceanic waters, respectively.

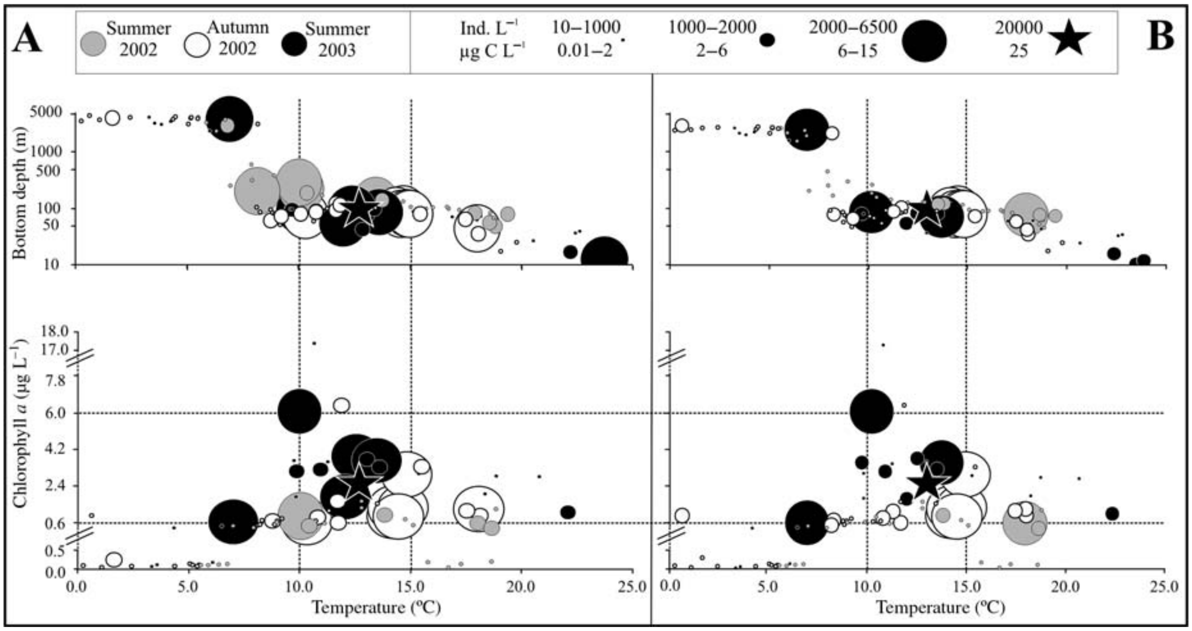

Fig. 3. Bubble plots of ciliate density (**A**) and biomass (**B**) in relation to environmental variables. Bottom depth was plotted on a logarithmic scale. Number of stations: 83 for chlorophyll *a* concentration and 111 for other variables.

Table IV) within such ranges than in the rest of the shelf-slope.

Taxonomic and size structure of ciliates

The ciliates recorded consisted of aloricate and loricate oligotrichs (class Oligotrichea), litostomatids (class Litostomatea), prostomatids (class Prostomatea) and an unidentified taxon. In terms of their mean absolute abundances, we found that: (i) aloricate oligotrichs (1080 ind. L^{-1} and 1.71 μg C L^{-1}) reached values higher by one order of magnitude with respect to loricate oligotrichs (116 ind. L^{-1} and 0.38 μg C L^{-1}), and by two orders of magnitude when compared with litostomatids (65 ind. L^{-1} and 0.08 μg C L^{-1}, represented by a 90% of *M. rubra*), prostomatids (9 ind. L^{-1} and 0.02 μg C L^{-1}) and the unidentified taxon (37 ind. L^{-1} and 0.03 μg C L^{-1}); (ii) microciliates (including some aloricate oligotrichs and all loricate oligotrichs, litostomatids and prostomatids) and nanociliates (comprising exclusively aloricate oligotrichs) reached similar mean densities (745 versus 562 ind. L^{-1}, respectively), but the

Table IV: Ciliate abundance in waters with temperature of 10–15°C and chlorophyll a of 0.6–6 μg L^{-1} as compared to that found in the rest of the shelf-slope by means of Mann–Whitney's test (statistic=U)

			Density (ind. L^{-1})				Biomass (μg C L^{-1})			
					Mann–Whitney				Mann–Whitney	
Factor	Range	Number of stations	>2000 (% of stations)	Mean	*U*	*P*	>6 (% of stations)	Mean	*U*	*P*
Temperature	10–15°C	42	33	2180	528	**0.001**	17	3.48	626	**0.022**
	< or >10–15°C	42	7	864			2	1.65		
Chlorophyll *a*	0.6–6 μg L^{-1}	47	26	1942	155	**0.001**	15	3.41	147	**0.001**
	< or >0.6–6 μg L^{-1}	15	7	628			7	1.28		

Significant results ($P < 0.05$) are shown in bold.

former fraction represented a relative contribution to biomass of 90% over nanociliates (2.05 versus 0.18 μg C L^{-1}); (iii) when passing from shelf-slope to oceanic waters, the abundance of nano- and micro-aloricate oligotrichs decreased two times, while loricate oligotrichs, litostomatids and the unidentified taxon decreased 4, 10 and 3 times, respectively, and prostomatids were no longer detected (Fig. 4).

Based on the relative density and biomass of the taxonomic classes and size fractions of ciliates, the following aspects were elucidated. First, the ordination of all the stations by multi-dimensional scaling reflected a relatively homogeneous distribution independent of the environment and period surveyed: the cloud of points based on density (Fig. 5A) tended to prolong towards two extremes due to the prevalence of micro- and nano-aloricate oligotrichs in 50 and 38% of the stations, respectively. The more compacted gathering of points yielded by the biomass (Fig. 5B) was also attributed to micro-aloricate oligotrichs (87%), whereas nanociliates dominated only in 1% of the points. The remaining points (12%), which escaped the central trends, were localized in shelf waters and responded to the dominance of the other microciliates.

