



Species composition and biogeography of diatoms in antarctic and subantarctic (Argentine shelf) waters (37–76°S)

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ABSTRACT

A large spatial scale study of the diatom species inhabiting waters from the subantarctic (Argentine shelf) to antarctic was made for the first time in order to understand the relationships between these two regions with regard to the fluctuations in diatom abundances in relation with environmental features, their floristic associations and the effect of the Polar Front as a biogeographic barrier. Species-specific diatom abundance, nutrient and chlorophyll-*a* concentration were assessed from 64 subsurface oceanographic stations carried out during the austral summer 2002, a period characterized by an anomalous sea-ice coverage corresponding to a “warm year”. Significant relationships of both diatom density and biomass with chlorophyll-*a* (positive) and water temperature (negative) were found for the study area as a whole. Within the Subantarctic region, diatom density and biomass values were more uniform and significantly (in average: 35 and 11 times) lower than those of the Antarctic region, and did not correlate with chlorophyll-*a*. In antarctic waters, instead, biomass was directly related with chlorophyll-*a*, thus confirming the important contribution of diatoms to the Antarctic phytoplanktonic stock. A total of 167 taxa were recorded for the entire study area, with *Chaetoceros* and *Thalassiosira* being the best represented genera. Species richness was maximum in subantarctic waters (46; Argentine shelf) and minimum in the Antarctic region (21; Antarctic Peninsula), and showed a significant decrease with latitude. Floristic associations were examined both qualitatively (Jaccard Index) and quantitatively (correlation) by cluster analyses and results allowed differentiating a similar number of associations (12 vs. 13, respectively) and two main groups of stations. In the Drake Passage, the former revealed that the main floristic change was found at the Polar Front, while the latter reflected the Southern ACC Front as a main boundary, and yielded a higher number of isolated sites, most of them located next to different Antarctic islands. Such differences are attributed to the high relative density of *Fragilariopsis kerguelensis* in Argentine shelf and Drake Passage waters and of *Porosira glacialis* and species of *Chaetoceros* and *Thalassiosira* in the Weddell Sea and near the Antarctic Peninsula. From a total of 84 taxa recorded in antarctic waters, only 17 were found exclusively in this region, and the great majority (67) was also present in subantarctic waters but in extremely low ($< 1 \text{ cell l}^{-1}$) concentrations, probably as a result of expatriation processes via the ACC–Malvinas Current system. The present results were compared with those of previous studies on the Antarctic region with respect to both diatom associations in regular vs. atypically warm years, and the distribution and abundance of some selected planktonic species reported for surface sediments.

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1. Introduction

Because of their role in silica cycling, carbon fixation/exportation from surface waters, and the generation of sedimentary

records (Smetacek, 1998; Chisholm, 2000; Falkowski, 2002; Armbrust, 2009), diatoms are perhaps the most important single cells of the oceans. In addition, the abundance levels and floristic associations of diatom species are also considered as sensitive indicators of environmental alterations such as climate change (Stoermer and Smol, 2001), a phenomenon to which polar regions are particularly vulnerable.

Antarctic marine ecosystems are mainly regulated both by the seasonal advance and retreat of marine sea-ice and by subsequent processes such as melting and glacial runoff, which favour the

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stabilisation of the water column during the austral summer. The Antarctic Circumpolar Current (ACC), the main pathway of exchange between the Atlantic, Indian and Pacific basins, encircles the Antarctic region, comprises permanent, circumpolar fronts and plays a critical role in the global ocean circulation and climate. Direct signals of interannual variations in the ACC circulation, the Antarctic sea-ice extent and the Antarctic Dipole, among other processes, can be detected in oceanic and shelf subantarctic marine ecosystems of the south-western Atlantic, thanks to the geographic proximity between the southern tip of South America and the Antarctic Peninsula at the Drake Passage.

The Drake Passage represents the main constriction for the flow of the ACC. At this sector, part of the ACC branches off and gives rise to the Malvinas Current (MC), which flows northward over the Argentine slope and outer shelf transporting saline, cold, nutrient-enriched waters (Peterson and Stramma, 1991). While the southern part of this shelf also receives low salinity waters entering from the Pacific via the Cape Horn Current, its northern counterpart is under the influence of the warm, salty, oligotrophic Brazil Current.

The diatoms of the Southern Ocean include close to 200 taxa (Scott and Thomas, 2005) and have been profusely studied both qualitatively and quantitatively. Most of these investigations, however, assessed areas of a restricted spatial scale, such as the Antarctic Peninsula (Kang et al., 2001; Varela et al., 2002; Garibotti et al., 2005) and the Weddell Sea (El-Sayed, 1971; Garrison and Buck, 1985; Garrison et al., 1987; Smetacek et al., 1992). Recent results from long-term studies carried out along the western Antarctic Peninsula (WAP) have revealed regional changes in phytoplankton structure and latitudinal shifts in the community composition, coinciding with changes in major herbivores (Montes-Hugo et al., 2009). Therefore, it still seems to be necessary to obtain a comprehensive, simultaneous view of distinct Antarctic ecosystems and/or of a wide range of latitudes as to the numerical fluctuations of diatoms and the structure of their assemblages. Moreover, to date, there are no studies covering simultaneously the Antarctic diatom communities and those of their closest subantarctic system, i.e. the Patagonian waters of the Argentine shelf (one of the largest and most productive shelves in the world). While the diatom flora from the latter region are relatively well known regarding the taxa present (cf., Ferrario and Galván, 1989; Sar et al., 2001, 2002), quantitative studies are very scarce and restricted either to single sites (Gayoso and Podestá, 1996) or to the distribution of potentially toxic species (Almandoz et al., 2007).

The uneven level of knowledge on the quantitative distribution of diatoms between these different regions represents a gap which thus far has impeded the analysis of critical issues such as the degree of interconnection between species-specific assemblages of subantarctic and antarctic waters, the effect of the Polar Front as a biogeographic barrier, the role of subantarctic diatoms in carbon production, and the extent to which the assemblages found in bottom sediments respond to those of the water column. Moreover, given the known functional role of many species in different oceanic processes (Le Quéré et al., 2005; Kemp and Dugdale, 2006), a key future step will be the incorporation of taxonomic and numerical information on diatoms into mathematical models.

In this context, the aim of the present work is to start filling this information gap by assessing both qualitatively and quantitatively, over a broad spatial scale, the diatoms inhabiting subantarctic shelf waters of the Patagonian region and antarctic waters, and by analysing for the first time the relationships between floristic associations and fluctuations of diatom abundances in relation with environmental features during the austral summer 2002.

2. Methods and materials

The study was based on materials collected on board the icebreaker *Almirante Irizar* during the austral summer 2002 (31 January–4 March) along a latitudinal transect from 41° to 76°S. Sixty-four subsurface (9 m deep) oceanographic stations were sampled by means of a suction pump in middle shelf and southern slope Patagonian waters, the Drake Passage, waters surrounding the tip and western side of the Antarctic Peninsula, and the Weddell Sea (Fig. 1, Table 1).

Samples for the analysis of diatoms were obtained by filtering 180–300 l of water through a 10 µm-mesh net and preserved with 5% buffered formaldehyde. In addition, 2–4 l of water was concentrated on GF/F filters and kept frozen for spectrophotometric quantification of chlorophyll-*a* according to Strickland and Parsons (1972), and 30 ml was collected and kept frozen at –20 °C for nutrient assessment (nitrates, phosphates and silicates) by a Technicon Autoanalyser. No nutrient samples were collected in the Weddell Sea. Temperature and salinity were measured from the same sampling depth by a continuous automated system equipped with Sea-Bird sensors (SBE 38 and 37, respectively) within the framework of the ARGAU Project (<http://dataipsl.ipsl.jussieu.fr/ARGAU/argau.htm>).

Diatom densities (cells l⁻¹) were estimated by cell counting under an inverted microscope (Uthermöhl technique) provided with phase contrast. For each sample, a minimum of 300 cells were counted and identified to ensure the statistical significance of the data. To estimate biomass (µg C l⁻¹), 30 cells were measured for calculation of biovolumes and further application of the diatom carbon conversion factor proposed by Menden-Deuer and Lessard (2000) ($\log_{10} \text{pg C cell}^{-1} = 0.811 \log_{10} \text{cell volume } [\mu\text{m}^3] - 0.541$).

When necessary, for the identification of species, the organic matter from frustules was eliminated by processing a subsample according to Simonsen (1974) and the specimens were further mounted onto glass slides using Naphrax. Diatom identifications were based on the works by Hustedt (1958), Cupp (1943), Hendey (1964), Simonsen (1974), Hasle and Syvertsen (1996), and Sar et al. (2001, 2002). Diatom species diversity was examined by assessing the number of taxa per sample, and by further application of the Shannon–Wiener diversity index (Shannon and Weaver, 1949; ln-based expression).

Two cluster analyses (UPGMA; Romesburg, 1984) were performed on diatoms: one based on the Jaccard Taxonomic Index (presence/absence of species) and aimed to evaluate mainly the relevance of the Polar Front as a biogeographic barrier, and another one based on correlation coefficients (transformed according to Hellinger; Legendre and Gallagher, 2001) of species-specific abundances and aimed at identifying floristic associations. The strength of the associations between diatom density/biomass values and environmental variables (macronutrients, temperature, salinity, chlorophyll-*a*) has been tested, for both the whole area under study and each of the hydrological regions considered (i.e. antarctic and subantarctic waters), by using Pearson's correlation (*r*), and taking into account only significance levels with *p* < 0.05.

