Distribution of spring phytoplankton (mainly diatoms) in the upper 50 m of the Southwestern Atlantic Ocean (30–61°S)

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This is the first study on diatom spatial patterns in relation to major oceanographic features along a megascale transect in the Southwestern Atlantic Ocean and provides a comparison with diatom distribution in surface sediments. Absolute abundances of diatoms, silicoflagellates and dinoflagellates (>10-μm fraction) were assessed in 80 bottle samples from 5 to 50 m, retrieved in November 1993 at 20 stations (30–61°S) along 53°W. Siliceous phytoplankton were scarce in the northern half of the transect and in the south of 57°S (100–150 cells L^{-1}), with a strong peak in the vicinity of the Polar Front (~200 000 cells L^{-1}), whereas dinoflagellates were more abundant at the northern stations (up to 24 000 cells L^{-1}). In the south of 50°S phytoplanktonic cell densities were loosely (but significantly, r = 0.54, P < 0.01) associated with chlorophyll a, whereas in the north of this latitude, this relationship disappeared (r = 0.018, P > 0.1). In total, 191 diatoms and 4 silicoflagellates were recorded. Changes in diatom assemblage compositions along the transect allowed identification of five discrete areas: Subtropical (29°S), Northern Transitional (34–41°S), Southern Transitional (43–48°S), Subantarctic (49–54°S) and Antarctic (55–59°S), each characterized by a set of typical species. Diversity changed little with latitude, but numbers of species were higher in the north of 40°S. Comparison of diatom assemblage makeup in the plankton and in the surface sediments shows very strong disagreements, whereby cold water species are very significantly over-represented in the sedimentary record, suggesting enhanced preservation and strong subsurface equatorward advection of the cold water taxa.

INTRODUCTION

The zooplankton of the Southwestern Atlantic Ocean has been a subject of many focused surveys and at least two major compilation efforts (Boltovskoy, 1981, 1999). Biogeographically oriented investigations have chiefly dealt with the latitudinal distribution of species and definition of areas of enhanced faunal turnover as a function of local currents, water masses and fronts. Animal groups used in these studies included several protists (Boltovskoy, 1970; Balech, 1986; Boltovskoy et al., 1996; Thompson et al., 1999, 2001; Thompson, 2001), as well as various multicellular taxa (Dadon and Boltovskoy, 1982; Mazzoni, 1983; Tarling et al., 1995; Esnal, 1999; Esnal and Daponte, 1999; etc.). Phytoplankton, on the contrary, have received considerably less attention. Regional studies have mainly dealt with spatial distribution patterns of nutrients and chlorophyll (Brandini et al., 2000; Barlow et al., 2002), whereas data on the distribution and abundance of phytoplankton species, in particular diatoms, are restricted to a few circumscribed

investigations (Lange, 1985, 1988; Lange and Mostajo, 1985; Gayoso and Podestá, 1996; Fernandes and Brandini, 1999; Gayoso, 1999).

Field measurements of primary production and chlorophyll *a* indicate that the Southwestern Atlantic host areas of enhanced phytoplankton output suggesting that diatoms may play an important role in this biomass buildup (Hasle, 1969; Esteves *et al.*, 1992; Sullivan *et al.*, 1993; Gayoso and Podestá, 1996; Fernandes and Brandini, 1999; Brandini *et al.*, 2000; Marañón *et al.*, 2000; Barlow *et al.*, 2002). However, the lack of adequate spatial coverage in synoptic or quasi-synoptic surveys, associated with the extreme temporal and spatial variability of the physical and biological properties in the dynamic Brazil–Malvinas Confluence Zone (BMCZ), makes assessment of overall phytoplankton patterns very complicated.

Investigation of distributional ranges of the diatoms present in the water column is important for the assessment of the biological attributes of this complex area. Species-specific surveys allow defining functionally meaningful biogeographic zonations (Beklemishev, 1969; Boltovskoy, 1986), as well as assess the origin, path and degree of mixture of different currents and water masses (e.g. Balech, 1986). Furthermore, thorough understanding of present distributional patterns of fossilizable microplankton organisms is a necessary condition for the use of their remains in sedimentary samples for paleoceanographic studies in general and for paleoclimatic interpretations in particular (Boltovskoy, 1994; Eynaud *et al.*, 1999). In this respect, contrary to the widely accepted notion that, in most regions of the world ocean, the sedimentary imprint is an adequate proxy of water column flora, preliminary analyses of the diatoms preserved in bottom sediments of the Southwestern Atlantic suggest that the signal is strongly biased toward the cold water components (Romero and Hensen, 2002).

The main goal of this work is to assess the species-specific distribution of diatoms and silicoflagellates recorded in the upper 50 m of the water column along a N–S transect in the Southwestern Atlantic between 30 and 61°S. Densities of thecate dinoflagellates (but not species identifications) are also included. The spatial patterns defined are interpreted in terms of the dynamics and the physical and chemical characteristics of the currents and water masses that characterize the area, allowing the identification of several sectors of enhanced species change, some of which coincide with physical fronts described for the area. Distributional ranges of selected species and species groups are compared in detail with data from the surface sediments.

Hydrology of the surface waters

The upper level circulation in the study area (47–57°W, 30–61°S) is dominated by two ocean currents flowing in opposite directions: the northbound Malvinas (Falklands) Current, which branches off the Antarctic Circumpolar Current (ACC or West Wind Drift), transporting cool, nutrient-rich Subantarctic waters along the western margin of the Argentine basin (Peterson and Stramma, 1991; Peterson, 1992), and the southbound Brazil Current (Fig. 1), which is warm, saline and relatively oligotrophic (Deacon, 1982; Peterson and Stramma, 1991). The area where the two come in contact with each other is the BMCZ, a very dynamic area between 30 and 46°S characterized by the interleaving and mixture of Subantarctic and Subtropical waters, as well as strong mesoscale features such as thermohaline fronts, rings, filaments and eddies (Olson *et al.*, 1988; Peterson, 1992; Mata and Garcia, 1996; Willson and Rees, 2000). Here, the Brazil Current detaches from the coast and starts meandering, turning first to the southeast (SE) and then to the northeast (NE) (Goni *et al.*, 1996), whereas the Malvinas Current makes a cyclonic loop returning to the SE.

The above-described hydrographic features define zones of enhanced horizontal gradients in several physical properties. Among the most conspicuous are the Subantarctic Front and the Polar Front (Fig. 1). The Subantarctic Front bounds the Malvinas Current up to ∼40°S following the 2000 m isobath (Peterson, 1992). The Polar Front or Antarctic Convergence according to Deacon (Deacon, 1982), located between 50 and 60°S depending on season and longitude, defines the area where cold (up to ∼4°C) waters of the ACC sink under the less dense Subantarctic surface waters and move north as Antarctic intermediate waters, probably as far north as 20–25°S (Lenz, 1975; Tsuchiya *et al.*, 1994). The area encompassed by the Subantarctic Front and the Polar Front is also known as the Polar Front Zone (Fig. 1).

In addition to these chiefly oceanic features, the area hosts several fronts associated with coastal processes. The Shelf Break Front is a stretch located along the Argentine continental shelf-break extending between ∼37 and 50°S (Guerrero *et al.*, 1999; Acha *et al.*, 2004). It is a major oceanographic feature along the southern South American Atlantic margin defined by the contact between Subantarctic shelf waters and cooler and more saline waters of the Malvinas Current. Along this feature, active vertical mixing is responsible for enhanced primary production estimated at 350–450 g C m^{-2} year^{-1} (Negri, 1993) and the concomitant high concentrations of zooplankton (Ciechomski and Sánchez, 1983; Dadon, 1984).
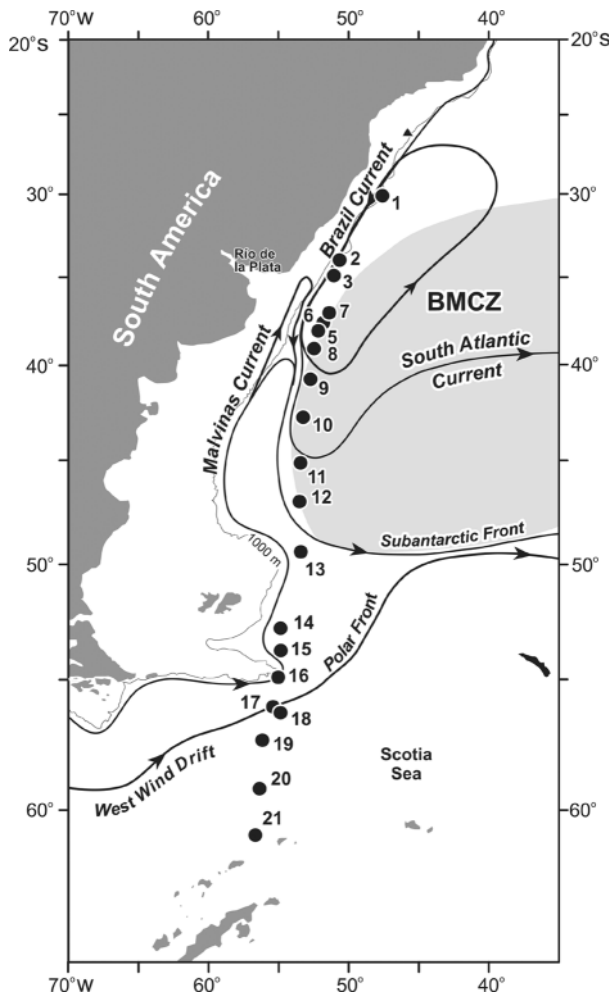
Fig. 1. Location of sampling stations and general surface circulation pattern, modified from Peterson and Stramma (Peterson and Stramma, 1991).

At 35–36°S the mouth of the Río de la Plata discharges ∼22 300 m^3 s^{-1} of fresh water into the sea (Guerrero *et al.*, 1997). The area influenced by fresh water runoff varies seasonally and geographically; during the winter, it extends up to 1300 km to the NE of the estuary, whereas in the summer, it mainly spreads offshore and along the coast reaching ∼31°S (Piola *et al.*, 2000).

METHOD

Within the framework of the Tango Batucada International Agreement (TABIA) project, a joint Brazilian–Argentine research program based on chemical and plankton sampling in the South Atlantic, water bottle (Niskin) samples were collected at 20 stations along a N–S transect located at 47–57°W and 30–61°S (Fig. 1,

Table I), onboard RV 'Barão de Teffé', in November 1993. Discrete samples were collected at 5, 10, 25 and 50 m in the water column. For each depth, a volume of 3–8 L was fractionated through a 10-μm mesh by reverse filtration and used for the estimation of the composition and abundance of the phytoplankton. Thus, all data reported here refer to the >10-μm fraction. Samples were preserved with 5% neutralized formaldehyde in sea water. Diatom and silicoflagellate counts and identifications were performed under an inverted microscope equipped with phase-contrast illumination in Utermöhl settling chambers (Utermöhl, 1958). The number of transects scanned in each chamber varied with algal density; at least 300 cells were counted and identified for each major group reported here (only relative abundance data were available for station 1). Diatoms were also identified in subsamples processed to clean the frustules from organic matter (Simonsen, 1974) and mounted in permanent slides with Naphrax mounting medium. Diatom identifications were chiefly based on Hustedt (Hustedt, 1930), Cupp (Cupp, 1943), Simonsen (Simonsen, 1974), Hasle and Syvertsen (Hasle and Syvertsen, 1996) and Sar *et al.* (Sar *et al.*, 2001, 2002); for silicoflagellates, the work of Takahashi and Blackwelder (Takahashi and Blackwelder, 1992) was used.