Second, the contribution of each group of ciliates to density as a function of latitude (Fig. 5C, E and G) reflected a higher contribution of micro-aloricate oligotrichs in waters of the north of the shelf until approximately 47–48°S (2002) or 43°S (2003) and in oceanic antarctic waters. On the other hand, nano-aloricate oligotrichs prevailed from those latitudes until 53 or 48°S, respectively, and in oceanic subantarctic waters. Loricate oligotrichs and litostomatids dominated in density and biomass (Fig. 5D, F and H) in the north of the transects during the summer (37°S and 41°S) and in the south of the middle shelf (53–55°S), where the contribution of the unidentified taxon also increased (51–52°S). The summer of 2003 was characterized by ca. 100% of micro- and nano-aloricate oligotrichs at 41 and 43.5°S, respectively, and the maximum contribution of prostomatids in biomass (17%; 48°S), whereas the autumn showed an increase in the presence of almost all taxonomic classes on the shelf.

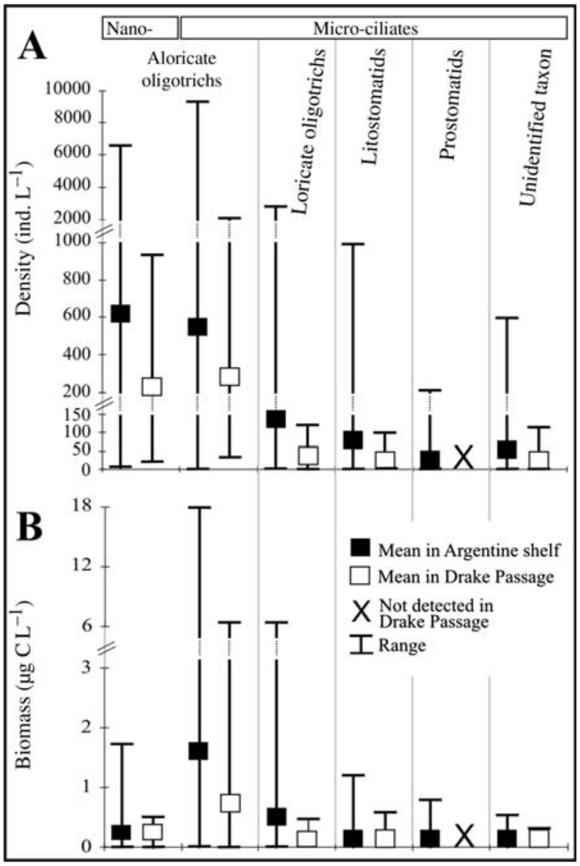

Fig. 4. Contrast of the absolute density (**A**) and biomass (**B**) of ciliates according to taxonomic classes and size fractions in shelf-slope and oceanic waters.

Finally, correlation results with environmental variables (Table V) showed that significant positive covariations within shelf-slope waters were limited to those of

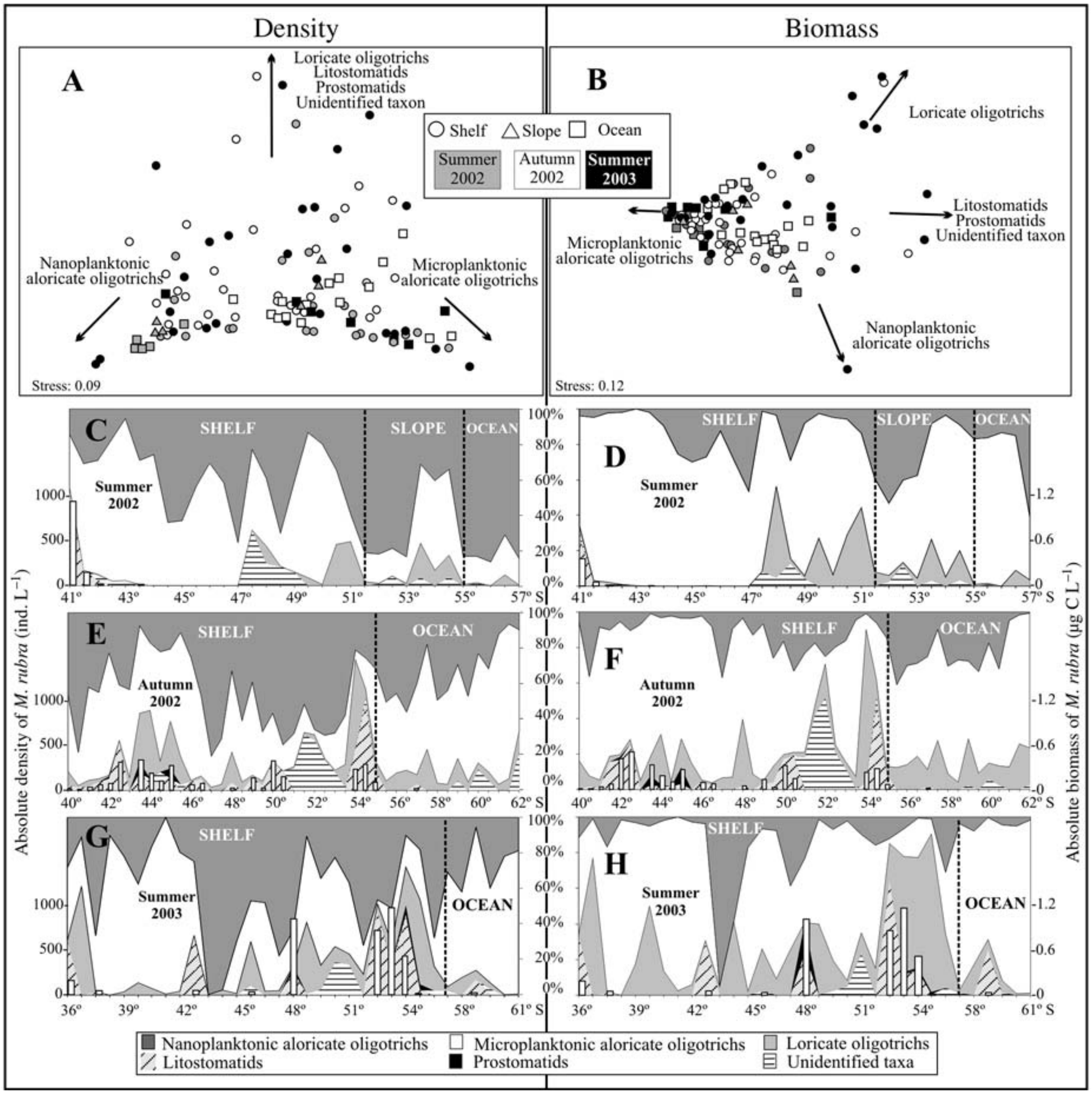

Fig. 5. Spatio-temporal distribution of the relative abundance and biomass of ciliates according to taxonomic classes and size fractions throughout the studied area and periods (**A–B:** MDS analyses; arrows indicate the direction in which the proportion of each group of ciliates increases) and per transect (**C–H:** area plots). Latitudinal profile of the absolute abundance of *Myrionecta rubra* (C–H: white bars).