The values of abundance found for Antarctic planktonic diatoms were compared with those reported in sediments by Crosta et al. (2005) and Armand et al. (2005), and the species were then classified, according to the criterion of these authors, as related to Open Ocean or Sea Ice. This procedure was followed on selected samples from three geographic sectors covered by both studies (the Drake Passage, waters off the Antarctic Peninsula and the south-eastern Weddell Sea: stations 35–37, 40–54 and 60–64, respectively; Fig. 1) and only on those taxa presenting a relative abundance of > 1% in one station at least.

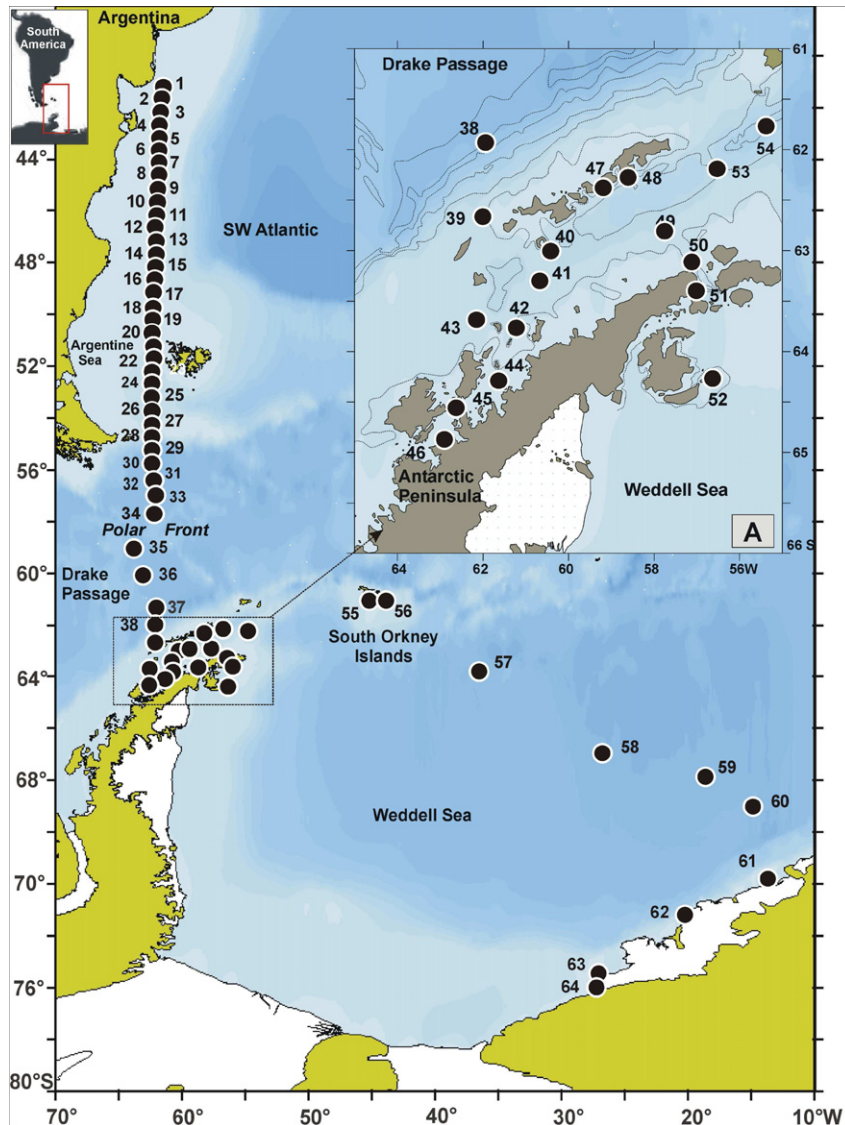


Fig. 1. Geographic location of the sites studied in subantarctic and antarctic waters during the austral summer (31 January–4 March 2002).

3. Results and discussion

3.1. General environmental features

The ACC comprises, from north to south, circumpolar fronts such as the Subtropical Front, the Subantarctic Front, the Polar Front and the Southern Antarctic Circumpolar Current Front (Joyce et al., 1978; Orsi et al., 1995), which affect the distribution of marine organisms. Among these, the Polar Front (PF) stands out as the most relevant, since it represents the sinking of Antarctic surface waters and its flowing northward below the subantarctic waters. Based on the surface position of the PF at the time of this study (ca. 58°S, Fig. 1), a general comparison of the environmental features measured during the late austral summer for both subantarctic and antarctic waters (stations: 1–34 and 35–64, respectively; Fig. 1) and for each one of the main studied regions is summarised in Table 1.

Temperature showed a regular decrease from 19 °C in Argentine shelf waters (41°S) to –1.69 °C in the southern Weddell Sea (75°55'S). Salinity, instead, exhibited an irregular pattern, with an average value slightly higher for antarctic waters. The lowest records (~33.4–33.5) corresponded to stations 8–20 on the Argentine shelf and to a few points in the antarctic waters (southern Weddell

Sea: station 60; Gerlache Strait: station 46), and are assumed to respond to the influence of typical shelf waters (Guerrero and Piola, 1997; Bianchi et al., 2005) and to ice-melting effects and advection of low salinity waters from the Bellingshausen Sea (Hofmann et al., 1996; García et al., 2002), respectively. Highest salinities (> 34), on the other hand, were found in most of the Weddell Sea stations, in concurrence with the observations by Hofmann et al. (1996). The influence of the Malvinas Current waters was found over the southern slope investigated (stations 21–28, Fig. 1).

While phosphate concentration did not show a clear trend along our transect, the mean values of nitrates, silicates and chlorophyll-*a* in antarctic waters were nearly four to five times higher as compared to subantarctic ones (Table 1). Silicates were uniformly low in both the Argentine shelf and the Drake Passage, and increased in the vicinity of the Antarctic Peninsula, while nitrates were greater in subantarctic waters of the Drake Passage. Chlorophyll-*a* followed the same increasing trend from subantarctic to antarctic waters, reaching values one order of magnitude higher in the latter.

In terms of sea-ice coverage, the period of spring–summer 2001/2002 can be considered unusual because of an anomalous atmospheric circulation resulting in persistent, strong, warm

Table 1
Average, standard deviation (in parenthesis), minimum and maximum values of abiotic variables, chlorophyll-*a* and diatom density and biomass for the entire transect, subantarctic and antarctic waters and main environments studied. Station codes according to Fig. 1.

Geographic Sector	Station no.	Temperature (°C)	Salinity (psu)	NO ₃ (μM)	SiO ₂ (μM)	PO ₄ (μM)	Chlorophyll- <i>a</i> (μg l ⁻¹)	Diatoms	
								Cells l ⁻¹	μg C l ⁻¹
All transect	1–64	6.88 (6.6) –1.69–19.12	33.85 (0.28) 33.43–34.42	5.57 (6.03) 0.15–23.7	11.87 (14.4) 0.61–60.5	2.60 (1.87) 0.41–8.92	1.15 (2.98) 0.02–18.6	41956 (119459) 0.84–777213	18.1 (43) 8.8 × 10 ⁻⁴ –254
Subantarctic waters	1–34	12.2 (4.48) 5.54–19.12	33.71 (0.23) 33.43–34.01	3.05 (3.36) 0.15–14.3	5.76 (4.50) 0.61–18.16	2.47 (1.63) 0.41–7.1	0.45 (0.44) 0.016–1.6	2478 (6326) 0.84–26143	2.99 (8.2) 8.8 × 10 ⁻⁴ –31.7
Argentine Shelf	1–21	15.28 (2.7) 10.32–19.12	33.56 (0.13) 33.43–33.83	1.06 (0.87) 0.15–3.26	6.21 (4.66) 0.61–18.2	2.47 (1.75) 0.50–7.1	0.54 (0.54) 0.016–1.6	260 (626) 0.8–2725	0.38 (0.83) 8.8 × 10 ⁻⁴ –2.9
Subantarctic Slope	22–28	8.76 (1.2) 6.74–10.22	33.85 (0.17) 33.67–34.08	4.47 (1.98) 2.2–8.5	4.20 (4.40) 0.61–12.8	1.90 (1.31) 0.41–4.39	0.51 (0.14) 0.36–0.65	263 (372) 6–1034	0.23 (0.32) 7 × 10 ⁻³ –0.94
Drake Passage (Oceanic)	29–38	4.90 (1.71) 2.64–6.80	33.93 (0.15) 33.72–34.08	10.57 (6.73) 4.30–23.73	8.53 (5.03) 2.14–15.35	2.55 (1.32) 0.79–4.47	0.13 (0.049) 0.06–0.2	24865 (48949) 1509–161848	14.17 (15.07) 1.47–37.21
Drake Passage (Subantarctic)	29–34	6.18 (0.54) 5.54–6.80	34.03 (0.048) 33.96–34.08	8.37 (3.62) 4.30–14.32	6.05 (4.39) 2.14–14.34	3.11 (1.33) 1.16–4.47	0.15 (0.03) 0.11–0.2	12822 (10319) 1509–26143	16.24 (14.89) 1.47–31.65
Antarctic waters	35–64	1.01 (1.66) –1.69–3.21	33.99 (0.26) 33.45–34.42	11.69 (6.79) 4.38–23.7	26.7 (19) 7.6–60.5	2.93 (2.38) 0.79–8.92	1.73 (3.94) 0.06–18.6	86698 (164492) 408–777213	32.7 (56.44) 0.24–254
Drake Passage (Antarctic)	35–38	2.97 (0.25) 2.64–3.21	33.76 (0.04) 33.72–33.81	13.87 (9.49) 5.41–23.73	12.24 (3.60) 7.63–15.35	1.71 (0.88) 0.79–2.55	0.07 (0.015) 0.06–0.09	42928 (79282) 2649–161848	11.57 (17.14) 1.576–37.21
Antarctic Peninsula	38–54	1.49 (1.10) –0.43–2.86	33.99 (0.27) 33.50–34.42	10.82 (5.79) 4.38–23.59	32.50 (19.67) 9.77–60.47	3.42 (2.65) 1.05–8.92	2.92 (5.30) 0.11–18.60	101930 (212761) 408–777213	44.91 (73.26) 0.24–254.51
Weddell Sea	55–64	–0.53 (1.46) –1.69–1.75	34.09 (0.26) 33.45–34.33	ND	ND	ND	0.56 (0.36) 0.06–1	79834 (91259) 551–227918	21.62 (24.9) 0.26–70.4

winds from the NNW (Turner et al., 2002; Massom et al., 2006). The south-eastern Weddell Sea and the NW and tip of the Antarctic Peninsula experienced positive and negative anomalies of ice concentration, respectively. Such conditions are assumed to have triggered the breakdown of the Larsen Ice Shelf (Turner et al., 2002), an event that occurred during this study (February 2002), and caused an unusually early and fast retreat of ice at the WAP, together with a great cutback in the ice coverage south of the Gerlache Strait (e.g., Marguerite Bay) and an abnormally high concentration of ice in the south-eastern Weddell Sea.