Temperature, nutrient and chlorophyll *a* (by fluorometry after extraction with 90% acetone) data used in this work have been reported by Brandini *et al.* (Brandini *et al.*, 2000), where the corresponding methods are also detailed. The positions of the main fronts traversed during the cruise were defined in a previous work chiefly on the basis of surface and vertical temperature profiles (Brandini *et al.*, 2000).

Because the aim of this survey was assessing geographic (latitudinal) shifts in diatom assemblages in association with major hydrographic features, for most biogeographic analyses, the species-specific quantitative values of each vertical profile were pooled (weighted mean). This procedure was further justified by the fact that the overall structure of the database was very strongly governed by the latitudinal gradient, whereas depth had a minor influence on the composition of the assemblages. This assumption was confirmed by the results of a cluster analysis using all the data points (i.e. non-pooled data), where sample-to-sample similarities clearly followed a latitudinal gradient rather than vertical patterns (Fig. 2).

Cluster analyses were based on Jaccard's index and the unweighted pair group method with arithmetic mean (UPGMA) algorithm (Romesburg, 1984).

Although all our taxonomic information (and, consequently, the biogeographic zonations proposed) is based on traditional, light-microscope systematics, we are aware of the fact that, in the last years, diatom taxonomy has

Table I: Date, location of sampling stations, number of diatom species and phytoplankton (>10 μm) densities

Station	Date (November 1993)	Latitude S	Longitude W	Number of diatom species	Diatoms	Silicoflagellates	Thecate dinoflagellates
1	6	29°42′06″	47°16′07″	81	ND	ND	ND
2	10	33°59′03″	51°14′12″	87	56 234	325	1780
3	11	35°00′03″	51°23′36″	69	519	175	521
5	12	37°35′12″	51°38′00″	54	69	4	15
6	12	37°15′06″	51°23′06″	36	934	1454	13 405
7	12	37°01′54″	51°12′00″	68	16 451	371	949
8	13	39°02′00″	52°07′00″	64	18 647	193	1329
9	14	40°59′00″	52°40′00″	37	161	4	131
10	15	42°59′00″	53°08′06″	34	766	61	205
11	15	45°00′12″	53°31′00″	45	2030	100	945
12	16	47°00′00″	53°50′00″	37	647	48	396
13	17	49°36′00″	54°12′00″	37	7645	199	702
14	18	53°05′00″	54°52′00″	37	2221	461	2007
15	19	53°54′18″	55°01′48″	50	20 216	1651	1181
16	20	55°03′00″	55°14′00″	45	4252	999	379
17	20	56°14′24″	55°30′54″	53	31 718	1133	679
18	20	56°20′23″	55°25′24″	56	67 984	6453	1055
19	20	57°15′42″	55°43′42″	46	35 865	1297	661
20	21	59°14′00″	56°16′00″	43	34 035	974	1111
21	21	61°00′00″	56°46′12″	40	2713	90	90

ND, no data.
Cell numbers (cells L^{-1}) are mean values for integrated 0–50 m water column based on depth-weighted figures for 5, 10, 25 and 50 m.

undergone changes because of new evidence from molecular studies. Thus, at least some of the taxa identified in our work are probably species groups rather than valid species (e.g., Lundholm and Moestrup, 2002; Lundholm *et al.*, 2002, 2003; Sarno *et al.*, 2005). Despite these shortcomings, we contend that the taxonomic changes involved do not affect significantly biogeographic zonations derived from numerical analyses. The outcome of multivariate techniques are very resilient, and meaningful trends emerge even when the databases used contain significant amounts of noise derived chiefly from the spurious absences of the uncommon species (Romesburg, 1984). Using the smaller ranges of the intervening taxa, rather than the larger ones of the corresponding species groups, would most probably add detail to the pattern rather than modify the overall scheme radically.

RESULTS AND DISCUSSION

Temperature

Sea surface temperature (SST) varied between 24°C at the northern end of the transect and 1°C at the south of the Polar Front (Fig. 3). SSTs were >18°C at stations 1–3, located in the north of the Brazil Current Front in Subtropical waters. At ~38°S, a strong drop in the SST and steepening of the isotherms indicated the presence of a lateral intrusion of colder waters. Temperatures decreased sharply within the BMCZ from 18°C at its northern end to ~7°C at 50°S, where the southern boundary of the BMCZ or Subantarctic Front (Peterson and Stramma, 1991; Saraceno *et al.*, 2004) or Falkland Escarpment Front (cf. Ikeda *et al.*, 1989) was identified. In Subantarctic waters of the Malvinas Current temperatures were homogeneous both horizontally and vertically, ranging between 7 and 5°C. The Polar Front was detected at ~56°S with SSTs decreasing sharply from 5 to 2°C and isotherms deepening to 200 m (Fig. 3 and Brandini *et al.*, 2000).

Nutrients, chlorophyll *a* and phytoplankton densities

Nutrient concentrations along the transect (not shown) increased gradually from north to south, with low values in the upper oligotrophic waters of the Brazil Current
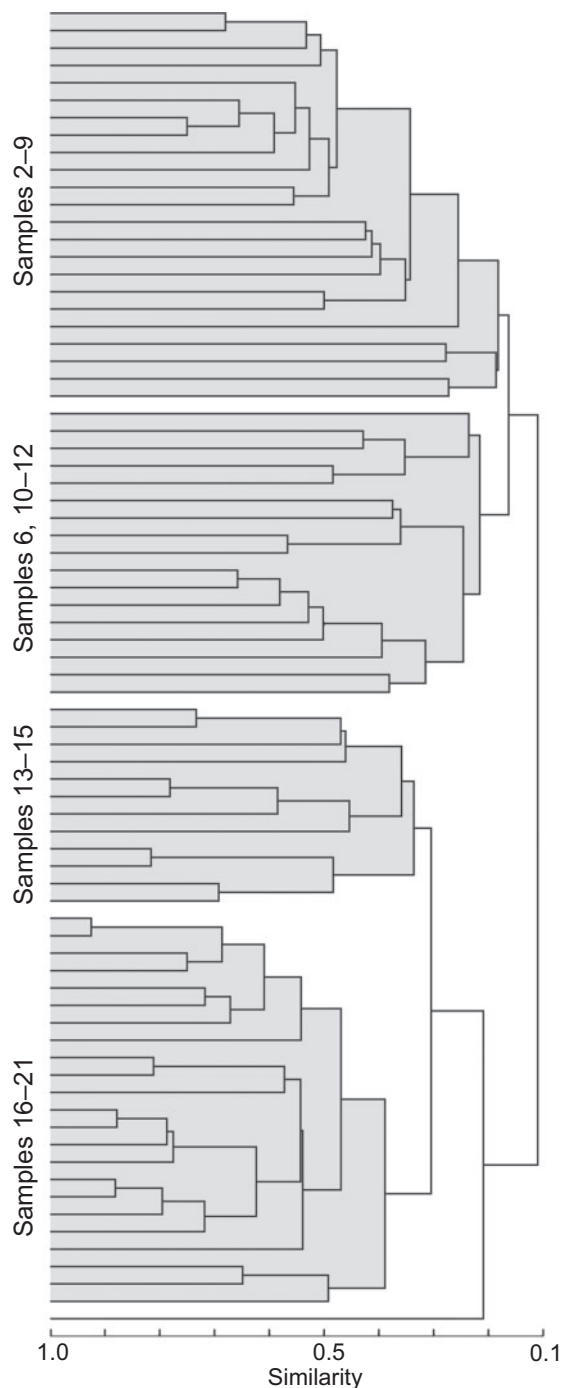
Fig. 2. Similarity between all samples investigated as shown by a cluster analysis based on their diatom inventories [Jaccard's index and unweighted pair group method with arithmetic mean (UPGMA)]. Notice that latitude, rather than depth, clearly structures the database (cf. Fig. 5).

and throughout most of the BMCZ and relatively high ones in the south of 56°S (see Fig. 3 in Brandini *et al.*, 2000).

Chlorophyll *a* concentrations varied between 0.14 and >3 μg L^{-1}; peak values usually occurred in the upper 25 m of the water column, chiefly in the area of the BMCZ (36–46°S) and in the vicinity of the Polar Front (Fig. 3); no major peaks below 50 m were observed (see Fig. 2 in Brandini *et al.*, 2000). This pattern agrees with previous surveys (Sullivan *et al.*, 1993; Podestá, 1997; Marañón *et al.*, 2000). Highest value (3.58 μg L^{-1}) were recorded at station 6 (37°15′); interestingly, the water temperature at this site was noticeably lower than both north and south of it (Fig. 3), and the plankton were dominated by cold water diatoms (*Asteromphalus hyalinus*, *Asteromphalus parvulus* and *Fragilariopsis ritscheri*), dinoflagellates (*Ceratium lineatum*, E. Balech, Buenos Aires, personal communication), tintinnids (Thompson *et al.*, 1999), foraminifers (Boltovskoy *et al.*, 1996), etc. These records suggest that the area was under the influence of laterally advected waters of the colder Malvinas Current (Brandini *et al.*, 2000). High chlorophyll *a* values may also have been enhanced by nutrients flushed out by the Río de la Plata estuary whose offshore influence was indicated by the presence of neritic diatoms (*Thalassiosira decipiens*) and fresh water Desmidiaceae.

With the exception of station 2, where diatoms were very abundant in the 5–25-m layer, phytoplankton were scarce in the northern half of the transect; concentrations of diatoms were ∼5000–10 000 cells L^{-1}, whereas those of the silicoflagellates varied around 100–150 cells L^{-1} (Fig. 3). At 56°S, in the vicinity of the Polar Front, there was a very strong peak in diatom (181 000 cells L^{-1}) and silicoflagellate abundances (10 353 cells L^{-1}), both at station 18 at 5 m (Fig. 3), dropping again at the south of 57°S. As opposed to the silica-bearing cells, dinoflagellate densities were lower at the southern end of the transect than farther north; peak values for this group (24 000 cells L^{-1}) occurred at station 6 (Fig. 3). In all cases, maximum densities were recorded in the uppermost 25 m. On average, diatoms accounted for 73% of all cells recorded (range: 6–96%); with lowest values at stations 6 and 9, where dinoflagellates and unidentified algae were dominant. Silicoflagellates represented on average 5.4% (0–18%) and dinoflagellates 17% (1.4–85%) of the numeric density.