temperature and salinity with microplanktonic aloricate oligotrichs and those of chlorophyll *a* concentration with loricate oligotrichs and prostomatids, while significant negative covariations were obtained for nanoplanktonic aloricate oligotrichs, loricate oligotrichs and the unidentified taxon with temperature, and for litostomatids with bottom depth. In oceanic waters, a significant and positive correlation was found for the relative density of nano-aloricate oligotrichs with temperature and salinity, together with an opposite trend for micro-aloricate oligotrichs.

The spatio-temporal distribution of *M. rubra* (Fig. 5C–H) revealed that in shelf waters, the species reached mean abundances of 90 ind. L^{-1} and 0.10 µg C L^{-1}, with maximum values ca. three times higher during both summers (up to 962 ind. L^{-1} and 1.16 µg C L^{-1}) than during autumn (337 ind. L^{-1} and 0.5 µg C L^{-1}), although it was found more frequently in this last period. Besides, its abundance on the shelf correlated significantly (Spearman's coefficient, $P < 0.05$) with bottom depth ($R = -0.29$ and -0.28 for density and biomass respectively; $n = 84$) and chlorophyll *a*

Table V: Spearman's coefficients between environmental factors and the relative density (D) and biomass (B) of taxonomic classes and size fractions

		Bottom depth	Temperature	Salinity	Chlorophyll *a*
Shelf -slope					
Nanoplanktonic aloricate oligotrichs	D	0.13	**−0.33**	−0.19	−0.17
	B	0.15	**−0.25**	−0.12	−0.29
Microplanktonic aloricate oligotrichs	D	−0.07	**0.51**	**0.42**	0.01
	B	−0.04	**0.36**	**0.40**	−0.04
Loricate oligotrichs	D	0.07	**−0.35**	−0.18	**0.39**
	B	0.07	**−0.33**	−0.21	**0.34**
Litostomatids	D	**−0.29**	0.03	−0.12	0.16
	B	**−0.31**	0.04	−0.12	0.17
Prostomatids	D	−0.10	0.02	0.01	**0.23**
	B	−0.11	0.03	0.02	**0.23**
Unidentified taxon	D	0.21	**−0.35**	−0.09	0.02
	B	0.22	**−0.40**	−0.13	0.00
Number of stations		84	84	84	62
Ocean					
Nanoplanktonic aloricate oligotrichs	D	−0.14	**0.67**	**0.69**	0.19
	B	−0.20	0.18	**0.38**	0.02
Microplanktonic aloricate oligotrichs	D	0.14	**−0.66**	**−0.69**	−0.34
	B	0.31	−0.03	−0.14	−0.10
Loricate oligotrichs	D	0.11	−0.13	−0.02	0.15
	B	0.19	−0.37	−0.09	0.02
Number of stations		27	27	27	21

Significant results ($P < 0.05$) are shown in bold.

concentration (only in biomass, $R = 0.21$; $n = 62$). Oceanic waters, instead, were characterized by isolated increases (up to 89 ind. L^{-1} and 0.06 μg C L^{-1}) only in the subantarctic sector (55 and 57°S: autumn 2002; 58.5°S: summer 2003).

Potential metabolic rates of aloricate oligotrichs

The expected linear relationship between the maximum growth rate of aloricate oligotrichs (Fig. 6A) and seawater temperature (Fig. 2B) encompassed a southward latitudinal decrease from 2.73 to 0.20 day^{-1}, although such rates were much more variable from the north of the area to 50–51°S than at the south of this latitude. Maximum consumption and production were, on average, 10.1 and 2.7 μg C L^{-1} day^{-1} for the shelf-slope, and 4.7 and 0.3 μg C L^{-1} day^{-1} for oceanic waters, respectively. As shown in Fig. 6B, the microplanktonic aloricate oligotrichs had mean values of biomass, consumption and production ca. 7 and 3.5 times greater (in neritic waters and oceanic waters, respectively) than nanoplanktonic cells. In both environments, however, the mean growth and ingestion rates were ca. 2-fold higher for the smaller fraction. The station carried out at 57°S–63°W in summer 2003 was excluded from this analysis, as it yielded biomass, consumption and production values one order of magnitude higher than the average for oceanic waters. Maximum production covaried significantly and negatively (Spearman's coefficient, $P < 0.05$) with bottom depth and latitude, while it correlated positively with temperature and chlorophyll *a* concentration (Table III).

DISCUSSION

Contrast of ciliate abundance and potential metabolic rates in neritic and oceanic waters

The relevance of the environments examined in this study is related to the circulation of the Antarctic Circumpolar Current, for which the Drake Passage represents its major chokepoint, and its impact on the rich subantarctic waters of the Argentine shelf through the Malvinas Current (Fig. 1). The transition from the Drake Passage to the Argentine shelf encompasses two sectors of clearly different bathymetric gradients, a very sharp one at the tip of Tierra del Fuego (ca. 55°S) and a gentler one west of the Burdwood Bank (52–55°S). The Malvinas Current flows along the outer shelf and the adjacent slope, also influencing the inner and middle shelf south of 51°S, a sector which shows a quasi-homogenous water column all along the year (Guerrero *et al.*, 1999; Sabatini *et al.*, 2004). The vertical homogeneity of the upper water column in both the south of the shelf and the Drake Passage would imply