3.2. Spatial distribution of diatoms in relation to summer environmental conditions

The overall diatom abundance within the area under study showed a range of six orders of magnitude for both density and biomass (Table 1). The main trend observed for the whole area involves a clear association of these two variables with chlorophyll-*a* ($r=0.5$ and 0.88 , respectively; $n=49$) and a significant increase in diatom density with the decrease in water temperature ($r=-0.37$; $n=63$). Nitrates and silicates were also inversely associated with temperature ($r=-0.740$ and -0.536 , respectively; $n=47$) but did not evince a relationship with diatom abundance.

Diatom density and biomass in the subantarctic region (mainly in Patagonian shelf waters; see below) presented relatively homogeneous values (Fig. 2), with mean values significantly lower than those of the Antarctic area (t -test, $p < 0.01$; 35 and 11 times lower). While the correlation analysis of density vs. biomass yielded a highly significant result ($r=0.99$; $n=30$) seemingly due to the general dominance of large species (e.g., *Rhizosolenia* spp.; Table 2), these two variables did not show a clear relationship with chlorophyll-*a*,

thus suggesting that the main contribution to phytoplankton during February 2002 was provided by groups other than diatoms. Diatom density and biomass of subantarctic waters were also found to covary positively with nitrates ($r=0.38$ and 0.41 , respectively; $n=33$) and salinity ($r=0.53$ and 0.44 , respectively; $n=33$) and negatively with temperature ($r=-0.5$ and -0.45 , respectively; $n=33$). This behavior is thought to respond primarily to the abundance increases recorded for the subantarctic oceanic waters of the Drake Passage, which, as compared to those of the Patagonian shelf and slope, exhibited mean density and biomass values up to two orders of magnitude higher (Maximum: 26 000 cells l⁻¹, 31.7 μg C l⁻¹, Fig. 2), together with two-fold higher nitrate concentrations (14 μM).

Patagonian middle-shelf waters, in particular, were characterized by a homogeneous scarcity of diatoms (mean: 260 cells l⁻¹, 0.38 μg C l⁻¹), chlorophyll-*a* (mean 0.54 μg l⁻¹) and macronutrients (Table 1; Fig. 2). Slight increases in diatom abundance (up to 3000 cells l⁻¹ and 3 μg C l⁻¹) were observed at the northern extreme of the transect (41–43°S), in concurrence with the influence of High Salinity Coastal Waters (Bianchi et al., 2005). The low abundances recorded in shelf waters during the late austral summer may be a consequence of the typical seasonal productivity cycle of temperate regions (Carreto et al., 1995), in which the input of nutrients into the euphotic zone is limited by a strong thermocline located 30–40 m deep (Guerrero and Piola, 1997). This can be confirmed by the low nitrate levels detected in all of the shelf stations (mean 1.1 μM), which are likely to be restrictive for algal growth (Quéguiner et al., 1997). Furthermore, the central fringe of the shelf has been previously characterized as presenting a strong spring bloom, a weak fall bloom, and low chlorophyll values throughout summer (Rivas et al., 2006), in agreement with our results, while the inner and outer shelf waters are productive even during most of the summer season as

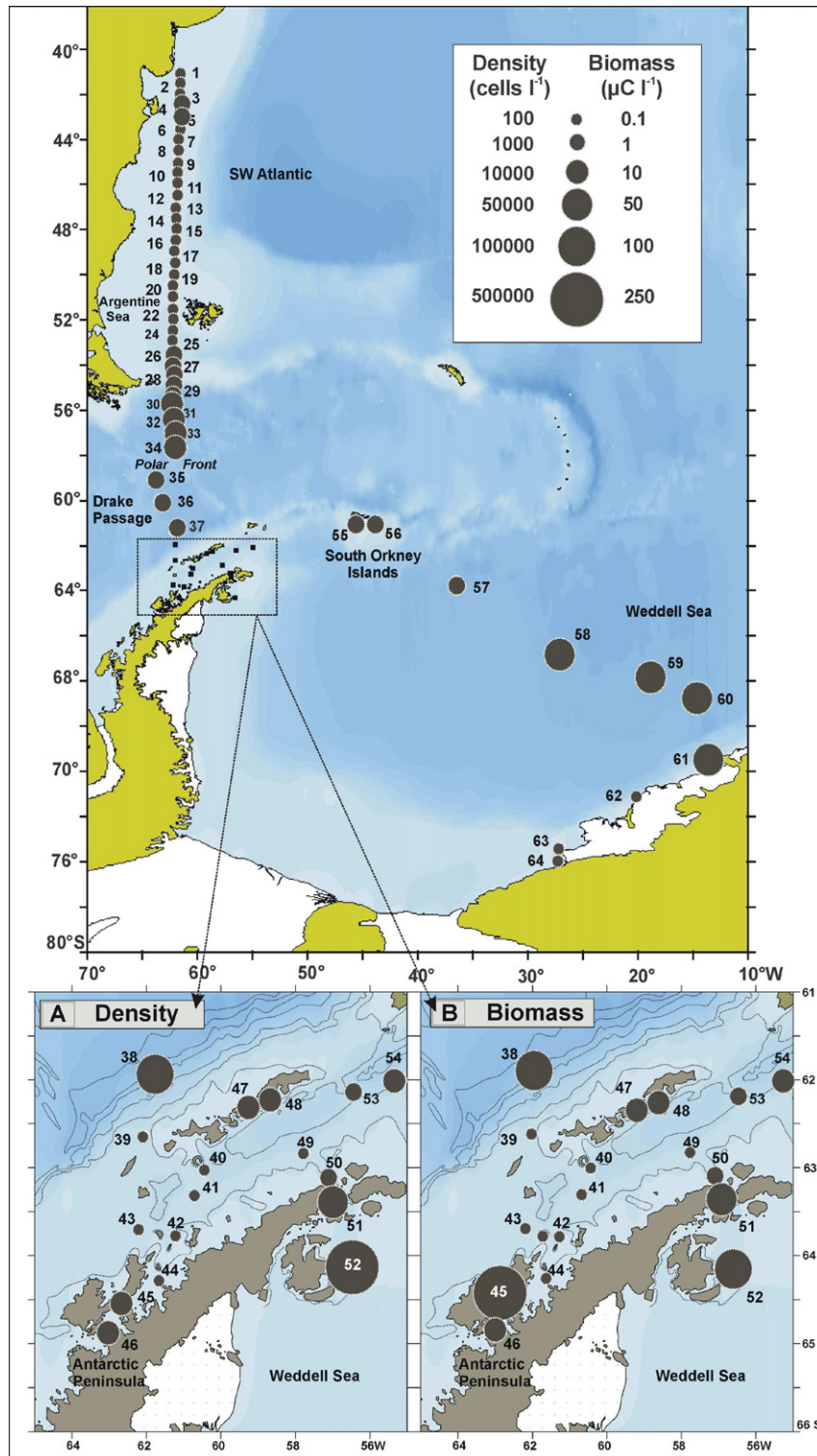


Fig. 2. Spatial distribution of the absolute density and biomass of diatoms in subantarctic and antarctic waters during the austral summer 2002. A, B: Detail of abundance values in waters surrounding the Antarctic Peninsula.

a result of the conditions generated by tidal fronts and the Shelf Break Front, respectively (Acha et al., 2004). Interestingly, the abundance levels of diatoms in waters of the Argentine shelf were similar to those previously mentioned as typical of the oligotrophic regions of the large oceanic gyres (Marañón et al., 2000).

The Polar Front is commonly associated with high diatom densities as a result of a greater availability of macro- and

micronutrients and the stability of the water column (de Baar et al., 1995; Quéguiner et al., 1997). However, in the present study, diatom abundances in the surroundings of the Polar Front were moderate to low (Fig. 2), in concurrence both with the trend reported for *in situ* chlorophyll during summer/autumn 2003 and 2006 (Franzosi et al., 2007) and with remote sensing data obtained in February 2000 and 2003 (<http://oceancolor.gsfc.nasa.gov>).