Phytoplankton concentrations assessed in this work were generally lower than those reported by Fernandes and Brandini (Fernandes and Brandini, 1999) for the same area and by Gayoso and Podestá (Gayoso and Podestá, 1996) in the BMCZ, which is not surprising given the remarkable temporal and geographic variability in ambient conditions and plankton concentrations characteristic of the Confluence area (Gayoso and Podestá, 1996; Willson and Rees, 2000; Barlow *et al.*, 2002; Saraceno *et al.*, 2005); however, in all surveys, diatoms were largely dominant.
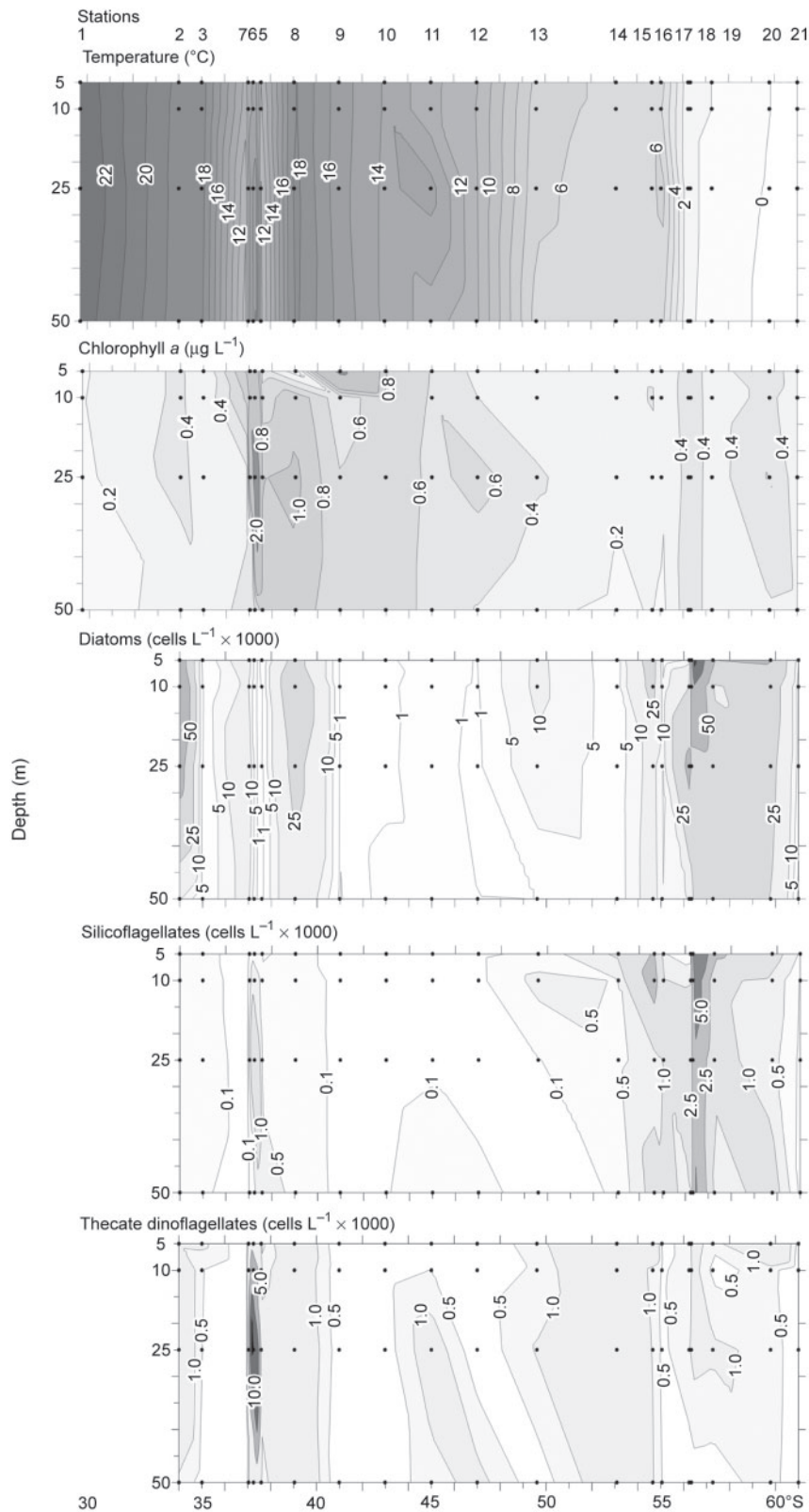
Fig. 3. Vertical profiles of temperature, chlorophyll *a* concentrations and cell numbers along the transect; chlorophyll data from Brandini *et al.* (Brandini *et al.*, 2000).

Peaks in pigment values (3.58 μg L^{-1} at station 6; Fig. 3) were characterized by moderate cell densities dominated by dinoflagellates (<25 000 cells L^{-1}). Conversely, in areas with the highest cell numbers (stations 2 and 18), chlorophyll *a* values were low (<0.6 μg L^{-1}; Fig. 3). Thus, when considering the entire transect, and especially in the north of 50°S, phytoplankton cell densities were uncoupled with concentrations of chlorophyll *a* ($r = -0.003$; $P > 0.1$). This lack of correlation in the north of 50°S may be because of the generally low association between phytoplanktonic biomass and chlorophyll *a* content (Kruskopf and Flynn, 2006). Alternatively, it may indicate that, in addition to the contribution of dinoflagellate pigment at station 6, nanophytoplankton (<10 μm) represented the bulk of primary producers. In the south of 50°S, on the contrary, association between chlorophyll *a* and phytoplankton cell numbers was much higher ($r = 0.54$; $P < 0.01$), probably because the taxonomic composition of the phytoplankton was more homogeneous here than in the northern section, and/or because diatom cells >10 μm hosted most of the chlorophyll in this area. This pattern agrees with previous observations that, within the BMCZ, ubiquitous nanoplanktonic diatoms and flagellates are an important contributor to total chlorophyll, whereas in the north of 35°S picoplankton (<2 μm) dominate phytoplankton biomass (Barlow *et al.*, 2002; Gibb *et al.*, 2000; Marañón *et al.*, 2000).

Species composition and biogeographic patterns

In total, 191 diatom species were identified (Appendix), ranging between 69 (station 2, 10 m) and 9 (station 9 at 5 and 50 m); the overall mean was 31 diatom species per sample. Most of these, however, were represented by very few individuals; on average, for the entire collection six species accounted for 50% of all diatom cells counted (36 species to reach 90% of the individuals). *Fragilariopsis kerguelensis* was by far the most abundant diatom, both in terms of absolute density (average for the entire collection: ~4000 cells L^{-1}) and in terms of relative abundance (mean: 23%). In agreement with its high proportions in sedimentary materials of this area (Crosta *et al.*, 2005), in the south of 47°S, *F. kerguelensis* usually accounted for >30% of the diatoms recorded. In terms of cell numbers, it was followed by *Thalassionema nitzschioides*, *Pseudo-nitzschia lineola*, *Chaetoceros rostratus*, *Leptocylindrus danicus*, etc. However, because throughout the collection densities were poorly correlated with occurrences, taxa most often present in the samples were often different from these: *Azpeitia tabularis* (present in 84% of the samples), *T. nitzschioides* (79%), *Corethron criophilum* (76%),

F. kerguelensis (75%), *Actinocyclus curvatulus* (67%), etc. Thirty-six species were recorded only once.

Four silicoflagellate species were identified in the collection, of which *D. speculum* was the most abundant reaching over 10 000 cells L^{-1} in the vicinity of the Polar Front (Fig. 3). To decrease numerical importance, it was followed by *Dictyocha messanensis*, *Distephanus pulchra* and *Dictyocha mandrai*, none of which exceeded 700 cells L^{-1}. *Distephanus pulchra* was restricted to the northern sector of the area surveyed (north of 40°S), whereas the other three had a more cosmopolitan distribution, ranging from 30 to 54–55°S (*D. messanensis*, *D. mandrai*) and to 61°S (*D. speculum*). These distributional patterns are in general agreement with the ecological preferences of these species reported for the South Atlantic (Eynaud *et al.*, 1999) and for other areas of the World Ocean (Poelchau, 1976; Takahashi, 1987; Takahashi and Blackwelder, 1992). To establish biogeographic diatom-based zones along the transect, we performed a cluster analysis using depth-integrated diatom data (Fig. 5). The first-order change in species composition was located between stations 12 and 13, at ~48°S. The northern area was further divided into three subzones: Subtropical (station 1), Transition North (stations 2–5 and 7–9) and Transition South (stations 6 and 10–12). The southern area showed two groups of stations: Subantarctic (stations 13–15) and Antarctic (stations 16–21).

To define diatom assemblages characteristic of each one of these geographic areas, we selected species according to the following criteria: (i) The relative abundance of the species should exceed 0.5% of all diatoms in at least one sample; (ii) the mean relative abundance of the species in the samples included in a particular geographical group should be >2 times higher than that in the entire collection; (iii) the species should be present in >80% of the samples of the geographical group it characterizes and (iv) the species should be present in <25% of the samples of any other group. These criteria were fulfilled by 42 diatom taxa. In addition to these, we also selected a set of nine diatoms clearly associated with the northern warm waters, stations 1–9 (mean relative abundance at stations 1–9 >1.4 times higher than at stations 13–21; present in >75% of stations 1–9 and <15% of stations 13–21) and a set of seven diatoms associated with the cold southern waters (stations 13–21, criteria opposed to above). Finally, we also identified a set of nine cosmopolitan or widely distributed diatoms composed of those taxa that were present in >30% of the samples of every geographical group defined (with the exception of the northernmost sample group which consisted of a single sample).

This procedure allowed pinpointing a total of 67 relatively abundant diatom species with reasonably

well-defined distributional ranges (Fig. 4). These 67 diatoms accounted for 72% of all the specimens identified. For the remaining 124 taxa, latitudinal distribution and abundance values were not consistent enough to derive their biogeographic affinities.

The results of these analyses are described as follows:

Station 1 (Subtropical)
A total of 81 diatom species were identified in this area. Twenty of them were restricted to station 1, but only two species were relatively abundant (>1% of the assemblage): *Chaetoceros danicus* and *Mastogloia rostrata*. The remaining 18 diatoms recorded at station 1 scarcely represented 3.6% of the cells identified in this sample. In addition to the above two, this area was characterized by 14 species most of which peaked at station 1 but were also present farther south, in the Northern Transitional area (stations 2–9). None of them were recorded in the south of 41°S (Fig. 4). These 16 characteristic species were generally represented by low numbers of individuals (0.2–4%) of the entire assemblage at station 1.

Stations 2–5, 7–9 (Northern Transitional)
In total, 119 diatom species were recorded in these samples, of which 20 were not found elsewhere; these restricted species were invariably of low abundance (mean proportion of the assemblages in these samples: 0.1%). Thirteen diatoms were found to adequately characterize this area; among these, *Chaetoceros contortus*, *Pseudo-nitzschia multiseries* and *C. rostratus* were particularly abundant (Fig. 4). With the exception of *Pseudo-nitzschia fraudulenta*, whose range extended to 55°S, these diatoms were practically absent in the south of 41°S.

Stations 6, 10–12 (Southern Transitional)
Although the area encompassed by these samples yielded 75 species, only one (*Coscinodiscus granii*) was restricted to it, and also a single diatom was found to characterize these samples (*Detonula pumila*) (Fig. 4).

Stations 13–15 (Subantarctic)
Only two species were restricted to the Subantarctic area (*Stephanopyxis turris* and *Thalassiosira allenii*) of 61 recorded in samples 13–15. No characteristic diatoms were identified according to the criteria defined above. *Eucampia antarctica* was particularly abundant in these samples (up to 14%), but it was also present in sizeable proportions in most Antarctic samples as well.

Station 16–21 (Antarctic)
Seventy-five diatoms were recorded in the Antarctic area; 20 of which were not found in the north of 53°S. Characteristic taxa included 12 species, mostly restricted to the Antarctic and Subantarctic, but some with sporadic occurrences as far north as 36°S (Fig. 4).

Several species were not unequivocally associated with a single group of stations defined by the clustering technique but were clearly more abundant at either the northern or the southern part of the transect. Nine diatoms were consistently present in considerable numbers in samples 1–5 and 7–9 and absent from Subantarctic and Antarctic waters (labeled 'warm water' in Fig. 4), and seven other species depicted the opposite trend (labeled 'cold water' in Fig. 4).

Finally, nine more diatoms were present throughout the transect at 80% of the stations; several of these were among the most abundant species in the collection (e.g. *T. nitzschioides*, *Nitzschia sicula*, etc.) (labeled 'Cosmopolitan' in Fig. 4).