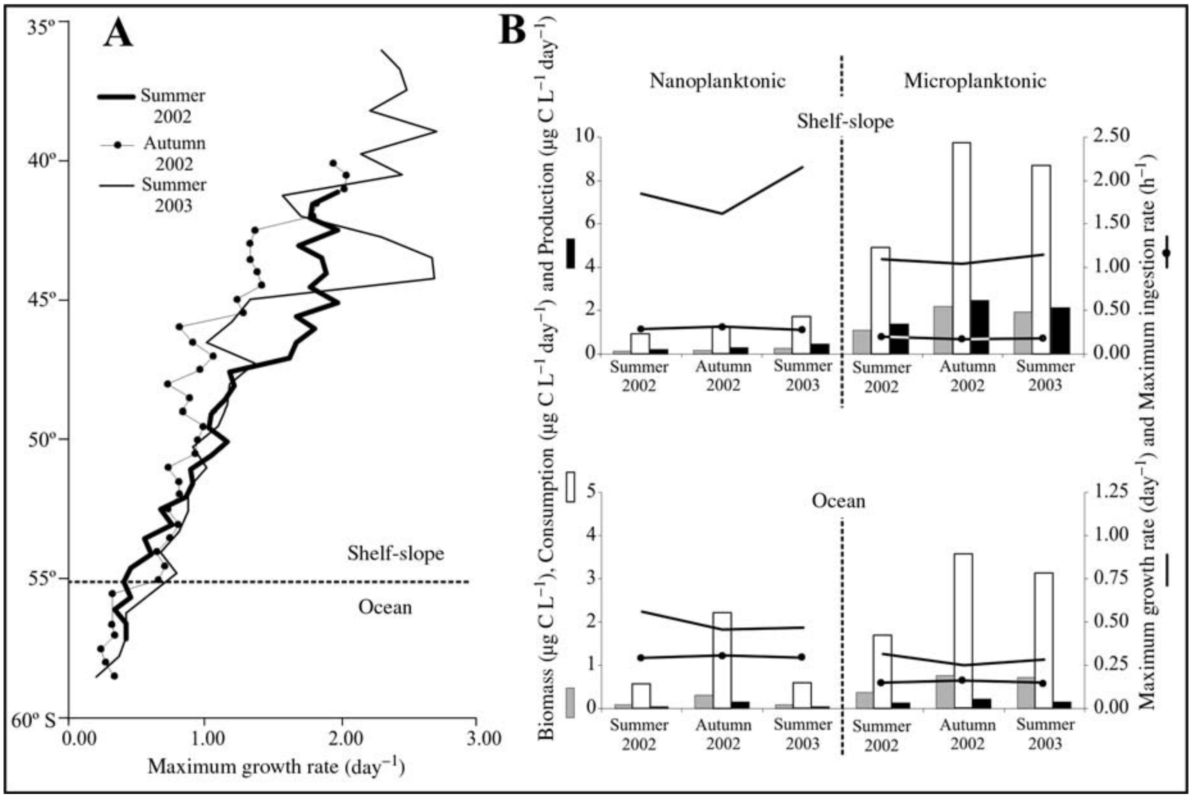

Fig. 6. Potential metabolic rates estimated for aloricate oligotrichs. (**A**) Latitudinal fluctuation of the maximum growth rate (averages per station). (**B**) Biomass and maximum values of growth rate, ingestion rate, consumption and production (averages for each size fraction in shelf-slope and oceanic waters).

that our sampling performed at 9 m depth reflects actual ciliate abundances quite satisfactorily, although these organisms have been observed to concentrate either in the upper 10–20 or 40–50 m in neritic and oceanic waters, respectively (Leakey *et al.*, 1996; Garrison *et al.*, 1998).

In this context, our data confirm that the mean density and biomass of ciliates decrease significantly when passing from neritic to oceanic waters (Figs 2E and F and 3; Tables I and II). Maximum values of ciliate abundance commonly found on the Argentine shelf (10^3 ind. L^{-1} and 10^1 µg C L^{-1}) and in the Drake Passage (10^2 ind. L^{-1} and 10^0 µg C L^{-1}) are comparable with those of other shelves (Verity *et al.*, 1996; Chiang *et al.*, 2003) and oceanic environments (Dolan and Marrasé, 1995; Dolan *et al.*, 1999; Fernandes and Brandini, 1999; Pitta *et al.*, 2001), while values one order of magnitude higher are found only exceptionally. In general, values of 10^4 ind. L^{-1}, and even 10^5 ind. L^{-1}, are reported for coastal environments linked to high levels of biological productivity, such as estuaries, bays and gulfs (Sanders, 1995; Modigh, 2001; Barría de Cao *et al.*, 2003; Kogan, 2005; Kim *et al.*, 2007). On the other hand, a drop of one order of magnitude from neritic to oceanic waters was also estimated for the potential maximum production of aloricate oligotrichs (Fig. 6B), which represented ca. 80% of total ciliate abundance in both environments.

The relationship of the bottom depth and latitude with the density and biomass of total ciliates was reflected only when considering the whole neritic-to-oceanic latitudinal range (Tables II and III). Instead, the potential maximum production of aloricate oligotrichs showed such trends when considering either all the area surveyed or only the shelf waters (Table III), in agreement with previous reports which indicate that ciliate production reaches higher values near the coast and as latitude decreases in a similar range in the northern hemisphere (Lynn and Montagnes, 1991). The difference in the trends detected for abundance and potential production may be attributed to the decrease in the maximum growth rates, which tends to be parallel to the latitudinal decrease in temperature (Figs 2B and 6A). However, while there is no evident change in maximum growth rates with bottom depth, the constant and gradual decrease in values estimated south of 51°S agrees with the more stable environmental conditions found in this sector due to the permanent influence of the Antarctic Circumpolar Current (Sabatini *et al.*, 2004).

In addition to the expected higher temperatures, the Argentine shelf waters were characterized by a mean chlorophyll *a* concentration ca. 10 times higher than the oceanic realm (Fig. 2D), thus partially explaining the differences in ciliate abundance and production between these environments. The direct relationships of both environmental factors with ciliate abundance and potential production in the whole area under study (Table III) are a clear trend that may be attributed to the positive effect of both food concentration and temperature on the numerical response of ciliates (Montagnes and Lessard, 1999).

Increases in ciliate abundance

Mechanisms and factors that regulate ciliate abundance are complex and still under debate. Top-down or bottom-up regulation, interactions between environmental conditions, mainly temperature and food resources, and their influence on metabolic rates have been examined (Nielsen and Kiørboe, 1994; Montagnes, 1996; Montagnes and Lessard, 1999; Weisse *et al.*, 2002). In this study, increases in ciliate abundance ($>2\ 10^3$ ind. L^{-1} and/or 6 μg C L^{-1}) were found under combined, probably optimum, and relatively intermediate ranges of temperature and chlorophyll *a* concentration (Fig. 3; Table IV). Although we did not test statistically possible interactions between factors, the trend found based exclusively on field data seems to be consistent enough for temperate shelf waters under late summer and early autumn conditions.