Table 2
Diatom density (cells l⁻¹), biomass (µg C l⁻¹), average carbon content per cell (µg C × 10⁻⁴ cells⁻¹) and dominant diatom species at the 10 stations of higher density from subantarctic and antarctic waters. The rank value of each parameter is based on the total number of stations assessed (64). Abbreviations for genera, as follows: Ch.: *Chaetoceros*; C.: *Corethron*; Cy.: *Cylindrotheca*; F.: *Fragilariopsis*; Tha.: *Thalassionema*; T.: *Thalassiosira*; P.: *Pseudo-nitzschia*; Ro.: *Roperia*; R.: *Rhizosolenia*; A.: *Actinocyclus*; D.: *Dactyliosolen*.

Station	Density		Carbon biomass		Mean C per cell		Dominant diatom species
	(cells l ⁻¹)	Rank	(µg C l ⁻¹)	Rank	(µg C 10 ⁻⁴ cells ⁻¹)	Rank	
ANTARCTIC WATERS							
52	777 213	1	156.03	2	2.0	59	<i>Ch. tortisimum</i> (85%)
51	447 075	2	117.96	3	2.6	55	<i>Ch. tortisimum</i> (72%)
59	227 918	3	70.39	5	3.1	52	<i>F. curta</i> (38%) <i>D. antarcticus</i> (13%) <i>P. lineola</i> (10%)
58	217 397	4	50.55	6	2.3	58	<i>Ch. dictyota</i> (74%)
38	161 848	5	37.22	8	2.3	57	<i>Ch. dictyota</i> (35%) <i>F. rhombica</i> (15%) <i>Ch. neglectus</i> (12%)
46	155 060	6	87.22	4	5.6	50	<i>F. curta</i> (47%) <i>F. rhombica</i> (7%) <i>P. lineola</i> (5%)
61	140 198	7	38.07	7	2.7	54	<i>F. curta</i> (38%) <i>Ch. neglectus</i> (18%) <i>Ch. dictyota</i> (14%)
60	118 007	8	34.23	9	2.9	53	<i>Ch. dictyota</i> (55%) <i>P. lineola</i> (16%)
45	115 162	9	254.51	1	22.1	1	<i>T. tumida</i> (47%) <i>A. spiritus</i> (13%) <i>F. curta</i> (12%)
55	76 068	10	8.06	17	1.1	60	<i>Ch. socialis</i> (95%)
SUBANTARCTIC WATERS							
34	20 604	13	30.90	11	15.0	8	<i>R. antarctica</i> (25%) <i>P. heimii</i> (18%) <i>Ch. convolutus</i> (11%)
33	18 496	14	31.65	10	17.1	5	<i>R. antarctica</i> (48%) <i>P. heimii</i> (20%)
32	7804	19	15.67	15	20.1	3	<i>F. kerguelensis</i> (15%) <i>P. heimii</i> (12%) <i>Ch. criophilus</i> (9%)
4	2725	25	2.92	22	10.7	25	<i>Ch. decipiens</i> (35%) <i>Ch. rostratus</i> (30%)
30	2377	27	1.51	33	6.4	45	<i>F. kerguelensis</i> (51%) <i>P. lineola</i> (13%)
29	1509	31	1.47	34	9.7	28	<i>F. kerguelensis</i> (37%) <i>Ro. tessellata</i> (18%)
5	1102	34	2.25	26	20.4	2	<i>Cy. closterium</i> (32%) <i>R. styliformis</i> (16%) <i>Ch. decipiens</i> (12%)
26	1034	35	0.94	36	9.0	33	<i>C. criophilum</i> (38%) <i>Tha. nitzschoides</i> (15%) <i>P. lineola</i> (13%)
3	599	37	0.70	37	11.6	20	<i>Ch. rostratus</i> (26%) <i>Ch. decipiens</i> (23%) <i>A. octonarius</i> (10%)
28	444	39	0.26	41	5.8	49	<i>F. kerguelensis</i> 39%) <i>P. lineola</i> (9%) <i>Tha. nitzschoides</i> (7%)

Values of diatom abundance (Fig. 2), chlorophyll-*a* and macronutrients (mainly nitrates and silicates) (Table 1) within the study area were significantly higher in antarctic waters as compared to the subantarctic region. However, only 30% of the stations south of the Polar Front yielded relatively high levels of diatom density (> 100,000 cells l⁻¹), biomass (> 50 µg C l⁻¹) and chlorophyll-*a* (> 1 µg l⁻¹), with the sites of maxima located close to the Southern Antarctic Circumpolar Current Front, around the tip of the Antarctic Peninsula, at the Gerlache Strait and at the Marginal Ice Zone (MIZ) in the south-eastern Weddell Sea (Fig. 2). The general features of these sites were in agreement with observations made by other authors during the austral summer (e.g., Sullivan et al., 1993; Villafañe et al., 1995; Kang et al., 2001; Rodríguez et al., 2002; Holm-Hansen et al., 2004): high phytoplanktonic abundances (especially of diatoms) associated with either the MIZ of the Weddell Sea (Stations 58–61; Nelson et al.,

1987), the vicinity of coastal glaciers and icebergs (Stations 51–52; Garibotti et al., 2005), and areas of upwelling of the SACCF (Station 38; Longhurst, 1998; Prézelin et al., 2000; Ward et al., 2002; Holm-Hansen et al., 2004), where iron concentrations, a limiting factor for this High Nutrient Low Chlorophyll region, have been reported as high (Martin et al., 1990; Boyd et al., 1995; Assmy et al., 2007).

Contrary to the trend observed for subantarctic waters, diatom abundances south of the Polar Front were relatively heterogeneous and biomass values showed a strong relationship with chlorophyll-*a* concentrations ($r=0.9$; $n=27$), thus confirming the relevant contribution of diatoms to the Antarctic phytoplanktonic stock. The dominance of small species (e.g., *Chaetoceros tortisimum*, *Chaetoceros dictyota*, *Chaetoceros socialis*, *Fragilariopsis curta*; Table 2) was reflected in the relatively low values of carbon concentration per cell. Diatom density and biomass were

significantly correlated but, as a consequence of differences in cells size, the association between these two parameters was weaker than that in the subantarctic waters (0.66 vs 0.99; $n=30$; Table 2). Station 45 was an exception to this trend, as both biomass and chlorophyll-*a* reached their highest levels there (254 $\mu\text{g C l}^{-1}$ and 18.6 $\mu\text{g l}^{-1}$, respectively; Fig. 2), despite a moderate value of density (115 000 cells l^{-1}) due to the dominance of large species such as *Thalassiosira tumida* and *Actinocyclus spiritus* (Table 2). Stations 45 and 52 (both located near the WAP, Fig. 2) were the richest ones in diatom biomass and Station 52 presented the maximum density (8.0×10^5 cells l^{-1}). The high density of diatoms in waters surrounding the tip of the Antarctic Peninsula (Fig. 2) was part of an important bloom, which occupied a good portion of the north-western Weddell Sea (<http://oceancolor.gsfc.nasa.gov>) and was associated with the

large negative anomaly of ice concentration reported for this region (Turner et al., 2002).

The lowest diatom abundances (400 cells l^{-1} , 0.24 $\mu\text{g C l}^{-1}$) and chlorophyll concentrations (0.06 $\mu\text{g l}^{-1}$) were recorded in the antarctic waters of the Drake Passage, Bransfield Strait and the southernmost sector of the Weddell Sea (Fig. 2). Several explanations can account for such a pronounced decrease in these parameters. First, the selective grazing on microplankton by salps and krill in waters off the Antarctic Peninsula and, particularly, in the Bransfield Strait (Frost, 1991; Gran et al., 1993; Villafañe et al., 1995; Cabal et al., 2002; Varela et al., 2002). Secondly, as discussed in Section 3.1, the early retreat of sea-ice in a warm year such as that of the present study results in an increase of phytoflagellates (e.g., cryptophytes) and salps (Moline et al., 2000) and a decrease in the concentration of microdiatoms. Finally, and in spite of the many investigations