In general terms, the ecological settings of the species recorded—as derived from their occurrence in our samples—agree well with previous information (Venrick, 1971; Simonsen, 1974; Hasle, 1976; Lange, 1985; Hasle and Syvertsen, 1996). Of the 63 species ascribed to warm and temperate waters by previous authors (Appendix), in our materials, 57 were either restricted to or very clearly peaked at stations of the northern half of the transect. *Nitzschia bicapitata* group and *N. sicula* peaked in warm and temperate waters as well but ranged as far south as 54–59°S, for which reason they were tentatively included in the cosmopolitan group (Fig. 4). The remaining four species (*Chaetoceros peruvianus*, *Lauderia annulata*, *S. turris* and *T. allenii*) in our materials had high or maximum relative abundances in Subantarctic or Antarctic waters; however, all four were very scarce in our samples (none exceeded 0.4% of the overall diatom assemblage at any given station), for which reason their distribution patterns cannot be adequately interpreted.

Similarly, very few of the 54 diatoms ascribed to the cold waters by previous authors had a conspicuous presence outside of the Subantarctic and Antarctic areas in our materials. The only notable exception is that of *A. tabularis,* which showed peaks in abundance around the Subantarctic Front but was rather abundant throughout the entire transect (Fig. 4). Hasle and Syvertsen (Hasle and Syvertsen, 1996) considered *A. tabularis* as a Subantarctic species; yet, its pattern in sediments of the South Atlantic indicates that it is cold tolerant but clearly associated with Tropical–Subtropical waters (Romero *et al.*, 2005).

For the 51 taxa regarded as cosmopolitan by previous authors, agreement with our results was somewhat lower. In our materials, *Actinocyclus octonarius*, *Chaetoceros affinis*, *Chaetoceros concavicornis*, *Coscinodiscus centralis*, *Coscinodiscus marginatus*, *Coscinodiscus radiatus*, *P. fraudulenta*, *P. multiseries*, *Pseudo-nitzschia pungens* and *Skeletonema costatum s.l.* were clearly associated with the northernmost warm waters
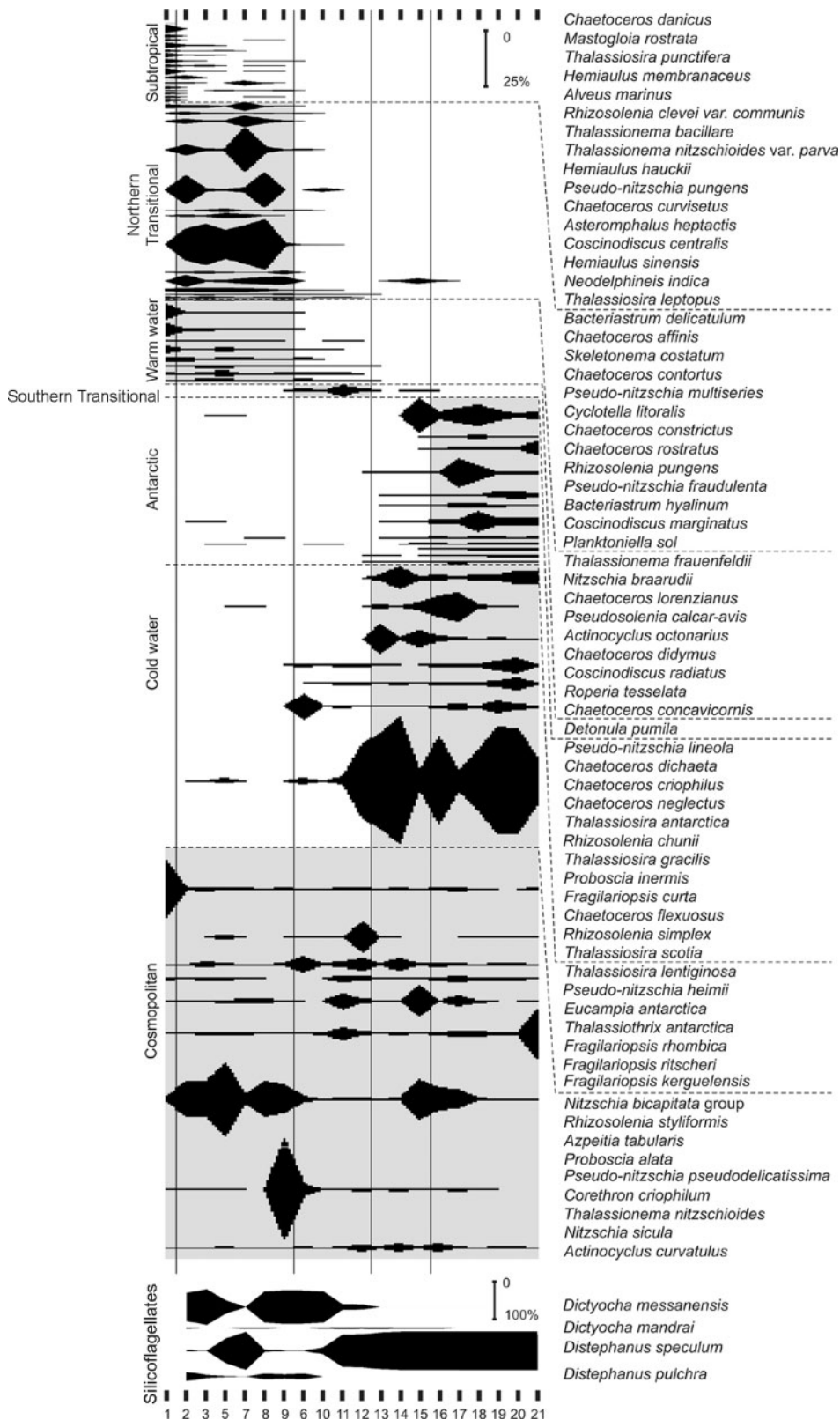
Fig. 4. Distribution of a selected group of diatom species and of the four silicoflagellates recorded in the area investigated. Notice that station sequence is modified to illustrate diatom assemblage zones.

(Fig. 4), whereas *P. lineola* was noticeably more abundant at the southern end of the transect. *Detonula pumila*, also cosmopolitan according to previous information (Hasle, 1976; Hasle and Syvertsen, 1996), was in our materials practically restricted to the Southern Transitional area. These disagreements are most probably because literature-based information on the ecological affinities of these species was often based on general review works (Hasle, 1976; Priddle and Fryxell, 1985; Medlin and Priddle, 1990; Hasle and Syvertsen, 1996) or on surveys from other areas (Simonsen, 1974), where different ecological settings may have led to a different interpretation of the environmental signal conveyed by their presence. Disagreements with the data of Romero and Hensen (Romero and Hensen, 2002) and Romero *et al.* (Romero *et al.*, 2005), in turn, respond to the blurring and distortion of the distribution pattern in sediments (see below).

The above-described biogeographic areas based on diatom assemblages reflect latitudinal changes in temperature and nutrients, as well as the location of fronts and water masses (Fig. 1). The assemblage recorded at station 1 (~30°S) is dominated by taxa typical of the Subtropical oligotrophic waters of the Brazil Current. Stations 2–12 are also clearly dominated by warm water diatoms, but the presence of cold water and cosmopolitan forms is here more conspicuous, especially in the southern part of the area (stations 10–12, Southern Transitional). As shown in Fig. 5, these stations are located in the BMCZ—Transition Zone or Subtropical–Subantarctic Convergence Zone (cf. Boltovskoy, 1970)—a large area of mixture of warm and cold waters with isolated cells and tongues of pure Subantarctic and Subtropical input (Boltovskoy, 1970; Boltovskoy *et al.*, 1999). Our data indicate that, at the time of the cruise, the transition from Subtropical to Subantarctic conditions was relatively smooth. However, sharp discontinuities in this trend were also present, as indicated by the dominance of cold water diatoms at station 6 (Figs 4 and 5), most probably because of lateral advection of colder Malvinas waters offshore (Fig. 3 and Brandini *et al.*, 2000). A similar cold water signal was also detected at this site in other surveys of the same collection, based on planktonic foraminifers (Boltovskoy *et al.*, 1996) and on tintinnids (Thompson, 2001). The southern limit of the Transition (BMCZ) was defined by the Subantarctic Front, located between our sampling stations 12 and 13 (Fig. 5). This front was characterized by a sharp decrease in temperature, a rise in the concentration of nutrients (Brandini *et al.*, 2000) and a strong species change whereby cold water taxa became clearly dominant in the assemblage (Fig. 5, right-hand panel). Interestingly, this area did not seem to host

characteristic species; most of the diatoms present in Subantarctic waters were also abundant in farther south or dwelled throughout the transect investigated (Fig. 4). Finally, in south of the Polar Front, a distinct Antarctic assemblage occurred; most of these species clearly peaked at the southernmost end but were also present, albeit usually in small proportions, in Subantarctic and Transitional waters (Fig. 4).

Comparison of the biogeographic zonation of the area based on our diatom data with those based on planktonic foraminifers (Boltovskoy *et al.*, 1996) and tintinnids (Thompson, 2001) recovered from the same samples shows very good overall agreement. All three groups indicate a sharp break between stations 1 and 2, and the Transitional–Subantarctic and Subantarctic–Antarctic boundaries are also either coincident or very close by (Fig. 6). On the contrary, ecological affinities of the species whose distributional ranges define the boundaries in question vary strongly between groups. Differences are particularly noticeable with the foraminifers: although diatom assemblages show a strong dominance of warm water cells from 30 to ~43°S (station 10, Fig. 5), warm water foraminifers drop to near-zero values around 37°S (Boltovskoy *et al.*, 1996). This difference is partly because foraminiferal assemblages are depth stratified, with deeper strata hosting higher proportions of cold water species than the surficial ones (Boltovskoy *et al.*, 1996). Alternatively, the higher lifespans of foraminifers, around 2–4 weeks (Spindler *et al.*, 1979; Hemleben *et al.*, 1989), as compared with those of the diatoms and the tintinnids, a few hours to 1–2 days (Guillard and Kilham, 1977; Burkill, 1982; Heinbokel, 1987) could facilitate extended expatriation through longer survival. This assumption is supported by the fact that, as mentioned above, cold water foraminifers have extended northward ranges at depth; it is conceivable that these specimens are expatriates that have already reached their sterile range but are still present in the water column because of their long lifespans.