The increases were detected only at 15% of the stations examined throughout the study, but represented 50% of total ciliate abundance, and practically all of them were located in Argentine shelf waters. As a consequence of the strong seasonality of this region, and in coincidence with the productivity levels based on satellite-measured surface chlorophyll *a* (Rivas *et al.*, 2006), both the ranges of temperature and chlorophyll *a* as well as the ciliate peaks were displaced in relation to latitude (Fig. 2B, D–F): in late summer, they were found in southern Patagonian waters (at 47–52°S and 45–53°S in 2002 and 2003, respectively), relatively later than the period when the phytoplanktonic bloom develops (November to December), whereas in early autumn they were found in northern Patagonian waters (43–45°S), when secondary peaks of chlorophyll *a* are detected, although the bloom occurs in spring (September to October). As the main peaks of ciliates are detected immediately after the phytoplankton bloom in other temperate environments (Nielsen and Kiørboe, 1994; Sanders, 1995; Modigh, 2001; Barría de Cao *et al.*, 2003; Johansson *et al.*, 2004; Kim *et al.*, 2007), ciliates may reach the highest abundances during austral spring and early summer in the Argentine shelf.

On the other hand, almost all the abundance increases were located close to the historical position of fronts of the Argentine shelf and the slope (Fig. 7), such as the Valdés Front, Atlantic Patagonia Cold Estuarine Front, El Rincón Front, tidal fronts of southern Patagonian waters and the shelf-break Front (Bava *et al.*, 2002; Acha *et al.*, 2004; Lucas *et al.*, 2005). However, only a few of such ciliate peaks coincided with the simultaneous drops of temperature and salinity detected in this study (Fig. 2B, C, E and F), possibly because fronts may be evident in deeper strata than the waters here examined.

Although fronts tend to be related to increased abundances for all the biological communities (Olson, 2002), our results also suggest that this trend may be altered. For instance, the effect of top-down regulation on ciliate density and biomass may be reflected by the lowest values detected in summer 2003 (Fig. 2E and F) both in the vicinity of the Valdés Front (42–44°S), where potential maximum growth rates are as high as in the north of the shelf due to the prevalence of nanociliates (Figs 5G and H and 6A), and in Grande Bay (51–52°S), since copepods and other metazoans reach the highest biomass in the same season and sectors (Ramírez and Sabatini, 2000; Sabatini and Álvarez Colombo, 2001; Sabatini *et al.*, 2004).

Moreover, the strongest evidence that fronts are not always related to high abundances emerges from those of the Drake Passage, such as the Subantarctic Front, Polar Front and Southern Antarctic Circumpolar Current Front (Orsi *et al.*, 1995), where both ciliate and chlorophyll *a* concentrations were low and homogeneous (Figs 2D–F and 7). Once again, this may be a consequence of seasonality: in these waters, satellite-measured surface chlorophyll *a* reflects that the phytoplankton bloom is mainly restricted to the vicinity of the Polar Front during early summer (December), while during the seasons surveyed here the bloom formation is limited principally due to low nutrient availability in the water column (Moore and Abbott, 2002). Instead, the only oceanic increase in ciliates (57°S–63°W, summer 2003) was located between the Subantarctic Front and the Polar Front, coinciding with an increase in temperature of ca. 1°C higher than the southern station and, according to loricate oligotrich species, comprised waters of subantarctic origin. This local increase may be associated with eddy activity, a phenomenon well documented in the Drake Passage, even in the same geographical position (Sprintall,

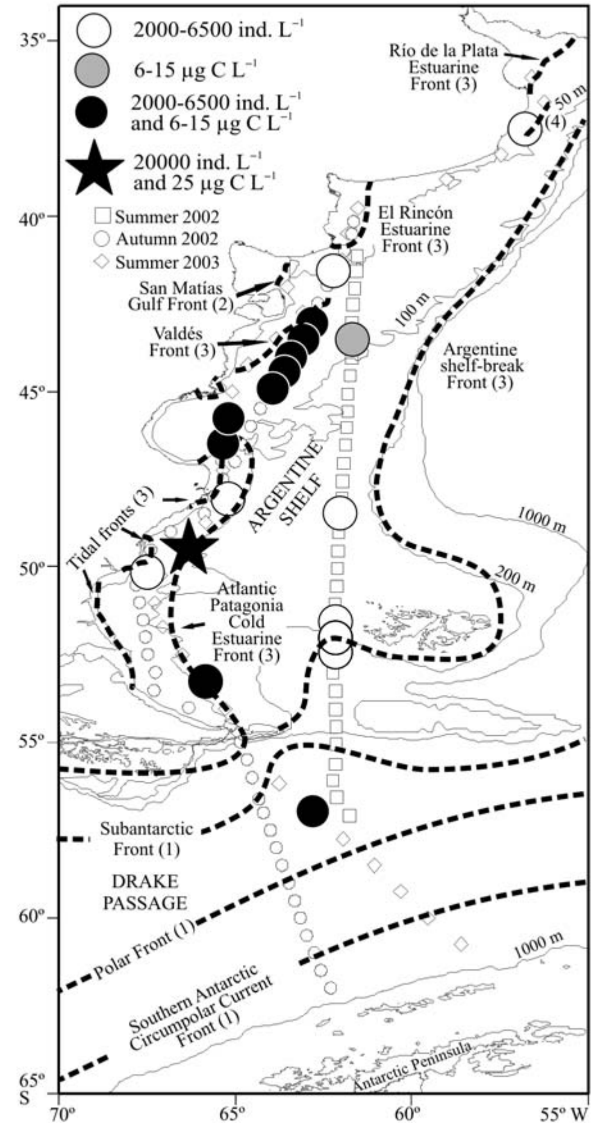

Fig. 7. Stations of maximum ciliate abundance in relation to historical position of fronts (incomplete lines; (1) Orsi *et al.*, 1995; (2) Bava *et al.*, 2002; (3) Acha *et al.*, 2004; (4) Lucas *et al.*, 2005). Increases in density, biomass or both parameters are indicated with white, grey or black symbols, respectively.