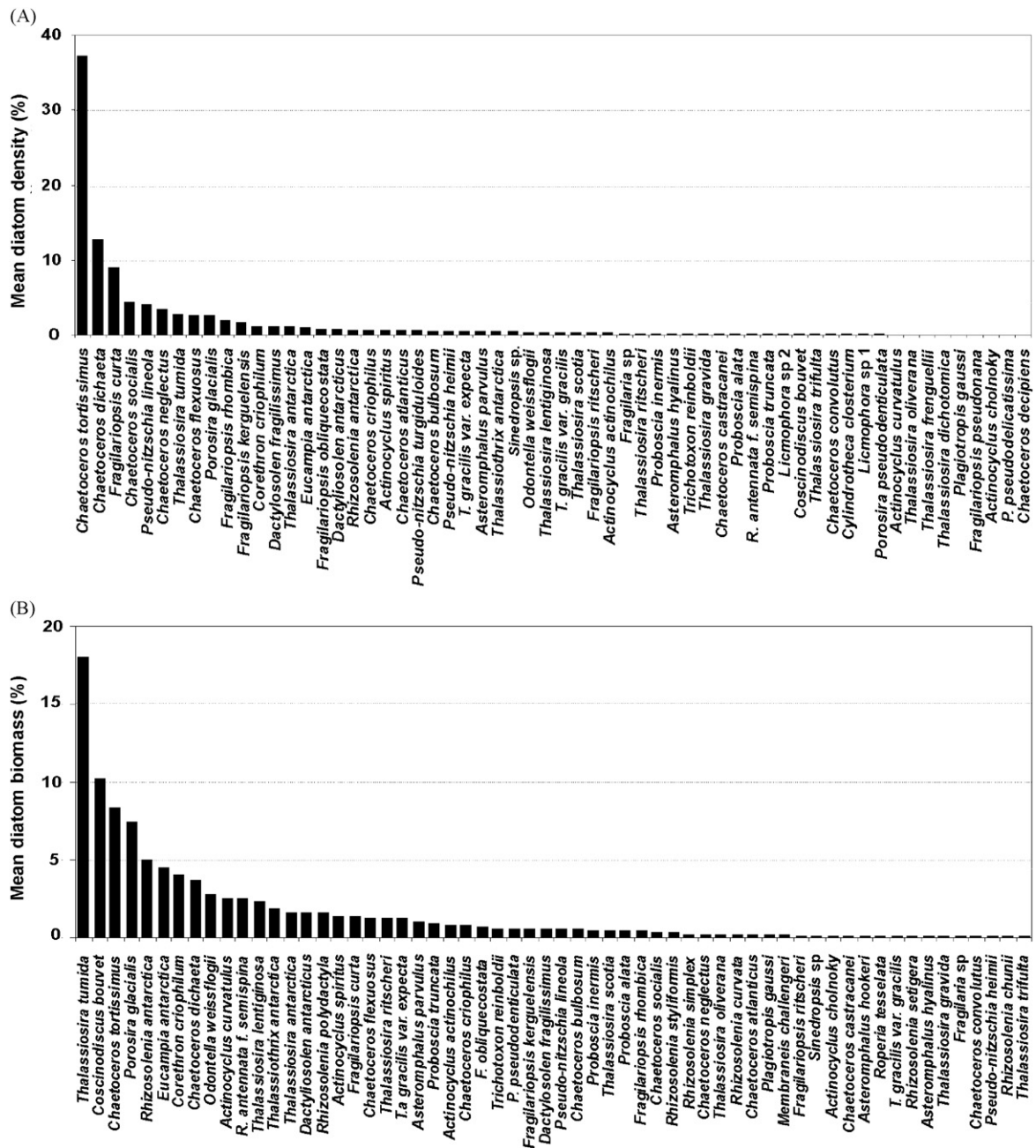


Fig. 3. Mean relative diatom species contribution (%) in density (A) and biomass (B) in relation with the total number of species recorded. Only the 60 more relevant species are included.

reporting phytoplanktonic blooms at the south-eastern end of the Weddell Sea in February (El-Sayed, 1971; <http://oceancolor.gsfc.nasa.gov>), during the period covered by our study, and as a result of the extremely high ice concentration (Turner et al., 2002), this sector (Stations 62–64) presented a particular scarcity of diatoms and phytoplankton in general (chlorophyll-*a* < 0.5 µg l⁻¹).

3.3. Geographic fluctuations of species abundance and diversity

A total of 167 taxa (included the *Nitzschia bicapitata* group) were recorded throughout the area studied, 143 of which were identified to the specific level. These species were grouped into 63 genera (see Appendix 1 in Supplementary Material), with *Chaetoceros* and *Thalassiosira* being the best represented. Most of the species showed very low densities, and only a few were numerically dominant (Fig. 3A), with *C. tortissimus* and *C. dichæta* representing

ca. 50% of the total cells counted (37% and 13%, respectively). A relatively different trend was observed in terms of biomass (Fig. 3B), since 50% of the contribution to total diatom carbon corresponded to the following five species: *T. tumida*: 18%, *Coscinodiscus bouvet*: 10%, *C. tortissimus*: 8.3%, *Porosira glacialis*: 7.4%, and *Rhizosolenia antarctica*: 5%.

The geographic distribution of each diatom taxa was included in Appendix 1 (Supplementary Material). While the great majority of the subantarctic (131 out of 150) and Antarctic taxa (75 out of 84) showed relatively low abundance levels (< 1% of total cells counted), those in the greatest concentrations were found to be different from the most widely distributed ones: highest mean relative abundances per station corresponded to *Corethron criophilum* (10%), *Fragilariopsis kerguelensis* (8.6%) and *F. curta* (6.8%) (Fig. 4A), while species occurring in > 75% of the stations were *F. kerguelensis*, *F. curta*, *Fragilariopsis rhombica*, *Thalassiosira gracilis*, *Thalassiothrix antarctica*, *Pseudo-nitzschia lineola* and

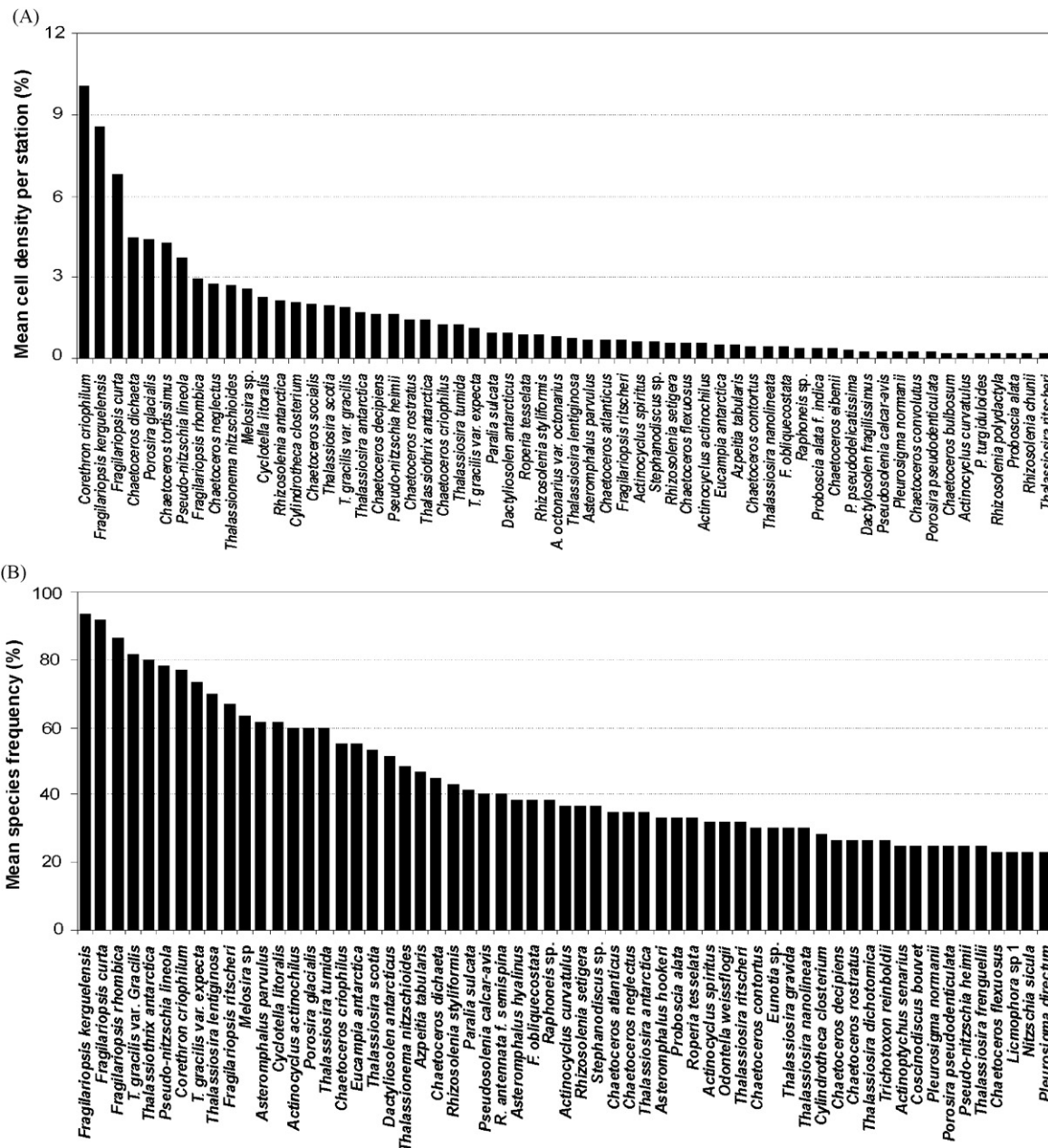


Fig. 4. Mean relative diatom species contribution (%) in density per station (A) and frequency of appearance (B) in relation to the total. Only the 60 more relevant species are included.

C. criophilum (Fig. 4B), which, according to Hasle and Syvertsen (1996), exhibit cold water preferences.

When considering only the taxa for which there are previous reports on ecological preferences (Appendix 1), it can be observed that throughout the studied area the prevailing species in terms of relative density and number are those typical of cold water (52% and 56%, respectively), followed by cosmopolite ones (43% and 36%, Fig. 5A and B). In some sites of the Antarctic region, cold water species were found to decrease their numerical relevance due to the dominance of cosmopolite taxa such as *C. tortissimus*, *C. socialis* and, to a lesser extent, *Pseudo-nitzschia lineola* and *Pseudo-nitzschia heimii*. At the northern end of the transect (Stations 1–5), on the other hand, a relatively high dominance of warm water species was observed (e.g. *Chaetoceros rostratus*, *Bacteriastrium hyalinum*, etc.).

The number of taxa per station ranged between 46 (Patagonian shelf waters) and 21 (waters surrounding the Antarctic Peninsula), with the Shannon–Wiener Index varying from 0.41 to 4.6

(Fig. 5C and D). In the patagonian and antarctic waters these parameters were higher and lower than the mean value (36 and 3.3), respectively. The decrease in the number of taxa recorded from subantarctic to antarctic waters (ca. 1.7 times) was statistically confirmed by a linear regression between species richness and latitude ($b = -0.28$; $p = 0.0007$). Yet, the latter accounted only for 18% of the total variability, probably as a consequence of species richness being higher at the southernmost sector of the Weddell Sea than, for instance, in the Drake Passage and the Bransfield Strait (Figs. 5 and 7).