Specific diversity

Diatom diversity (as measured by the Shannon–Wiener index) and number of species were not associated with depth (Fig. 7) but rather followed a latitudinal pattern. The latitudinal variation in specific diversity depicted three more-or-less well-defined peaks: at 30°S (station 2), at 46°S (station 11) and at 56°S (stations 17 and 18) (Fig. 7, upper panel). Comparison of this pattern with the distribution of the total number of species recorded at each station shows that although the first diversity peak is clearly associated with a higher number of taxa at the northernmost end of the transect, increases in the
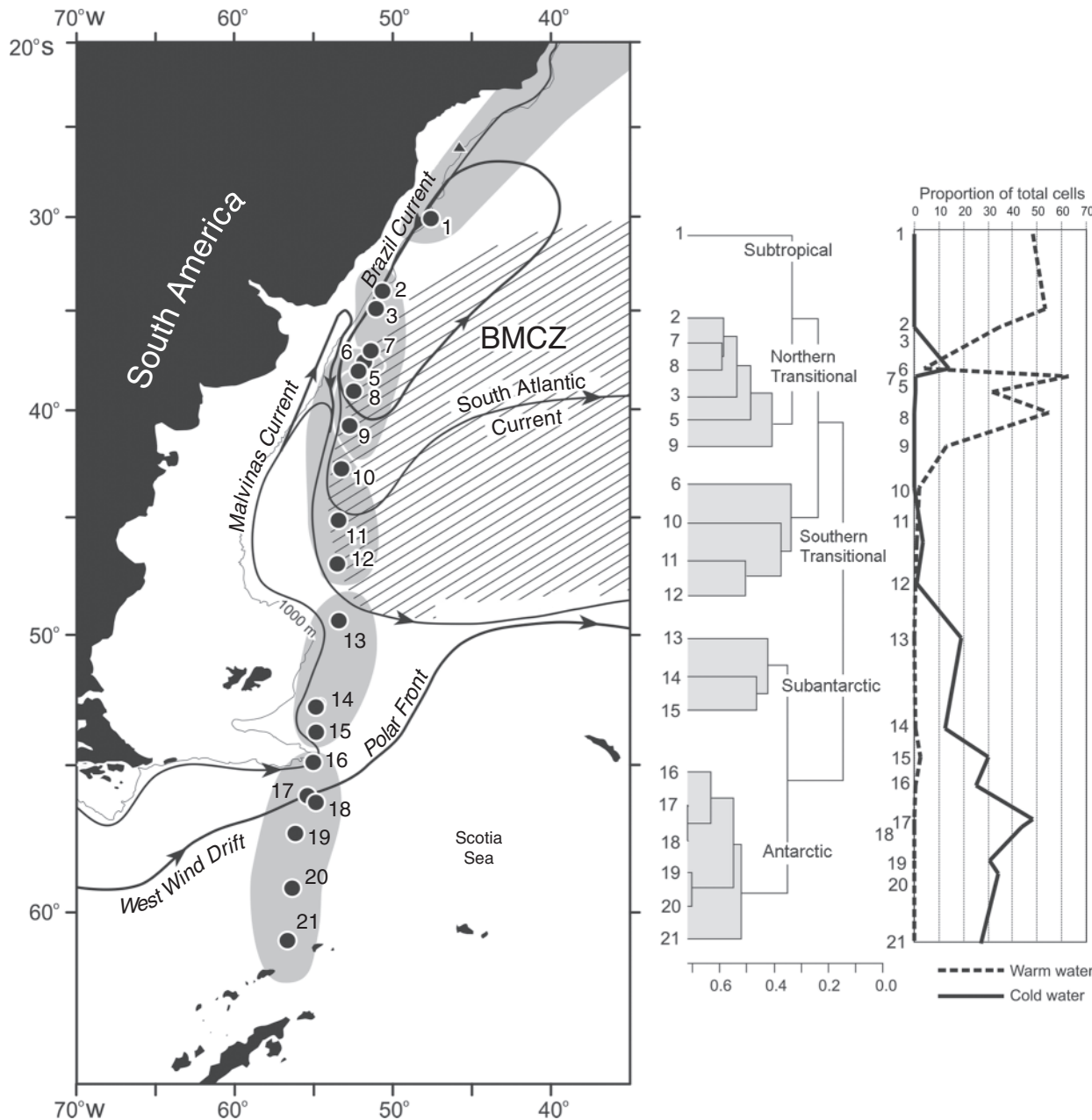
Fig. 5. Geographic zonation of the area based on the diatom depth-integrated data for the sites surveyed [Jaccard's index and unweighted pair group method with arithmetic mean (UPGMA)]. Curves on right-hand side of the graph show proportions of warm water (Subtropical, Northern Transitional and warm water in Fig. 4) and cold water (Antarctic and cold water in Fig. 4) individuals at each site.

number of species at the other two are very minor (Fig. 7, lower panel). These slight increases in species number combined with an increase in the evenness contributed to boosting diversity index values.

The north–south trend in diatom species numbers does not agree with the widely acknowledged pattern of more or less gradually decreasing species richness figures toward higher latitudes (Ricklefs and Schluter, 1993; Briggs, 1996; Hayek and Buzas, 1997; Thompson, 2004).
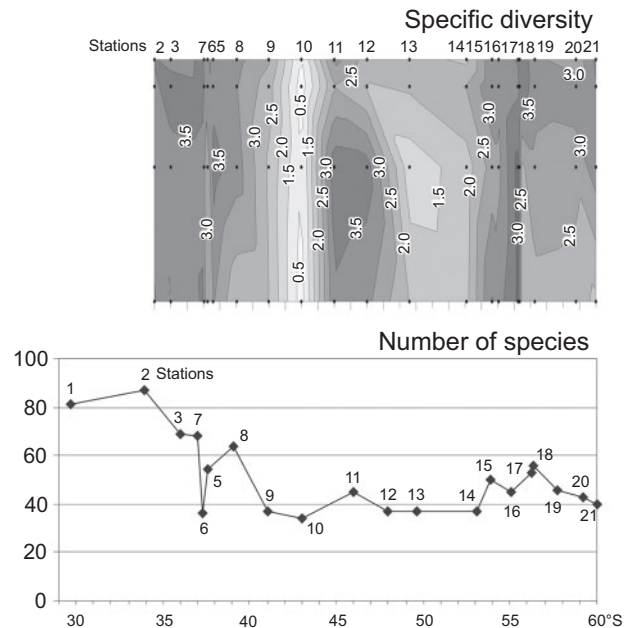
Furthermore, diatom values also differ from data for the zooplankton of the same area. On the basis of compiled data for 16 zooplankton groups (1432 species in total), Boltovskoy *et al.* (Boltovskoy *et al.*, 2003) calculated the numbers of species inhabiting the different biogeographic areas of the South Atlantic. For the zooplankton, species numbers drop gradually from the Central–Subtropical area to the Antarctic, where inventories are ~40% of those in the subtropics (Fig. 8). For the diatoms, on the

Fig. 6. Comparison of the biogeographic zonation of the area based on diatom data (this work) with those based on planktonic foraminifers (Boltovskoy *et al.*, 1996) and tintinnids (Thompson, 2001).

Fig. 7. Diatom specific diversity, as measured by the Shannon–Wiener index, log base 2 (Shannon and Weaver, 1949) and numbers of diatom species per station (all depths pooled) along the transect surveyed.
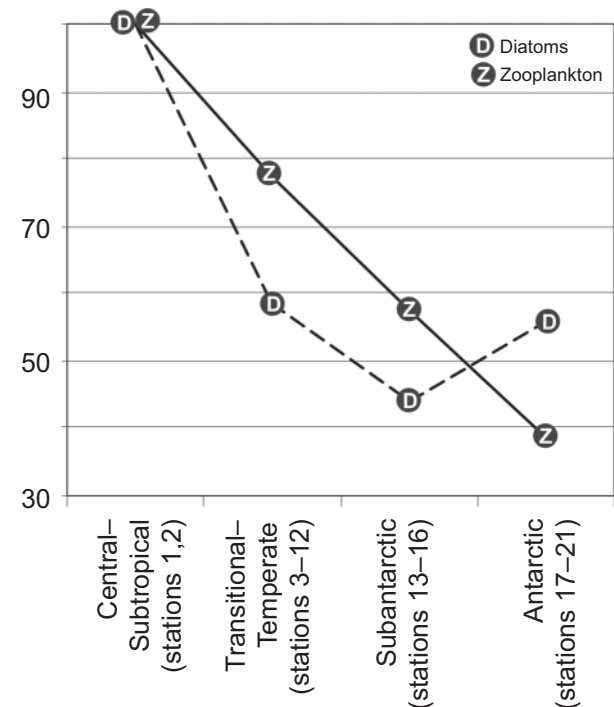
Fig. 8. Numbers of zooplankton species present in the different biogeographic areas of the South Atlantic, based on data from Boltovskoy *et al.* (Boltovskoy *et al.*, 1999), compared with similar figures for the diatoms recorded in the present survey. All figures are in relative values.

contrary, inventories in the south of the subtropics remain more or less stable and are even somewhat higher in the Antarctic than in the Subantarctic (Fig. 8).

These differences have interesting implications for biogeographic and paleobiogeographic or paleoecologic purposes. Phytoplanktonic fossilizable remains have often been considered better current and water mass indicators and paleoindicators because of their inability to survive for extended periods away from the photic layer (thus minimizing transport by subsurface currents), their higher abundances and because of their shorter lifespans (thus decreasing sterile expatriation phenomena) (e.g. Boltovskoy, 1994). Whereas highly diversified and very abundant diatoms seem to be less sensitive to environmental changes in traits such as diversity and number of species,

thus reducing the potential usefulness of these attributes. Analysis of these diversity attributes from repeated sampling along similar transects in several years may reveal if the observed trends are persistent in that region.

Diatom assemblages in the water column versus in the surface sediments

Romero and Hensen (Romero and Hensen, 2002) investigated the diatom assemblages retrieved in 60 surface sediment samples, 47 of which are located almost directly under our stations 1–13 (Fig. 9). This allowed a close comparison of water column versus sedimentary compositional data aimed at checking whether for the diatoms, in this area, patterns in the sediments reflect those in the overlying plankton. Romero and Hensen (Romero and Hensen, 2002) identified a total of 194 diatom species, which compares very favorably with our inventory of 191 taxa. Also, the overall numbers of diatoms characteristic of warm waters, cold waters and neritic environments were very similar in the two collections. In addition, the occurrence of freshwater diatoms in both collections was
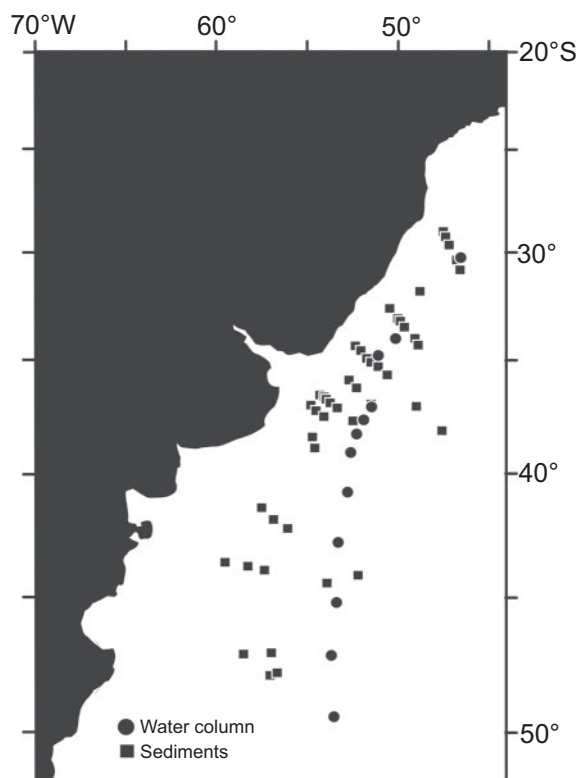
Fig. 9. Location of the water column samples used in this survey and the sedimentary materials where diatoms were analyzed by Romero and Hensen (Romero and Hensen, 2002). Figure does not include sedimentary samples located too far east or north from the water column transect and therefore not used for comparative analyses.

mainly restricted to the area of influence of the Rio de la Plata outflow.

However, on a species-to-species basis, of the 209 diatoms recorded in the sediments or the water column (considering the overlapping area only, Fig. 9), only 79 (38%) were present in both collections, whereas the remaining 121 were absent from either collection (Fig. 10).