2003), and which is known to influence the abundance and distribution of loricate oligotrichs in the area (Alder and Thompson, 2000).

Environmental factors related to the taxonomic and size structure of ciliates

Sub-surface temperature and salinity helped to explain the latitudinal distribution of taxonomic classes and size fractions of ciliates from shelf-slope and oceanic waters, while, with a few exceptions, a practically null effect of bottom depth and chlorophyll *a* concentration was reflected (Table V). On the shelf, microplanktonic aloricate oligotrichs prevailed when temperature and salinity reached relatively higher values, showing maximum contributions in the mixed, coastal waters surrounding Buenos Aires during 2003, although extending their dominance to the south of San Jorge Gulf during 2002 (Fig. 2B and C and 5C–H). Considering the evidence obtained mostly from the same sampling cruises examined in this study, which indicates that in sub-surface shelf waters the mean value of net primary production was 34 μg C L^{-1} day^{-1} (Schloss *et al.*, 2007) and the phytoplankton biomass was dominated by cells <10 μm (Almandoz *et al.*, 2007), the main food resource for micro-aloricate oligotrichs (Rassoulzadegan *et al.*, 1988), our theoretical estimations suggest a potential to consume ca. 30% of primary production for these organisms, with maximum consumption and production ca. one order of magnitude higher than nanociliates (Fig. 6B).

The proportions of other microciliates (loricate oligotrichs, litostomatids and prostomatids) also increased where the water column is permanently mixed, such as restricted points of the coast of Buenos Aires and near Blanco Cape, which are subject to wind action or tidal forces, and in the southern border of the shelf. Ciliates other than oligotrichs were relatively rare, and prostomatids were not detected in oceanic waters (Fig. 4), possibly because of their fragmentary distribution, although they may be able to reach high abundances in some periods (Pierce and Turner, 1992).

In contrast, nanoplanktonic aloricate oligotrichs prevailed on the stratified side of the Valdes Front (summer 2003) and in the Low Salinity Coastal Water band (autumn 2002), which is caused by the flux of diluted waters entering from the Pacific Ocean (Bianchi *et al.*, 2005). Both sectors are characterized by the highest densities of bacterioplankton on the Argentine shelf (Alder and Franzosi, 2004). On the other hand, the drop in the abundance of nanoaloricate oligotrichs in oceanic waters from the subantarctic to the antarctic regime followed the decrease in both temperature and salinity (Fig. 2B and C), and the bacterioplankton: nanoflagellate biomass ratio reported for the Drake Passage (Pedrós-Alió *et al.*, 1996). Thus, in agreement with previous conclusions (Montagnes *et al.*, 1988; Setälä and Kivi, 2003; Johansson *et al.*, 2004), the structure of ciliate assemblages according to taxonomic classes and cell size may be defined by quality rather than quantity of food, and by the availability of larger or smaller cells which can develop under permanent mixing of the water column or stratified conditions.

Finally, the distribution and abundance of *M. rubra* was described for the first time in the south-western Atlantic, being only detected in the inner and middle bands of the Argentine shelf, and less frequently in subantarctic waters of the Drake Passage (Fig. 5C–H). Although the positive relationship found for its biomass with the chlorophyll *a* concentration in the shelf waters may suggest a contribution of the species to this variable, such a contribution was estimated as very low (mean = 0.3%), considering a specific cellular content of chlorophyll *a* of 10–60 pg cell^{-1} (Johnson and Stoecker, 2005). The maximum contribution (5%) was estimated for the scarce stations where the species reached density values of 10^3 ind. L^{-1}. Both on the Argentine shelf and in the Drake Passage, densities were one order of magnitude lower than in other neritic (Nielsen and Kiørboe, 1994; Montagnes *et al*., 1999) and oceanic environments (Montagnes *et al*., 2008), including antarctic waters (Edwards *et al*., 1998), possibly because this autotrophic species generally peaks in spring (Sanders, 1995).

In conclusion, the main contrast found for ciliates between Argentine shelf and Drake Passage waters, along a range of ca. 30 degrees of latitude, is the decrease in density, biomass and potential production, due to the reduction in food availability and the latitudinal decline in temperature. At the taxonomic level, aloricate oligotrichs are clearly dominant in both environments, the most evident difference being the absence of prostomatids in oceanic waters. Instead, their size structure seems to be related to the quality of food associated with the stability of the water column, as nano- and microciliates tend to predominate under stratification and mixing conditions, respectively. Local increases in ciliate abundance were significantly linked to combined ranges of temperature and chlorophyll *a* concentration, and also to fronts and eddies of the shelf and oceanic waters, respectively. Finally, the estimations based on aloricate oligotrichs suggest that microplanktonic cells may be quantitatively relevant in the transference of carbon through the planktonic food web of the Argentine shelf waters in summer and autumn, showing the potential to consume more than a quarter of the net primary production. Although food availability, intra- and interspecific variability, mixotrophy or predation are not considered by the empirical equations used here to estimate the potential metabolic rates, and in spite of methodological differences, our estimations are comparable with the values obtained by means of similar theoretical procedures (Dolan and Marrasé, 1995; Montagnes *et al*., 1999; Modigh, 2001; Johansson *et al*., 2004) or *in situ* experiments (Nielsen and Kiørboe, 1994).

The trends found for the structure and abundance of ciliates and for the metabolic rates of aloricate oligotrichs constitute a field baseline for further approaches centred on the evaluation of the abundance of mixotrophic ciliates, the relevance of the ciliate peaks in relation to growth or biomass accumulation and for experimental studies aimed at enhancing the knowledge of their role in both carbon flux and the microbial food web of south-western Atlantic waters.

ACKNOWLEDGEMENTS

We are grateful to Lic. G. Visbeek for his technical assistance during the installation of the continuous sampling system. We also thank to the ARGAU Project (Argentina-France) for making data on abiotic variables available to us. Two anonymous reviewers contributed with helpful comments to improve the manuscript.

FUNDING

This work was supported by a fellowship granted to L.S. by Consejo Nacional de Investigaciones Científicas y Técnicas—CONICET, and by fundings from the same institution (PIP 0246), Agencia Nacional de Promoción Científica y Tecnológica (PICT 7-9108), and Instituto Antártico Argentino (Proyecto No. 58) granted to V.A.