3.4. Biogeographical trends and the Polar Front

The cluster analysis based on the Jaccard Index (Fig. 6A) yielded two main groups of stations (a northern group and a southern group, with five and seven sub-groups, respectively) clearly divided by the Polar Front and in correspondence with the

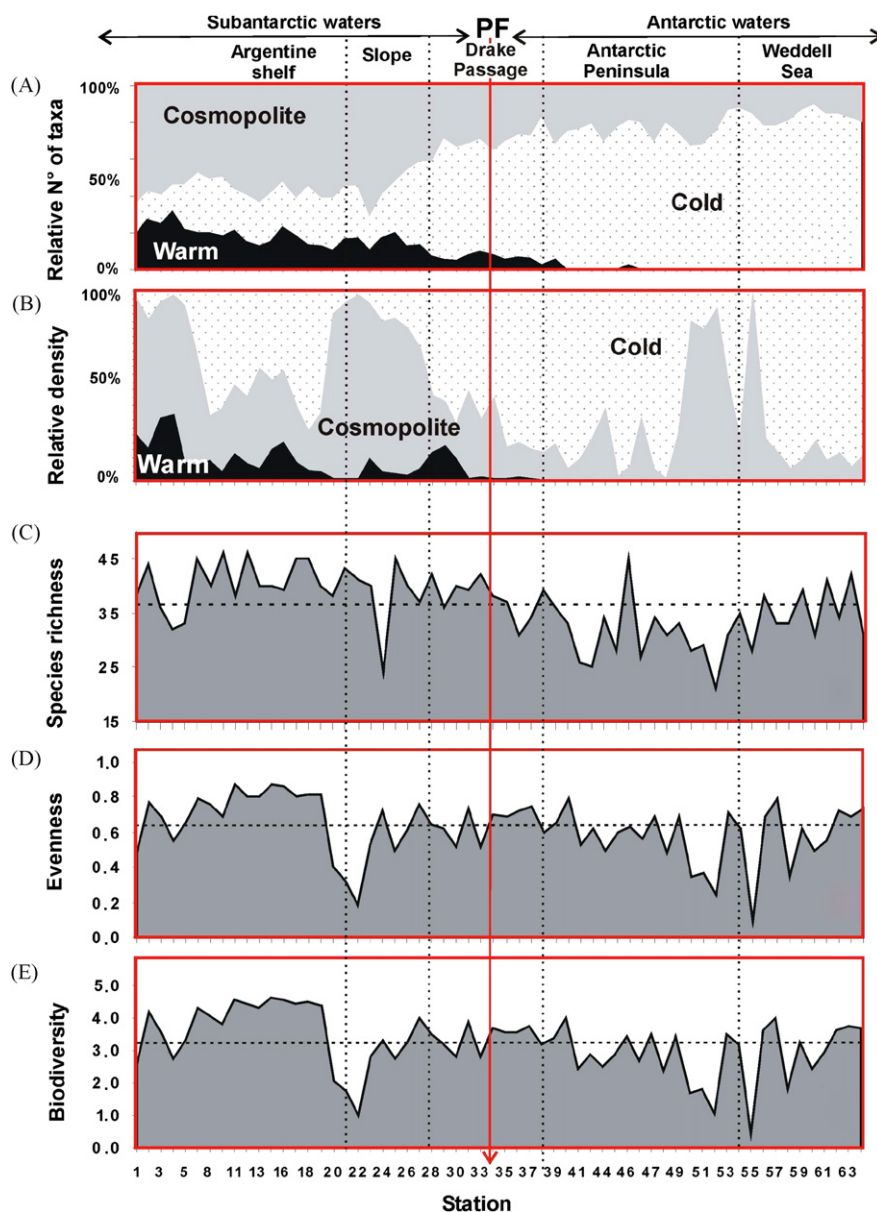


Fig. 5. Latitudinal distribution of the relative number (A) and relative density (B) of cosmopolite, warm and cold waters taxa, diatom species richness (C), evenness (D) and Shannon–Wiener diversity (E). Ecological preferences of diatom species are according to Hasle and Syvertsen (1996), Lange and Mostajo (1985), Simonsen (1974), Hustedt (1958), Medlin and Priddle (1990), Rines (1999), Sar et al. (2001), and Johansen and Fryxell (1985). Taxa without a reported ecologic preference (see Appendix 1) were excluded from A and B.

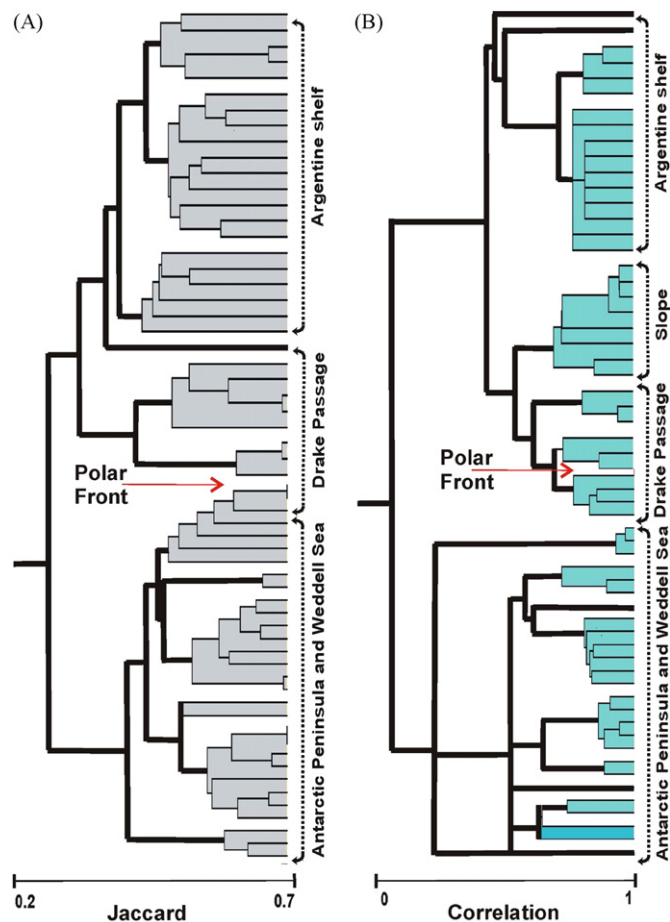


Fig. 6. Hierarchical cluster analysis (UPGMA) based on the presence/absence of species (Jaccard Taxonomic Index: A) and species-specific densities (correlation coefficient: B).

Subantarctic and Antarctic regions. Only one site located at 52°26'S (Station 24) remained isolated from the rest due to a local decrease in the total number of species identified.

A total of 83 taxa of the 150 identified for subantarctic waters were exclusive of this region, with 124 species being detected in less than 50% of the stations. The distribution of taxa according to ecological preferences showed a domain of cosmopolites (59.4%) followed by 32% of cold water species (Fig. 5A and B, Appendix 1 in Supplementary Material). Patagonian shelf waters (Stations 1–21, Fig. 1), in particular, hosted 18.8% of warm water taxa (e.g., *C. rostratus*, *Pseudosolenia calcar-avis*, *Thalassiosira nanolineata*, *Thalassiosira nodulolineata* and *Roperia tesselata*) and 24.5% of cold water taxa (*F. kerguelensis*, *F. rhombica*, *F. curta* and *T. gracilis*).

On the other hand, from a total of 84 taxa identified for antarctic waters, only 17 were found exclusively in this region, and the great majority (58) was present in less than 50% of the stations. The Antarctic and Subantarctic regions shared a total of 67 taxa, with this number representing 49% of the total found in shelf Patagonian waters and the adjacent slope.

The Drake Passage region was characterized by the presence of species exclusive of cold waters (*Rhizosolenia polydactyla*, *R. antarctica*, *R. crassa*, *R. curvata*, *R. simplex* and *R. chunii*) jointly with others frequently occurring as far as the southern Weddell Sea (*Rhizosolenia antennata* f. *semispina*, *C. dicaeta*, *C. atlanticus* and *C. criophilus*).