Comparison of the dominant taxa also points to very significant differences. Table II shows that 18 diatoms are necessary to account for the 10 most abundant forms in both databases. With the exception of *T. nitzschioides*, which ranked second both in the plankton and in the sediments, the remaining nine taxa varied widely in relative abundance and in rank (Table II). A similar disparity is observed when comparing the mean proportions of the taxa recorded in both collections (Fig. 11).

Although the above differences point at strong dissimilarities between the two data sets, they do not show that the temperature signal conveyed by the assemblage on the seafloor differs from the one in the water column. To assess this difference, we calculated the proportions of cells belonging to warm water and cold water species along the transect occupied. Because the locations of plankton and sediment samples are not identical, within each collection, we pooled the data in 5° latitude bins (Fig. 12). In the sediments between 36 and 41°S, the cold water signal is over twice as strong as the warm water one. In contrast, in the plankton, cold water diatoms are most abundant only in the south of 46°S (Fig. 5), whereas in the north of 41°S, the warm water signal is >6 and up to 4000 times stronger than the cold water one (Fig. 12). Although the two most abundant Antarctic diatoms in the sediments (*F. kerguelensis* and *Thalassiosira lentiginosa*) account for over half of all diatoms as far north as 35°S (Fig. 13), in the water column, they are only important in the south of 47°S.

Despite the temporal disparity of biological and sedimentary collections, our results indicate that sedimentary assemblages are a very poor proxy of diatom composition in the photic layer and that, along the entire transect, the sedimentary signal is very strongly biased toward colder waters. Romero and Hensen (Romero and Hensen, 2002) noticed this mismatch and stated that the diatom imprint in core top sediments mainly represents an Antarctic-originated signal, whereas *in situ* produced specimens supply a minor portion of the siliceous remains. This Antarctic signal can be traced as far north as 27°S, with *F. kerguelensis*, *T. lentiginosa* and the resting stage of *Thalassiosira antarctica* as indicative of the intensity of the equatorward displacement of Antarctic source water masses (Romero and Hensen, 2002).

Comparison of the planktonic and the sedimentary assemblages indicates that, as suggested by Romero and Hensen (Romero and Hensen, 2002), selective dissolution
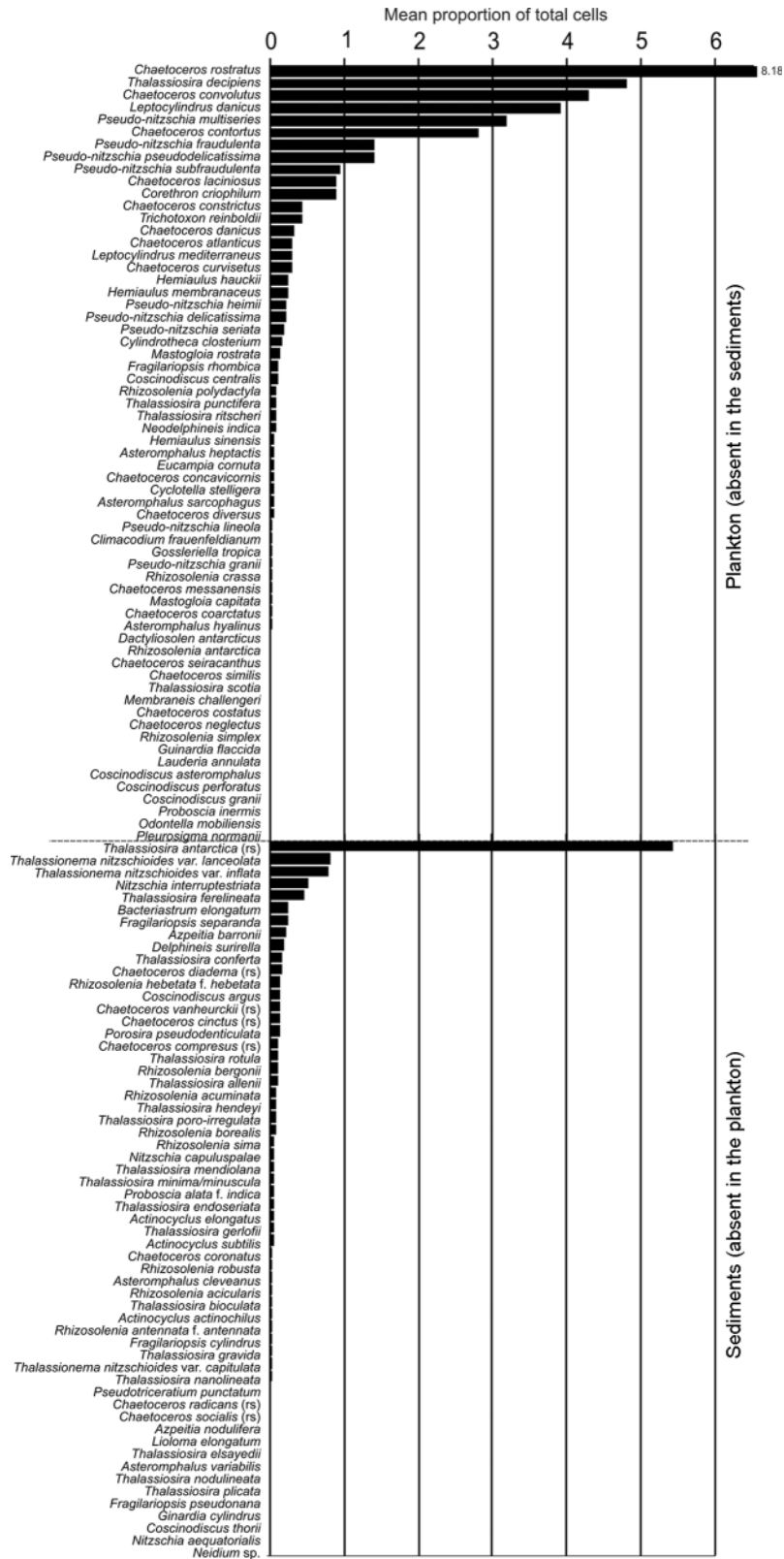
Fig. 10. Mean proportions in the water column samples (this work) of the species absent in the sediments (Romero and Hensen, 2002) and vice versa (rs, resting spores).

Table II: Comparison of the overall percentage contributions and ranks of the 10 most abundant diatom species in the water column (this study) and the surface sediments (Romero and Hensen, 2002)

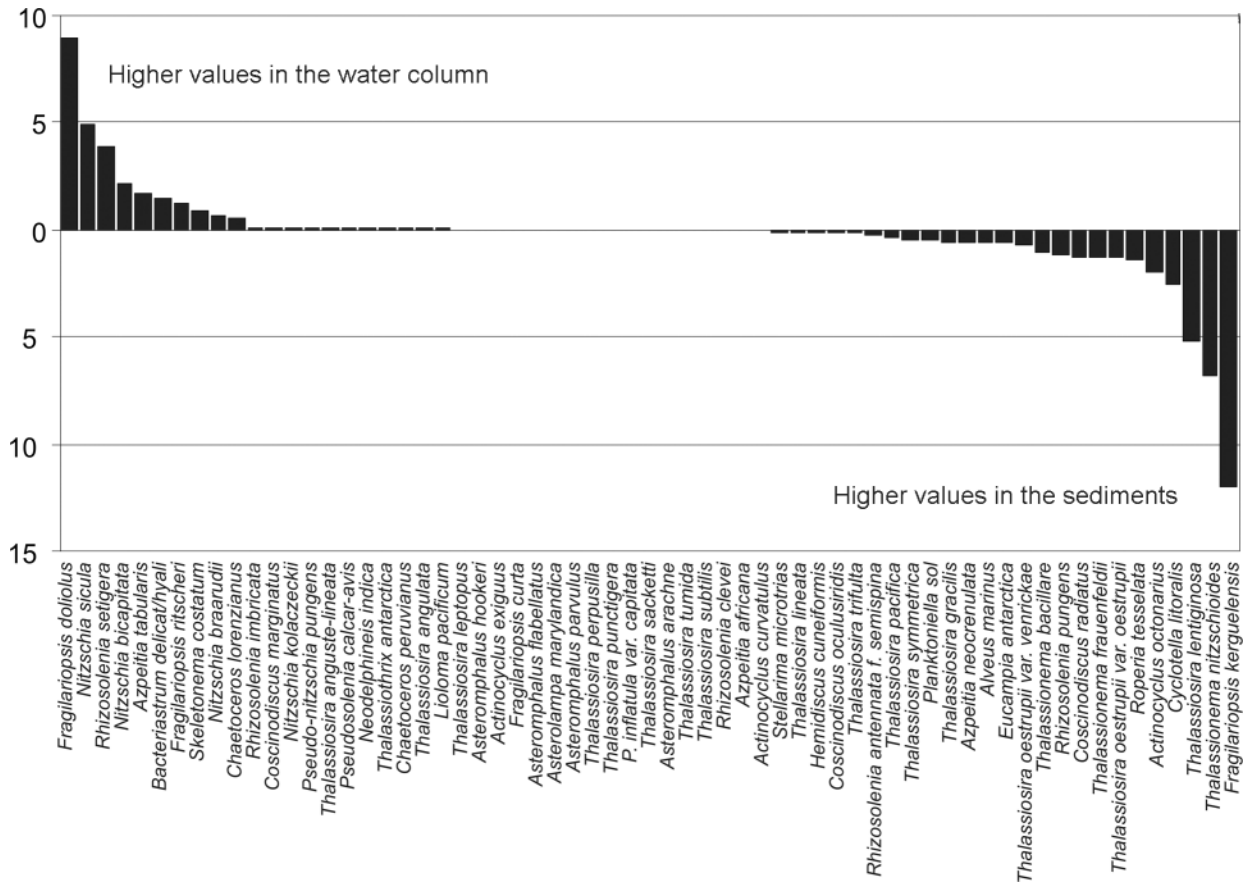|	Water column (%)	Sediment (%)	Water column (rank)	Sediment (rank)
Fragilariopsis doliolus	10.4	1.5	1	13
Thalassionema nitzschioides	9.9	16.7	2	2
Fragilariopsis kerguelensis	8.5	20.6	3	1
Chaetoceros rostratus	8.2	NR	4	–
Nitzschia sicula	5	0.01	5	143
Thalassiosira decipiens	4.8	NR	6	–
Chaetoceros convolutus	4.3	NR	7	–
Rhizosolenia setigera	4	0.1	8	76
Leptocylindrus danicus	3.9	NR	9	–
Pseudo-nitzschia multiseries	3.2	NR	10	–
Azpeitia tabularis	1.8	3.1	14	6
Actinocyclus octonarius	0.6	2.6	30	8
Roperia tesselata	0.6	2	31	10
Cyclotella litoralis	0.24	2.8	46	7
Thalassiosira lentiginosa	0.21	5.5	52	3
Paralia sulcata	0.01	3.1	121	5
Thalassiosira antarctica	NR	5.3	–	4
Chaetoceros sp.	–	2.5	–	9

NR, not recorded.

plays an important role in these disagreements. Antarctic diatoms (e.g. *F. kerguelensis*, *T. lentiginosa* and several others) are known to have heavily silicified frustules and high preservation potential (Crosta *et al.*, 2005), which contributes to enhance their proportions in mixed warm water and cold water sedimentary assemblages. Seasonal variability may also play a role in these mismatching patterns insofar as much of the area transected is known to undergo important seasonal shifts, especially between 30 and 35°S (Boltovskoy, 1970). Equatorward displacement of settling frustules by northbound subsurface and deep currents has been proposed by several authors (Burckle and Stanton, 1975; Burckle and Cooke, 1983; Jones and Johnson, 1984) as an important distorting effect in the study area as well. However, in the Southwestern Atlantic southward-moving subsurface currents are probably as important as the northward ones (Reid *et al.*, 1977). Thus, the resulting displacement of a random settling particle may have an important southward component as well. We suggest that the predominantly northward displacement reflected in the plankton versus sediments mismatching pattern is largely because of a complex interaction where biological factors play an important role. Planktonic organisms carried equatorward by surface or subsurface currents can sink in the water column in search of a colder stratum where they can extend their survival. Subsequent displacements will force the organism to

continue descending (if equatorward expatriation persists), allow it to return to the surface (if it is reversed) or perish and sediment (if its tolerance threshold is exceeded). Autotrophic organisms, which depend on light for extended survival and have often a more limited capacity to maintain a given depth range, can be subject to the same phenomenon through grazing by zooplankton. As opposed to expatriation toward the equator, poleward advection of plankters should not result in a descent in the water column (as it would not contribute to extended survival), thus minimizing the occurrence of warm-water remains outside of their living ranges (Boltovskoy, 1988, 1994).