REFERENCES

Acha, E., Mianzán, H., Guerrero, R. *et al*. (2004) Marine fronts at the continental shelves of austral South America. Physical and ecological processes. *J. Mar. Syst*., **44**, 83–105.

Alder, V. and Thompson, G. (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. and Broady, P.(eds), *Antarctic Ecosystems: Models for Wider Ecological Understanding*. New Zealand, pp. 203–214.

Alder, V. and Franzosi, C. (2004) Abundancia del picoplancton en el Mar Argentino y el Océano Antártico. *V Simposio Argentino y I Latinoamericano sobre Investigaciones Antárticas*. Argentina.

Almandoz, G., Ferrario, M., Ferreyra, G. *et al*. (2007) The genus *Pseudo-nitzschia* (Bacillariophyceae) in continental shelf waters of Argentina (Southwestern Atlantic Ocean, 38–55°S). *Harmful Algae*, **6**, 93–103.

Barría de Cao, M., Pettigrosso, R., Parodi, E. *et al*. (2003) Abundance and species composition of planktonic Ciliophora from the wastewater discharge zone in the Bahía Blanca Estuary, Argentina. *Iheringia Ser. Zool*., **93**, 229–236.

Bava, J., Gagliardini, D., Dogliotti, A. *et al*. (2002) Annual distribution of remote sensed sea surface temperature fronts in the Southwestern

Atlantic Ocean. *29° Inter Symposium of Remote Sensing of Environment*. Argentina.

Behrenfeld, M. and Falkowsky, P. (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.*, **42**, 1–20.

Bianchi, A., Bianucci, L., Piola, A. *et al*. (2005) Vertical stratification and air-sea CO2 fluxes in the Patagonian shelf. *J. Geophis. Res.*, **110**, C07003. 10.1029/2004JC002488.

Chiang, K.-P., Lin, C.-Y., Lee, C.-H. *et al*. (2003) The coupling of oligotrich ciliate populations and hydrography in the East China Sea: spatial and temporal variations. *Deep-Sea Res. II*, **50**, 1279–1293.

Dolan, J. and Marrasé, C. (1995) Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993. *Deep-Sea Res. I*, **42**, 1965–1987.

Dolan, J., Claustre, H. and Vidussi, F. (1999) Planktonic ciliates in the Mediterranean Sea: longitudinal trends. *Deep-Sea Res. I*, **46**, 2025–2039.

Edwards, E., Burkill, P. and Sleigh, M. (1998) Microbial community structure in the marginal ice zone of the Bellingshausen Sea. *J. Mar. Syst.*, **17**, 87–96.

Fernandes, L. and Brandini, F. (1999) Microplankton communities in the Southwestern Atlantic Ocean: biomass and distribution in November/1992. *Rev. Bras. Oceanogr.*, **47**, 189–205.

Field, J., Clarke, K. and Warwick, R. (1982) A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.*, **8**, 37–52.

Garrison, D., Gowing, M. and Hughes, M. (1998) Nano- and microplankton in the northern Arabian Sea during the Southwest Monsoon, August–September 1995. A US-JGOFS study. *Deep-Sea Res. II*, **45**, 2269–2299.

Guerrero, R., Baldoni, A. and Benavides, H. (1999) Oceanographic conditions at the southern end of the Argentine continental slope. *INIDEP Doc. Cient.*, **5**, 7–22.

Hansen, P., Bjørnsen, P. and Hansen, B. (1997) Zooplankton grazing and growth: scaling within the 2–2000 μm body size range. *Limnol. Oceanogr.*, **42**, 687–704.

Johansson, M., Gorokhova, E. and Larsson, U. (2004) Annual variability in ciliate community structure, potential prey and predators in the open northern Baltic Sea proper. *J. Plankton Res.*, **26**, 67–80.

Johnson, M. and Stoecker, D. (2005) Role of feeding in growth and photophysiology of *Myrionecta rubra*. *Aquat. Microb. Ecol.*, **39**, 303–312.

Kim, S., Gil Park, M., Moon, C. *et al*. (2007) Seasonal variations in phytoplankton growth and microzooplankton grazing in a temperate coastal embayment, Korea. *Estuarine Coastal Shelf S.*, **71**, 159–169.

Kogan, M. (2005) *Estudio de la composicón especifica, abundancia y distribución espacial del microzooplancton en el estuario del Río de La Plata*. University of Buenos Aires, Argentina.

Leakey, R., Burkill, P. and Sleigh, M. (1996) Planktonic ciliates in the northwestern Indian Ocean: their abundance and biomass in waters of contrasting productivity. *J. Plankton Res.*, **18**, 1063–1071.

Lucas, A., Guerrero, R., Mianzán, H. *et al*. (2005) Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34–43°S). *Estuarine Coastal Shelf S.*, **65**, 405–420.

Lynn, D. and Montagnes, D. (1991) Global production of heterotrophic marine planktonic ciliates. In Reid, P., Turley, C. and Burkill, P.(eds), *Protozoa and Their Role in Marine Processes.* NATO ASI publication, Springer Verlag, New York, pp. 281–307.

Lynn, D. and Small, E. (2002) Ciliophora. In Lee, J., Leedale, G. and Bradbury, P.(eds), *The illustrated guide to the Protozoa.* Lawrence, Kansas, pp. 371–656.

Modigh, M. (2001) Seasonal variations of photosynthetic ciliates at a Mediterranean coastal site. *Aquat. Microb. Ecol.*, **23**, 163–175.

Montagnes, D. (1996) Growth responses of planktonic ciliates in the genera *Strobilidium* and *Strombidium*. *Mar. Ecol. Prog. Ser.*, **130**, 241–254.

Montagnes, D. and Lessard, E. (1999) Population dynamics of the marine planktonic ciliate *Strombidinopsis multiauris*: its potential to control phytoplankton blooms. *Aquat. Microb. Ecol.*, **20**, 167–181.

Montagnes, D., Lynn, D., Roff, J. *et al*. (1988) The annual cycle of heterotrophic planktonic ciliates in the waters surrounding the Isles of Shoals, Gulf of Maine: an assessment of their trophic role. *Mar. Biol.*, **99**, 21–30.

Montagnes, D., Poulton, A. and Shammon, T. (1999) Mesoscale, finescale and microscale distribution of micro-and nanoplankton in the Irish Sea, with emphasis on ciliates and their prey. *Mar. Biol.*, **134**, 167–179.