The cluster analysis based on the correlation coefficient (Figs. 6B and 7), allowed differentiating a number of associations (13) similar

to that based on the Jaccard Index, but also revealed five different main aspects, as follows:

- 1) The first-order change of the correlation cluster separated two main groups of stations divided by the Southern Antarctic Circumpolar Current Front instead of the Polar Front: a northern group comprising Argentine shelf waters and the Drake Passage (Stations 1–39), and a southern group encompassing the Weddell Sea and waters surrounding the Antarctic Peninsula. Such differentiation is attributed to the high relative density of *F. kerguelensis* in the northern group (see Section 3.2, Fig. 4A and B) and to the dominance of *P. glacialis* and of the species of *Chaetoceros* and *Thalassiosira* in the southern one (Figs. 6B and 7).
- 2) A higher number of isolated stations was evidenced. From the floristic point of view, these sites showed a weak relationship with the assemblages found throughout the area, and were located either in subantarctic waters of the northern end of our transect (Stations 1 and 2) or in antarctic waters surrounding different islands (e.g., South Shetland: Station 40; South Orkney: Station 55; Gerlache Strait: Station 45). This fact is thought to respond to sectors of higher environmental heterogeneity due to the mixture of warm waters from coastal and oceanic origins, and to island effects, respectively, which might have pushed in favour of the increase in number of some particular species. For instance, and in terms of abundance of cosmopolite and warm species, Stations 1 and 2 showed a similar structure to that found at the immediately southern ones (Stations 3–5). Despite this, the structure of the species assemblages was different (Fig. 7). A different situation was found at Stations 38 and 46 (Drake Passage and Gerlache Strait, respectively), which appeared geographically isolated though dominated by the same species prevailing in the southern Weddell Sea (Sub-groups 12 and 13, respectively).
- 3) In terms of contribution of warm water species, subantarctic Drake Passage waters were second only to the northern extreme of the Patagonian shelf. Among these warm water species, *R. tesselata* increased in number exclusively at this sector, although it also occurred in very low densities in the Argentine shelf and the slope. This species is known for its thermophilic preferences (Hasle and Syvertsen, 1996). In sediments, its highest frustule abundances are mentioned for the Subtropical Front, yet it was also observed to frequently occur as far as in the Subantarctic Front (Romero et al., 2005). Its presence in subantarctic waters of the Drake Passage is thus probably associated with the circulation of the Cape Horn Current, which transports relatively warm waters from the Pacific, and/or to the increase in nitrate concentration (see Section 3.1).
- 4) The abundance level of the dominant species within each of the different associations detected for the Antarctic region is thought to reflect distinct stages of the seasonal succession that is initiated at the margins of the retreating ice (Garibotti et al., 2005). Northward from the southern Weddell Sea there is a transition from associations dominated by sea-ice-related species typical of initial stages (e.g., *F. curta*, Sub-group 13, Fig. 7) to an association dominated by species less related to ice (e.g., *C. dicaeta*, *C. neglectus*, etc., Sub-group 12, Fig. 7) that also hosts some species of open waters (e.g., *C. criophilus*, *C. criophilum*, *T. antarctica*, *F. kerguelensis*, *F. rhombica*, *P. lineola*, *P. heimii*, etc., Sub-groups 10, 11 and 6; Fig. 7), the presence of which is thought to reflect advanced stages of the seasonal cycle (Garrison et al., 1987; Villafañe et al., 1995). The significant dominance of the cosmopolite species *C. tortissimus* and *C. socialis* at the tip of the Antarctic Peninsula and the vicinity of the South Orkney Islands (Group 9 and Station 55, Fig. 7) is likely to respond to rich, strongly stratified coastal waters generated by

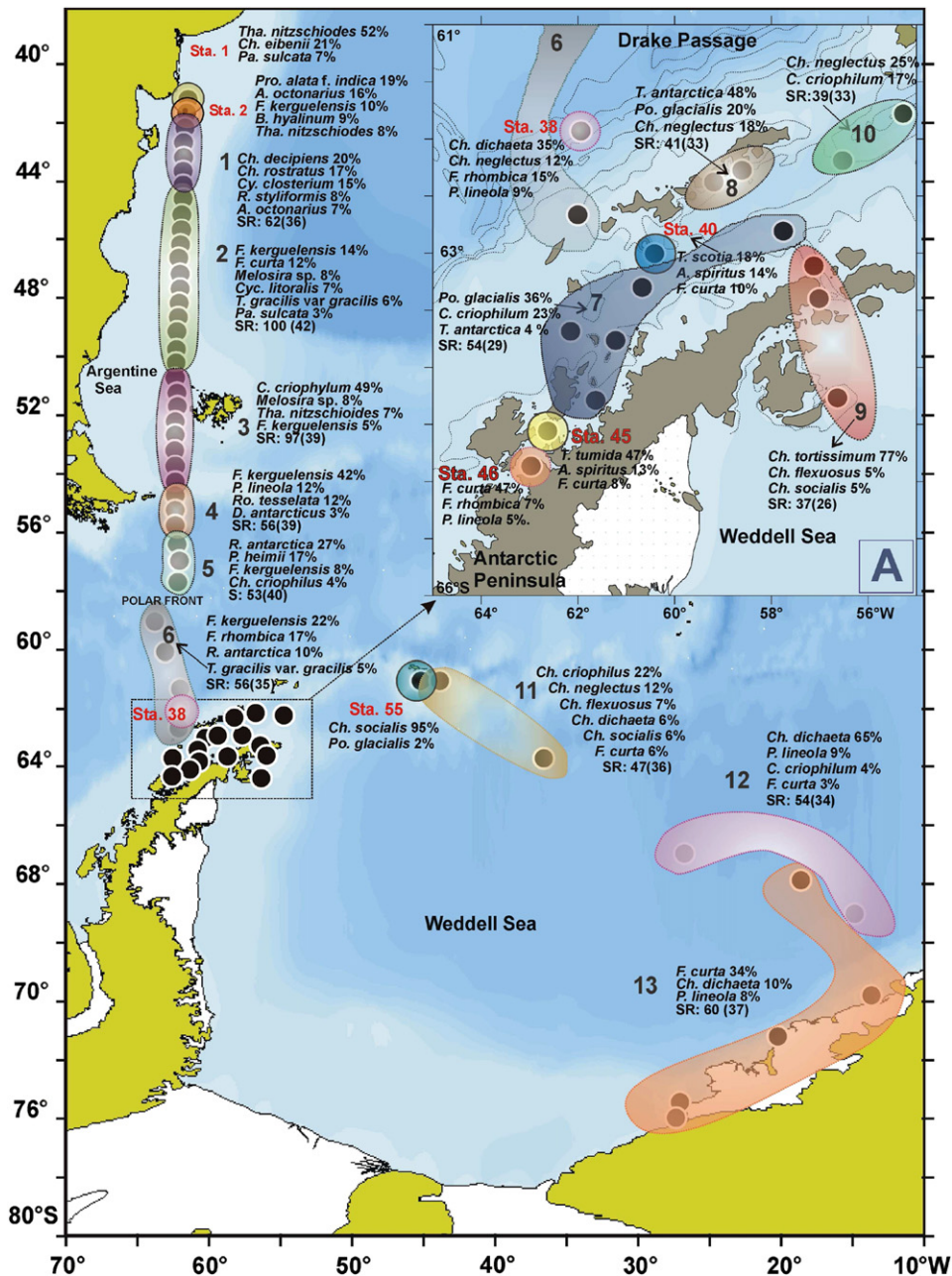


Fig. 7. Biogeographic zonation resulting from the cluster analyses based on diatom species-specific densities (see Fig. 6B). Numbers 1 to 13 indicate Sub-groups of stations. SR: Species richness, followed by mean number of taxa per sub-group of stations (in parenthesis). Abbreviations for genera, as follows: *Ch.*: *Chaetoceros*; *C.*: *Corethron*; *Cy.*: *Cylindrotheca*; *Cyc.*: *Cyclotella*; *F.*: *Fragilariopsis*; *Tha.*: *Thalassionema*; *T.*: *Thalassiosira*; *Pa.*: *Paralia*; *Pro.*: *Proboscia*; *Po.*: *Porosira*; *P.*: *Pseudo-nitzschia*; *Ro.*: *Roperia*; *R.*: *Rhizosolenia*; *A.*: *Actinocyclus*; *D.*: *Dactyliosolen*.

the permanent input of melt water from glaciers and sea-ice (Crosta et al., 1997; Stickley et al., 2005).

- 5) The high abundance of *P. glacialis* in the Bransfield Strait (Sub-group 7) represented a change in comparison with the diatom associations previously reported for the area (Estrada and Delgado, 1990; Kang et al., 2001). As it occurs with *Thalassiosira antarctica*, this species reaches high abundance levels in coastal, sea-ice related waters of the Weddell Sea and the Bellingshausen (El-Sayed, 1971; Smetacek et al., 1992; Savidge et al., 1995; Pike et al., 2008). In this respect, we could speculate that its dominance in the Strait may respond to fluxes of water from the Weddell Sea, probably originating in relation with the Larsen Ice Shelf, as has been proposed to explain the high concentration of *T. antarctica* in such sectors (Bodungen et al., 1986;

Smetacek et al., 1992). However, considering the fact that the extreme atmospheric anomalies during the spring/summer 2001–2002 decreased the advection of waters from the southeastern Weddell Sea to the northern Antarctic Peninsula (Turner et al., 2002), it is more probable that the increases in *P. glacialis* in the Bransfield Strait could be a consequence of water advection from the WAP (Bellingshausen Sea) to the Strait.

3.5. Comparison between the diatom species selected and their abundances in plankton and sediments of the Antarctic region

In their analysis of core top sediment samples from the Antarctic region, Armand et al. (2005) and Crosta et al. (2005)

Table 3
Comparison between the mean relative contribution and (range) of diatom species present in a varying number of plankton (P) and sediment (S) samples collected in the Drake Passage ($P=3$, $S=2$), waters off the Antarctic Peninsula ($P=15$, $S=24$), and the south-eastern Weddell Sea ($P=5$, $S=1$). Open Ocean/Sea-Ice affinities and relative contributions of species in sediments are according to Crosta et al. (2005) and Armand et al. (2005). Highest values in both plankton and sediments among the different regions are denoted in bold.