Although for most groups of pelagic organisms, distributional studies are based on samples of their living assemblages, for some provided with hard, fossilizable skeletal structures, including the diatoms, their remains in the sediments are often the main source of distributional information. As a matter of fact, for some groups, most of the information available to date, in particular on their specific distribution patterns, is based on sedimentary materials, whereas plankton-based studies are very scarce and fragmentary. This is partially because of the very significant input of geologically oriented investigations in this field but also largely because comprehensive information on the distribution of these organisms is more readily, easily and economically obtained from bottom sediments than from plankton collections. Indeed, sedimentary

Fig. 11. Differences in the mean relative abundance of the diatom species in the water column (this work) and in the sediments (Romero and Hensen, 2002) of the Southwestern Atlantic Ocean. Graph includes species recorded in both collections only.
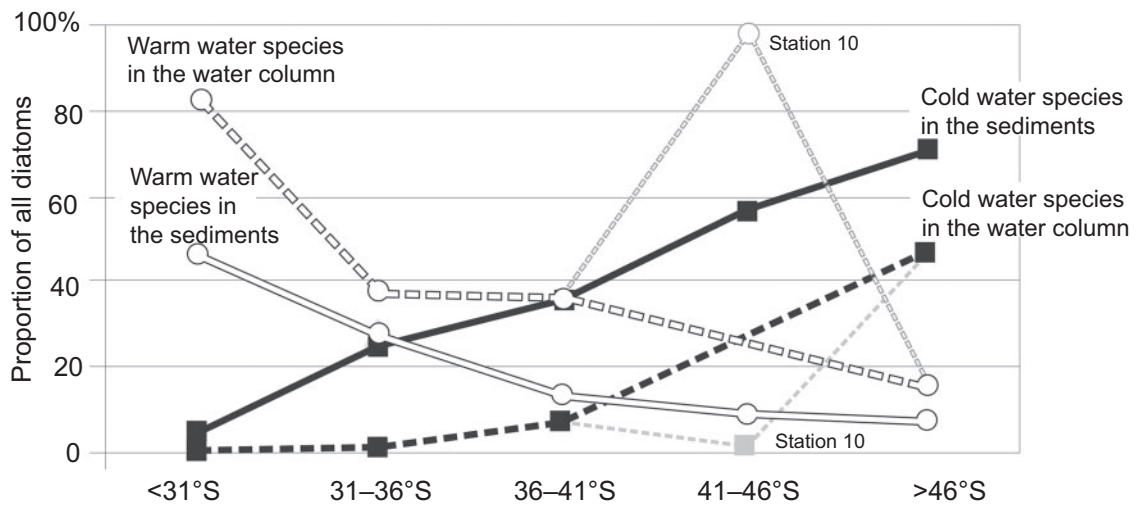
Fig. 12. Proportions of warm water and cold water diatoms at different latitudinal offsets along the transect surveyed in the 0–50 m layer water column (our data) and in the surface sediments, data from Romero and Hensen (Romero and Hensen, 2002). Station 10 (our material) was set apart by the fact that it hosted unexpectedly large proportions of warm water diatoms, most probably because it sampled a Subtropical eddy.
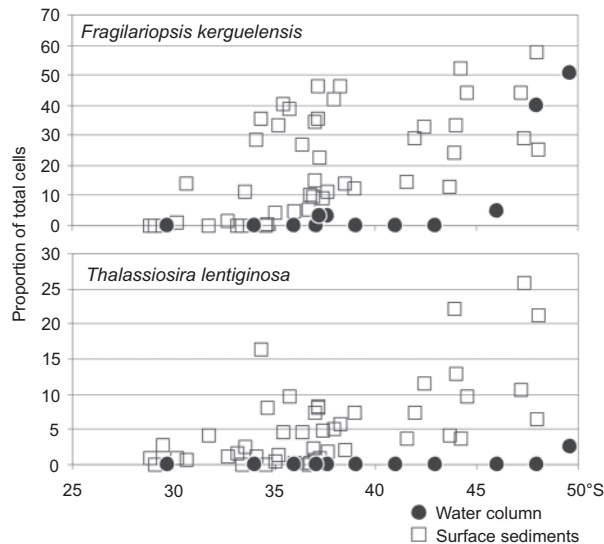
Fig. 13. Comparison of the proportions of the two most abundant cold water diatoms in bottom sediment samples, data from Romero and Hensen (Romero and Hensen, 2002) and in the water column (this work).

materials have some advantages over water column samples, including larger sample sizes, better availability and the provision of time-integrated data (Boltovskoy, 1994), which contributed to their wide use in biogeographic surveys. Furthermore, sedimentary materials are widely used in paleobiogeographic and paleoclimatic investigations; much of our current knowledge of glacial to interglacial climatic changes in the open ocean are based on the interpretation of differences between recent versus last glacial maximum distribution patterns of coccolithophorids, diatoms, foraminifers and radiolarians (e.g. CLIMAP Project Members, 1976). Use of surface sediment materials (rather than water column data) is validated by the implicit or explicit assumption that patterns in the sediments, while not identical to those in the overlying waters, are a very good proxy of the latter. However, this assumption has seldom been explicitly addressed and demonstrated (Boltovskoy, 1994). Our results show that, in the Southwestern Atlantic Ocean, diatom distribution patterns in the sediments differ very significantly from those in the plankton, and the distortions involved are similar to those recorded for the foraminifers in the same area (Boltovskoy *et al.*, 1996), and for other planktonic organisms elsewhere (Boltovskoy, 1994).

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APPENDIX 1

Species list and relative abundance data. First set of square brackets: mean relative contribution of the species to the diatom assemblage at the stations surveyed; second

set of square brackets: proportion of stations where the species was recorded. Code letters give general ecological preferences of the species as derived from the literature sources indicated. C, cold; Co, cosmopolitan; N, neritic; O, oceanic; T, temperate; W, warm; SA, subantarctic; F, freshwater. Literature sources: A, Hasle and Syvertsen (1996); B, Lange (1985); C, Simonsen (1974); D, Hustedt, (1958); E, Hendey (1964); F, Medlin and Priddle (1990); G, Priddle and Fryxell (1985); H, Rines (1999); I, Romero *et al.* (2005); J, Romero and Hensen (2002).

Achnantes sp. [0.011] [25]

Achnanthes brevipes Agardh [0.069] [30] N Co (B)

Actinocyclus actinochilus (Ehrenberg) Simonsen [0.043] [20] O C (A,B)

Actinocyclus cholnoky (Grunow) Van Landingham [0.006] [5] C (6)

Actinocyclus curvatulus Janisch [0.897] [95] N Co (A,B)

Actinocyclus exiguus Fryxell and Semina [0.022] [10] C (A)

Actinocyclus octonarius Ehrenberg [0.360] [45] N Co (A,B)

Actinocyclus spiritus Watkins [0.059] [5] C (A)

Actinoptychus senarius (Ehrenberg) Ehrenberg [0.007] [25] N Co (B)

Actinoptychus vulgaris Schumann [0.007] [5] N T (B)

Alveus marinus (Grunow) Kaczmarska and Fryxell [0.069] [15] W (A)

Amphora sp. [0.015] [5] F

Asterolampa marylandica Ehrenberg [0.001] [5] O W (A,C)

Asteromphalus arachne Brébisson [0.005] [10] O W (C)

Asteromphalus flabellatus (Brébisson) Greville [0.001] [5] W (C)

Asteromphalus heptactis (Brébisson) Ralfs [0.040] [5] Co (C)

Asteromphalus hookeri Ehrenberg [0.344] [45] N/O C (B,D)

Asteromphalus hyalinus Karsten [0.245] [50] N/O C (B,D)

Asteromphalus parvulus Karsten [0.208] [45] N/O C (B,D)

Asteromphalus sarcophagus Wallich [0.035] [15] W (C)

Aulacoseira granulata Thwaites [0.033] [10] F

Azpeitia africana (Janisch ex Schmidt) Fryxell and Watkins [0.014] [10] W (A)

Azpeitia neocrenulata (Van Landingham) Fryxell and Watkins [0.005] [5] W (A)

Azpeitia tabularis (Grunow) Fryxell and Sims [1.620] [100] O C, SA (A,B)

Bacteriastrum comosum Pavillard [0.009] [10] W (A)

Bacteriastrum delicatulum Cleve [0.442] [30] W/T (A)

Bacteriastrum hyalinum Lauder [0.466] [40] N/O W/T (A,B)

Banquisia belgicae (Van Heurck) Paddock [0.079] [15] C (A)

Cerataulina pelagica (Cleve) Hendey [0.074] [15] N Co (A,B)

Chaetoceros affinis Lauder [0.129] [40] N Co (A,B)

Chaetoceros atlanticus Cleve [0.732] [50] O Co (A,B)

Chaetoceros bulbosum (Ehrenberg) Heiden [0.024] [15] C (G)

Chaetoceros castracanei Karsten [0.105] [15] C (A)

Chaetoceros coarctatus Lauder [0.010] [5] W (A)

Chaetoceros contortus Schütt [1.680] [40] Co (H)

Chaetoceros concavicornis Manguin [0.037] [45] O Co (A,B)

Chaetoceros constrictus Gran [0.263] [25] N T (A,B)

Chaetoceros convolutus Castracane [2.568] [15] O T (A,B)

Chaetoceros costatus Pavillard [0.002] [5] W/T (A)

Chaetoceros criophilus Castracane [0.463] [30] C (A)

Chaetoceros curvisetus Cleve [0.179] [20] N W/ T (A,B)

Chaetoceros danicus Cleve [0.201] [5] N T Co? (A,B)

Chaetoceros debilis Cleve [0.204] [10] N Co (A)

Chaetoceros decipiens Cleve [1.597] [60] N/O Co (A,C)

Chaetoceros dichaeta Ehrenberg [0.121] [25] C (A)

Chaetoceros didymus Ehrenberg [0.366] [35] N W/T (A,B)

Chaetoceros diversus Cleve [0.030] [20] W (A)

Chaetoceros flexuosus Mangin [0.079] [30] C (A)

Chaetoceros laciniosus Schütt [0.537] [30] T (A)

Chaetoceros lorenzianus Grunow [0.368] [35] N/O W (A,B)

Chaetoceros messanensis Castracane [0.011] [20] W (A)

Chaetoceros neglectus Karsten [1.259] [35] C (A)

Chaetoceros pendulus Karsten [0.014] [5]

Chaetoceros peruvianus Brightwell [0.045] [30] N/O W/T (A,B)

Chaetoceros rostratus Lauder [4.907] [35] W (A)