Montagnes, D., Allen, J., Brown, L. *et al*. (2008) Factors controlling the abundance and size distribution of the phototrophic ciliate *Myrionecta rubra* in open waters of the North Atlantic. *J. Eukaryot. Microbiol.*, **55**, 457–465.

Moore, J. and Abbott, M. (2002) Surface chlorophyll concentrations in relation to the Antarctic Polar Front: Seasonal and Spatial Patterns from Satellite Observations. *J. Mar. Syst.*, **37**, 69–86.

Müller, H. and Geller, W. (1993) Maximum growth rates of aquatic ciliated protozoa: the dependence on body size and temperature reconsidered. *Arch. Hydrobiol.*, **126**, 315–327.

Nielsen, T. and Kiørboe, T. (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol. Oceanogr.*, **39**, 508–519.

Olson, D. (ed.) (2002) *Biological—Physical interactions in the sea. The Sea. Biophysical dynamics of ocean fronts.*. Vol. 12. Wiley, New York.

Orsi, A., Whitworth, T., III and Nowlin, W., Jr (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res. I*, **42**, 641–673.

Pedrós-Alió, C., Calderón-Paz, J., Guixa, N. *et al*. (1996) Microbial plankton across Drake Passage. *Polar Biol.*, **16**, 613–622.

Pierce, R. and Turner, J. (1992) Ecology of planktonic ciliates in marine food webs. *Rev. Aquat. Sci.*, **6**, 139–181.

Piola, A. and Rivas, A. (1997) Corrientes en la plataforma continental. In Boschi, E.(ed.), *El mar argentino y sus recursos pesqueros. Antecedentes históricos de las exploraciones en el mar y las características ambientales*. Vol. 1. Publicaciones Especiales INIDEP, Mar del Plata, Argentina, pp. 119–132.

Pitta, P., Giannakourou, A. and Christaki, U. (2001) Planktonic ciliates in the oligotrophic Mediterranean Sea: longitudinal trends of standing stocks, distributions and analysis of food vacuole contents. *Aquat. Microb. Ecol.*, **24**, 297–311.

Putt, M. and Stoecker, D. (1989) An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. *Limnol. Oceanogr.*, **34**, 1097–1103.

Ramírez, F. and Sabatini, M. (2000) The occurrence of Calanidae species in waters off Argentina. *Hydrobiologia*, **439**, 21–42.

Rassoulzadegan, F., Laval-Peuto, M. and Sheldon, R. (1988) Partitioning of the food ration of marine ciliates between pico- and nanoplankton. *Hydrobiologia*, **159**, 75–88.

Rivas, A., Dogliotti, A. and Gagliardini, D. (2006) Seasonal variability in the satellite-measured surface chlorophyll in the Patagonian Shelf. *Cont. Shelf Res.*, **26**, 703–720.

Romero, S., Piola, A., Charo, M. *et al*. (2006) Chlorophyll-a variability off Patagonia based on SeaWiFS data. *J. Geophis. Res.*, **111**, C05021. doi:10.1029/2005JC003244.

Sabatini, M. and Álvarez Colombo, G. (2001) Seasonal pattern of zooplankton biomass in the Argentinian shelf off southern Patagonia (45°–55°S). *Sci. Mar.*, **65**, 21–31.

Sabatini, M., Reta, R. and Matano, R. (2004) Circulation and zooplankton biomass distribution over the southern Patagonian shelf during late summer. *Cont. Shelf Res.*, **24**, 1359–1373.

Safi, C., Griffiths, F. and Hall, J. (2007) Microzooplankton composition, biomass and grazing rates along the WOCE SR3 line between Tasmania and Antarctica. *Deep-Sea Res. I*, **54**, 1025–1041.

Sanders, R. (1995) Seasonal distributions of the photosynthesizing ciliates *Laboea strobila* and *Myrionecta rubra* (*Mesodinium rubrum*) in an estuary of the Gulf of Maine. *Aquat. Microb. Ecol.*, **9**, 237–242.

Schloss, I., Ferreyra, G., Ferrario, M. *et al*. (2007) Role of plankton communities in sea–air variations in pCO2 in the SW Atlantic Ocean. *Mar. Ecol. Prog. Ser.*, **332**, 93–106.

Setälä, O. and Kivi, K. (2003) Planktonic ciliates in the Baltic Sea in summer: distribution, species association and estimated grazing impact. *Aquat. Microb. Ecol.*, **32**, 287–297.

Sprintall, J. (2003) Seasonal to interannual upper-ocean variability in the Drake Passage. *J. Mar. Res.*, **61**, 27–57.

Stoecker, D., Gifford, D. and Putt, M. (1994) Preservation of marine planktonic ciliates: losses and cell shrinkage during fixation. *Mar. Ecol. Prog. Ser.*, **110**, 293–299.

Strickland, J. and Parsons, T. (1972) A practical handbook of sea-water analysis. *J. Fish. Res. Board. Can.*, **167**, 1–311.

Utermöhl, H. (1958) Zur vervolkommung der quantitativen phytoplankton-methodik. *Mitteilung Internationale Vereinigung fuer Theoretische unde Amgewandte Limnologie*, **9**, 1–38.

Verity, P. and Langdon, C. (1984) Relationship between lorica volume, carbon, nitorgen, and ATP content of tintinnids in Narragansett Bay. *J. Plankton Res.*, **6**, 859–868.

Verity, P., Paffenhofer, G.-A., Wallace, D. *et al*. (1996) Composition and biomass of plankton in spring on the Cape Hatteras shelf, with implications for carbon flux. *Cont. Shelf Res.*, **16**, 1087–1116.

Weisse, T., Stadler, P., Lindström, E. *et al*. (2002) Interactive effect of temperature and food concentration on growth rate: a test case using the small freshwater ciliate *Urotricha farcta*. *Limnol. Oceanogr.*, **47**, 1447–1455.

Zar, J. (ed.) (1999) *Biostatistical Analysis*, Fourth edition. Prentice-Hall, Inc, New Jersey.

Zarauz, L., Irigoien, X. and Fernandes, J. (2008) Modelling the influence of abiotic and biotic factors on plankton distribution in the Bay of Biscay, during three consecutive years 2004–06. *J. Plankton Res.*, **30**, 857–872.