		Antarctic Peninsula		Drake Passage		SE Weddell Sea	
		P	S	P	S	P	S
OPEN OCEAN RELATED SPECIES	<i>Fragilariopsis kerguelensis</i>	21.5 (18–25)	51 (30–75)	1.1 (0–5)	2.5 (0–5)	5.6 (0.4–12)	0.5
	<i>Thalassiosira lentiginosa</i>	5.2 (3.6–6.6)	15 (10–20)	1.1 (0–5.4)	0.6 (0–5)	0.2 (0–0.4)	1.5
	<i>Thalassiosira oliverana</i>	0.54 (0.3–0.7)	2 (0–5)	0.03 (0–0.4)	0.5 (0–1)	0.06 (0–0.2)	0.5
	<i>Thalassiosira gracilis</i>	5.5 (4.6–6.3)	3.5 (2–5)	2.3 (0–11)	1.3 (0–20)	0.19 (0–0.5)	1.5
	<i>Thalassiothrix</i> spp.	1.9 (0.5–4.5)	1 (0–2)	1.7 (0–5.7)	0.5 (0–1)	0.62 (0.2–1.1)	0.5
	<i>Rhizosolenia polydactyla</i> , <i>R. curvata</i> , <i>R. crassa</i>	0.62 (0–1.9)	0.5 (0–1)	0	0.5 (0–1)	0	0.5
	<i>Rhizosolenia antennata</i> var. <i>semispina</i>	0.21 (0.2–0.3)	2 (0–5)	0.26 (0–1.6)	0.5 (0–2)	0.04 (0–0.12)	0.5
	SEA-ICE RELATED SPECIES	<i>Actinocyclus actinochilus</i>	0.06 (0–0.2)	1 (0–2)	1.2 (0–7.3)	0.5 (0–1)	1.8 (0.1–3.2)
<i>Chaetoceros</i>		12.1 (2.1–24)	16 (5–30)	25 (0–93)	87.5 (75–100)	25 (8–58)	40
<i>Fragilariopsis curta</i>		0.7 (0.3–0.9)	2.5 (1–5)	5.1 (0.1–46)	2.3 (0–20)	27.2 (3.5–38)	40
<i>Fragilariopsis cylindrus</i>		0	0.5 (0–1)	0.04 (0–0.6)	0.63 (0–3)	0.44 (0–1.6)	2
<i>Fragilariopsis obliquecostata</i>		0	0.5	0.44 (0–2.8)	0.5	2.5 (0–7)	3.5
<i>Fragilariopsis rhombica</i>		16.9 (7–24)	0.5 (0–1)	2.3 (0–8)	0.54 (0–2)	1.8 (0.1–3.4)	0.5
<i>Fragilariopsis ritscheri</i>		0.14 (0–0.4)	0.5	0.37 (0–3)	0.5	3 (0.02–5)	1.5
<i>Porosira glacialis</i>		0.09 (0–0.26)	0.5	17.6 (1.4–41)	0.54 (0–2)	0.5 (0.1–1.2)	0.5
<i>Porosira pseudodenticulata</i>		0	0.5	0.43 (0–3)	0.5	1.5 (0.1–3.1)	0.5
<i>Stellarima microtrias</i>		0	0.5 (0–1)	0	0.5 (0–1)	0.32 (0.1–1)	0.5
<i>Thalassiosira antarctica/scotia</i>		1.1 (0.3–2.2)	3.5 (2–5)	14.6 (0–52)	6.1 (2–20)	0.22 (0–0.8)	7.5
<i>Thalassiosira tumida</i>		0.4 (0.2–0.6)	0.5 (0–1)	4.2 (0–47)	0.5 (0–1)	0.12 (0–0.3)	0.5

established a clear distinction between species related to sea-ice conditions and those of the open ocean. When following this classification, we found that the assemblages from the Antarctic sector of the Drake Passage (Stations 35–37) can be considered as typical of the open ocean, while those from the surroundings of the Antarctic Peninsula (Stations 40–54) and the south-eastern Weddell Sea (Stations 60–64) are related to sea-ice conditions. The comparison between the data provided by these authors and the relative abundance of the species selected from our plankton samples (Table 3) revealed that there is a general coincidence in the contribution of the different taxa to the sediment and water assemblages of each sector. The strongest coincidences observed between sediment and plankton samples were the dominance of *F. kerguelensis* in open ocean assemblages, and that of *F. curta* and *Chaetoceros* spp. in areas of sea-ice. The high numbers and wide distribution observed for the genus *Chaetoceros* in the present study explain its dominance in both sediment traps (> 90%) and top sediment samples (> 60%) from the vicinity of the Antarctic Peninsula (Crosta et al., 1997; Buffen et al., 2007). Species of *Chaetoceros* belonging to the sub-genus *Hyalochaete* are frequently associated with spring blooms (Stickley et al., 2005). According to Buffen et al. (2007), the significant concentrations of *Chaetoceros* in superficial sediments of the north-western Weddell Sea, next to the Antarctic Peninsula, reflect episodes of very high spring productivity. The intense bloom of *Chaetoceros* detected in our study (February 2002) suggests that such high productivity period lasts until the end of the warm season.

Some notable discrepancies were found, nevertheless, regarding two species and two assemblages. In the first place, and based on the analysis of sediments, *F. rhombica* is mentioned as a generally scarce species related to the ice cover (Armand et al., 2005). Yet, our records indicate remarkably high concentrations of this species in the open oceanic waters of the Drake Passage and south-western Atlantic (Olguín et al., 2006) as well as in a large part of Patagonian shelf waters, thus suggesting the necessity of revision of its environmental affinity. Secondly, while sediment

analyses postulate *R. antennata* var. *semispina* as associated with open waters, the extremely low densities in which this taxon occurred in our samples did not allow us to establish its ecological affinity.

Some of the discrepancies detected are thought to be due to the small and spatially restricted data set used for the comparison. For instance, the assemblage comprising *R. polydactyla*, *R. curvata* and *R. crassa* occurs in sediments and has a similar density in the three sectors under comparison; however, our record of these species in the Drake Passage (more precisely, around the Polar Front) suggests an affinity towards open waters. Finally, the distribution of *Actinocyclus actinochilus*, *Stellarima microtrias*, *P. glacialis* and *T. tumida* in the plankton of either the Weddell Sea or waters off the Antarctic Peninsula demonstrates the affinity of these species for sea-ice conditions. Sedimentary records, instead, reveal significant concentrations only within specific locations of the Ross Sea and Prydz Bay (Eastern Antarctica) and the pronounced seasonal fluctuations of the sea-ice at these sites (Armand et al., 2005) can be compared to those typically occurring in the south-eastern Weddell Sea and south-western Bransfield Strait, sectors that hosted the highest densities of these species in the water column (Table 3). The low numbers in sediments can be explained either by the patchy distribution of some of these species (e.g., that of *T. tumida*, which varied from 1% to 47% in sediments and the water column, respectively) or by the exceptional occurrence of other species (e.g., *P. glacialis*; 2% vs. 41%) due to the unusual environmental conditions during the time of our study (see Section 3.1).

4. Conclusions

The transect studied allowed both assessing for the first time the summer abundance of diatom species and the structure of their associations in subantarctic waters of the Argentine-middle Patagonian shelf, and confronting them with those recorded in

antarctic waters during a period characterized by atypically warm conditions. Our results indicate that middle shelf waters are remarkably poor in diatom abundance, chlorophyll-*a* and nutrients (particularly nitrates). The lack of correlation between diatom abundance and chlorophyll-*a* suggests that the main contribution to the phytoplanktonic pool in this vast region is provided by organisms other than diatoms.

South of the Polar Front, on the other hand, the marked correlation between chlorophyll-*a* and diatoms reveals the relevant contribution of the latter to total Antarctic phytoplankton. While the highest values of diatom biomass were registered for a limited sector of the Gerlache Strait, the maximum densities corresponded to waters around the tip of the Antarctic Peninsula. These areas have previously been mentioned as important CO₂ sinks (Anadón et al., 2002) but in fact configure exceptions to the general trend, as diatom abundances in the rest of the WAP were rather low, presumably due to the intense grazing pressure by krill, which is abundant in this region (Ducklow et al., 2006).

Although the decrease in species richness with increasing latitude is still a paradigm in ecology (Gaston, 2000), some investigations have placed in doubt this concept based on increased number of species detected for certain groups in the Antarctic region (Gray, 2001). In this regard, our study verified a significant fall in diatom species richness from subantarctic to antarctic waters, although its relationship with latitude justifies only weakly the observed variability. The Weddell Sea was found to host slightly more species than the Drake Passage; however, the latter region was expected to show a higher richness because of the ACC circulation, the relative proximity of the Antarctic Peninsula to the southern tip of South America, and the resulting combination of taxa from different origin.

The qualitative/quantitative hierarchical analysis of diatom data allowed drawing of the following conclusions: (1) the Southern Antarctic Circumpolar Current Front and, primarily, the Polar Front are associated with significant floristic changes, thus representing biogeographical barriers for most Antarctic diatom species; (2) diatoms are good indicators of regional environmental changes: the anomalous conditions of the ice cover during the spring–summer 2001–2002 period were reflected in the structurally altered associations, as can be derived from their comparison against those of “normal years” for the WAP, a zone that has experienced one of the highest rates of regional climatic change in the last 50 years; (3) northward expatriation processes of polar taxa *via* the ACC–Malvinas Current system, as well as southward expatriation of warm water taxa down to the southern shelf by coastal shelf water circulation and the Brazil Current are of particular importance; (4) middle shelf, subantarctic waters represent a large transition zone hosting cold, warm and cosmopolite species; (5) ca. 90% of the taxa recorded in subantarctic waters were irrelevant in terms of concentrations, and many of them are likely to correspond to organisms expatriated chiefly from the south; this kind of phenomena can result in distortions when species richness is used as a tool for the assessment of the latitudinal gradient of diversity (at least for planktonic organisms provided with a rigid structure) and also suggests the need for future studies covering the seasonal distribution of diatoms in Patagonian waters in order to find out to what extent the low levels of abundance of most species within this region relate to temporal fluctuations during summer.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2010.09.031.

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