Chaetoceros seiracanthus Gran [0.006] [10] W/T (A)

Chaetoceros similis Cleve [0.004] [10] ? (A)

Climacodium frauenfeldianum Grunow [0.020] [5] W (A)

Cocconeis spp. [0.013] [10]

Corethron criophilum Castracane [2.153] [85] O Co (A,B)

Coscinodiscus asteromphalus Ehrenberg [0.001] [5] O Co (A,B)

Coscinodiscus centralis Ehrenberg [0.058] [25] O Co (A,B)

Coscinodiscus granii Gough [0.000] [5] N Co (A,B)

Coscinodiscus marginatus Ehrenberg [0.065] [40] N Co (A,B)

Coscinodiscus perforatus Ehrenberg [0.001] [5] N/O Co (B)

Coscinodiscus oculus-iridis Ehrenberg [0.001] [5] O Co (B)

Coscinodiscus radiatus Ehrenberg [0.115] [50] N/O Co (A,B)

Cyclotella litoralis Lange and Syvertsen [0.145] [40] N T (A)

Cyclotella stelligera Cleve and Grunow [0.050] [10]

Cylindrotheca closterium (Ehrenberg) Lewin and Reinmann [0.100] [20] Co (A)

Cymbella sp. [0.000] [5] (F)

Dactyliosolen antarcticus Castracane [0.083] [35] O C (A,B)

Detonula pumila (Castracane) Gran [0.310] [30] N Co (A,B)

Diploneis sp. [0.000] [5]

Ditylum brightwellii (West) Grunow [0.008] [25] N Co (A,B)

Endictya sp. [0.026] [15]

Eucampia antarctica (Castracane) Manguin [1.335] [40] C (A)

Eucampia cornuta (Cleve) Grunow [0.037] [35] O W (A,B)

Fragilaria striatula Lyngbye [0.003] [5] N (E)

Fragilariopsis curta (Van Heurck) Hustedt [0.243] [45] C (A)

Fragilariopsis doliolus (Wallich) Medlin and Sims [6.284] [55] O W (A,C)

Fragilariopsis kerguelensis (O'Meara) Hustedt [20.178] [85] O C (A,B)

Fragilariopsis rhombica (O'Meara) Hustedt [0.700] [60] C (A)

Fragilariopsis ritscheri Hustedt [1.353] [50] C (A)

Gomphonema sp. [0.011] [10]

Gossleriella tropica Schütt [0.020] [5] W (A)

Grammatophora sp. [0.004] [5]

Guinardia flaccida (Castracane) Peragallo [0.001] [10] N Co (A,B)

Hantzschia sp. [0.030] [10] F

Haslea trompii (Cleve) Simonsen [0.000] [5] C (A)

Hemidiscus cuneiformis Wallich [0.010] [5] W (A)

Hemiaulus hauckii Grunow [0.149] [25] N W/T (A,C)

Hemiaulus membranaceus Cleve [0.145] [15] W (A)

Hemiaulus sinensis Greville [0.040] [10] N W/T (A,B)

Lauderia annulata Cleve [0.004] [15] W/T (A)

Leptocylindrus danicus Cleve [2.352] [25] Co (A)

Leptocylindrus mediterraneus (Peragallo) Hasle [0.151] [30] Co (A)

Licmophora sp. [0.001] [5]

Lioloma pacificum (Cupp) Hasle comb. nov. [0.292] [35] W/T (A)

Mastogloia capitata Cleve [0.010] [10] W (C)

Mastogloia rostrata (Wallich) Hustedt [0.075] [5] O W (C)

Membraneis challengeri (Grunow) Paddock [0.099] [40] C (F)

Membraneis imposter Paddock [0.010] [5] C (F)

Navicula directa (Smiyh) Ralfs [0.210] [20]

Navicula distans (Smiyh) Ralfs [0.078] [15]

Neodelphineis indica (Taylor) Hasle [0.041] [10] W/T (A)

Neodenticula sp. [0.003] [10]

Nitzschia bicapitata Group [2.022] [85] O W/T (A,B)

Nitzschia braarudii Hasle [0.430] [35] W/T (A)

Nitzschia kolaczeckii Grunow [0.100] [30] O W (C)

Nitzschia sicula (Castracane) Hustedt [3.066] [75] N/O W (A,B)

Odontella mobiliensis (Bailey) Grunow [0.000] [10] N Co (A,B)

Paralia sulcata (Ehrenberg) Cleve [0.009] [5] N Co (A,B)

Pinnularia sp. [0.008] [10] F

Plagiotropis gaussi (Heiden) Paddock [0.020] [10] C (F)

Planktoniella sol (Wallich) Schütt [0.126] [45] W (A)

Pleurosigma directum Grunow [0.200] [50] Co (A)

Pleurosigma normanii Ralfs [0.000] [5] N Co (A,B)

Porosira pseudodenticulata (Hustedt) Josué [0.042] [20] C (A)

Proboscia alata (Brightwell) Sundström [0.495] [70]

Proboscia inermis (Castracane) Jordan and Ligowski [0.103] [40] C (F)

Pseudo-nitzschia delicatissima (Cleve) Heiden [0.293] [20] Co (A)

Pseudo-nitzschia fraudulenta (Cleve) Hasle [1.026] [45] N/O Co (A,B)

Pseudo-nitzschia granii (Hasle) Hasle [0.018] [5] C/T (A)

Pseudo-nitzschia heimii Manguin [1.704] [40] Co (A)

Pseudo-nitzschia inflatula var. capitata Simonsen [0.012] [15]

Pseudo-nitzschia lineola (Cleve) hasle [2.319] [40] Co (A)

Pseudo-nitzschia multiseries (Hasle) Hasle [1.903] [35] Co (A)

Pseudo-nitzschia pseudodelicatissima (Hasle) Hasle [1.934] [70] Co (A)

Pseudo-nitzschia pungens (Grunow ex Cleve) Hasle [0.097] [10] N Co (A,B)

Pseudo-nitzschia seriata (Cleve) Peragallo [0.131] [15] T (A)

Pseudo-nitzschia subfraudulenta (Hasle) Hasle [0.558] [35] W/T (A)

Pseudo-nitzschia turgidula (Hustedt) Hasle [0.250] [10] Co (A)

Pseudo-nitzschia turgiduloides (Hasle) Hasle [0.403] [15] C (F)

Pseudosolenia calcar-avis (Schulze) Sundström [0.068] [35] N/O W/T (A,B)

Rhizosolenia antennata f. antennata (Ehrenberg) Brown [0.016] [10] C (A)

Rhizosolenia antennata f. semispina Sundström [0.226] [25] C (A)

Rhizosolenia chunii Karsten [0.281] [40] C (F)

Rhizosolenia clevei var. communis Sundström [0.107] [20] W (A)

Rhizosolenia crassa Schimper [0.043] [35] C (A)

Rhizosolenia curvata Zacharias [0.025] [20] C (A)

Rhizosolenia antarctica Karsten [0.423] [25] C (D)

Rhizosolenia hebetata f. semispina (Hensen) Gran ? [0.020] [10] C (F)

Rhizosolenia imbricata Brightwell [0.093] [40] N Co (A,B)

Rhizosolenia polydactyla Castracane f. polydactila [0.116] [30] C (A)

Rhizosolenia pungens Cleve-Euler [0.185] [40] N (A)

Rhizosolenia setigera Brightwell [2.651] [65] N Co (A,B)

Rhizosolenia simplex Karsten [0.157] [35] C (A)

Rhizosolenia styliformis Brightwell [0.925] [45] N/O Co (B)

Roperia tesselata (Roper) Grunow [0.338] [50] N/O W/Co ? (A,B)

Skeletonema costatum s.l. (Greville) Cleve [0.560] [35] N Co (A,B) Note: recent molecular genetic studies have shown that Skeletonema costatum-like species comprise eight distinct entities (Sarno *et al.*, 2005)

Stellarima microtrias (Ehrenberg) Hasle and Sims [0.009] [10] C (A)

Stephanodiscus sp. [0.000] [5] F

Stephanopyxis turris (Arnott) Ralfs [0.014] [5] N W/T (A,B)

Thalassionema bacillare Kolbe [0.111] [20] W (A)

Thalassionema frauenfeldii (Grunow) Hallegraeff [0.044] [35] W/T (A)

Thalassionema nitzschioides var.parva (Heiden) Moreno-Ruiz [0.090] [20] W (I)

Thalassionema nitzschioides (Grunow) Grunow ex Hustedt [8.133] [90] N Co (A,B)

Thalassiosira allenii Takano [0.002] [5] W/T (A)

Thalassiosira angulata (Gregory) Hasle [0.038] [10] Co (B)

Thalassiosira anguste-lineata (Schmidt) Fryxell and Hasle [0.087] [60] N Co (A,B)

Thalassiosira antarctica Comber (vegetative cell) [0.404] [35] N/O C (A,B)

Thalassiosira dichotomica (Kozlova) Fryxell and Hasle [0.045] [10] C (F)

Thalassiosira decipiens (Grunow) Jørgensen [2.884] [35] N (A)

Thalassiosira delicatula Ostenfeld in Borgert [0.003] [5] N/O Co (A,B)

Thalassiosira eccentrica (Ehrenberg) Cleve [0.035] [35] N Co (A,B)

Thalassiosira frenguellii Kozlova [0.211] [50] C (F)

Thalassiosira frenguelliopsis Fryxell and Johansen [0.047] [30] C (F)

Thalassiosira gracilis (Karsten) Hustedt [1.244] [45] N/O C (A,B)

Thalassiosira gravida Cleve [0.061] [25] N/O C (A,B)

Thalassiosira lentiginosa (Janisch) Fryxell [1.793] [45] O C (A,B)

Thalassiosira leptopus (Grunow) Hasle and Fryxell [0.040] [5] W (A)

Thalassiosira lineata Jousé [0.227] [50] O W (A,B)

Thalassiosira oestrupii var. oestrupii (Ostenfeld) Hasle [0.312] [55] O W/T (A,B)

Thalassiosira oestrupii var. venrickae Fryxell and Hasle [0.446] [65] W/T (A)

Thalassiosira oliverana (O'Meara) Mak [0.041] [25] C (G)

Thalassiosira pacifica Grand and Angst [0.006] [20] Co (A)

Thalassiosira perpusilla Kozlova [0.079] [25] C (A)

Thalassiosira poroseriata (Ramsfjell) Hasle [0.059] [15] Co (A)

Thalassiosira punctifera (Grunow) Fryxell [0.051] [15] N/O (C)

Thalassiosira punctigera (Castracane) Hasle [0.094] [15] N/O W/T (A,B)

Thalassiosira ritscheri (Hustedt) Hasle [0.065] [45] C (A)

Thalassiosira sacketti Fryxell [0.010] [5] W (J)

Thalassiosira scotia Fryxell and Hoban [0.112] [40] C (F)

Thalassiosira symmetrica Fryxell and Hasle [0.010] [5] Co (C)

Thalassiosira simonsenii Hasle and Fryxell [0.001] [5] N/O W/T (A,B)

Thalassiosira subtilis (Ostenfeld) Gran [0.010] [5] O W/T (A,B)

Thalassiosira trifulta Fryxell [0.137] [60] N/O C (A,B)

Thalassiosira tumida (Janisch) Hasle [0.186] [45] N/O C (A,B)

Thalassiothrix antarctica Schimper ex Karsten [0.909] [55] N/O C (A)

Trichotoxon reinboldii (Van Heurck) Reid and Round [0.303] [35] C (A)