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PART I

Multiannual trends in fronts and distribution of nutrients and chlorophyll in the southwestern Atlantic (30–62°S)

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Abstract

This paper presents the first data on the vertical distribution of chlorophyll and nutrients in the upper layers of the southern southwestern Atlantic and interprets it in relation to frontal systems and the general hydrographic features. The survey covered quasi-synoptically the area between 30 and 62°S, at the beginning of the austral summers of three consecutive years (1993 through 1995). Our results show a rather consistent oceanographic structure, with similar patterns of chlorophyll and nutrient distributions with latitude. Outstanding features present throughout the three seasons are two zones of high phytoplankton production, where chlorophyll concentrations of > 1 μg/l seem to occur frequently. The first is the upper euphotic zone of the Brazil–Malvinas Confluence Zone between approximately 36 and 50°S. The second is centered on subsurface layers of the Antarctic Surface Water south of the Polar Front as far as 62°S. The rest of the area covered shows low chlorophyll concentrations (< 0.4 μg/l), due either to nutrient limitation in the oligotrophic subtropical waters of the Brazil Current or to excessive

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turbulence and upper-layer instability in the energetic Malvinas Current. The occurrence of a permanent meander around 38°S coincided with the cyclonic retroflexion of the Malvinas Current, causing upwelling of deep water. The ecological implications of this eddy-induced upwelling are discussed.

Keywords: Thermal fronts; Nutrients; Chlorophyll; Brazil–Malvinas Confluence Zone; Polar front; Southwestern Atlantic

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1. Introduction

Upper layers in the pelagic realm between the tropics and the Antarctic are characterized by large thermally homogeneous regions (= thermostads) circumscribed by oceanic fronts where strong horizontal thermal gradients occur within narrow (60–100 miles) latitudinal bands. In the South Atlantic, the most conspicuous fronts are the Subtropical Convergence and the Polar Front (Deacon, 1937; Gordon, 1971; Emery, 1977), which meander around the globe and coincide with remarkable accumulations of phytoplankton biomass (Lutjeharms et al., 1985). Many authors have analyzed the thermal structure of these features and their distribution in the Southern Ocean (Edwards and Emery, 1982; Lutjeharms and Valentine, 1984; Lutjeharms, 1985). Phytoplankton accumulation along these fronts in the South Atlantic, South Pacific and Indian Oceans has been discussed repeatedly (Fukuchi, 1980; Fukuchi and Tamura, 1982; Allanson et al., 1981; Lutjeharms et al., 1985; Taniguchi et al., 1986; Fukuchi et al., 1986; Watanabe and Nakajima, 1982). However, despite the considerable number of chlorophyll measurements performed in the past 3 decades, the mechanisms reponsible for phytoplankton development along these fronts are still poorly understood since, with few exceptions (Watanabe and Nakajima, 1982; Fukuchi and Tamura, 1982), only surface data were considered; this has seriously limited interpretations of the physical phenomena responsible for enhanced phytoplankton growth.

In the southwestern Atlantic, between 30 and 62°S, the dynamics of the pelagic ecosystem are mainly governed by the interaction of the Brazil and the Malvinas currents (roughly between 36 and 50°S) flowing in opposite directions. Farther south in the Drake Passage and western Scotia Sea, the dynamics are dominated by the narrow Polar Front.

Between 38 and 45°S our sections run along the mean position of the Brazil–Malvinas Confluence (Fig. 1). The front is sharp but shows substantial space–time variations forming a large area of intense mixing of subtropical and subantarctic waters. This area is characterized by sharp horizontal and vertical changes in temperature, salinity and nutrients (Gordon and Greengrove, 1986; Gordon, 1989; Ikeda et al., 1989; Bianchi et al., 1993) that, in turn, define conspicuous biological gradients and areas where subtropical and subantarctic species are found (Boltovskoy, 1981a,1986; Boltovskoy, 1970,1981b). We refer to this area as the Brazil–Malvinas Confluence Zone (BMCZ).

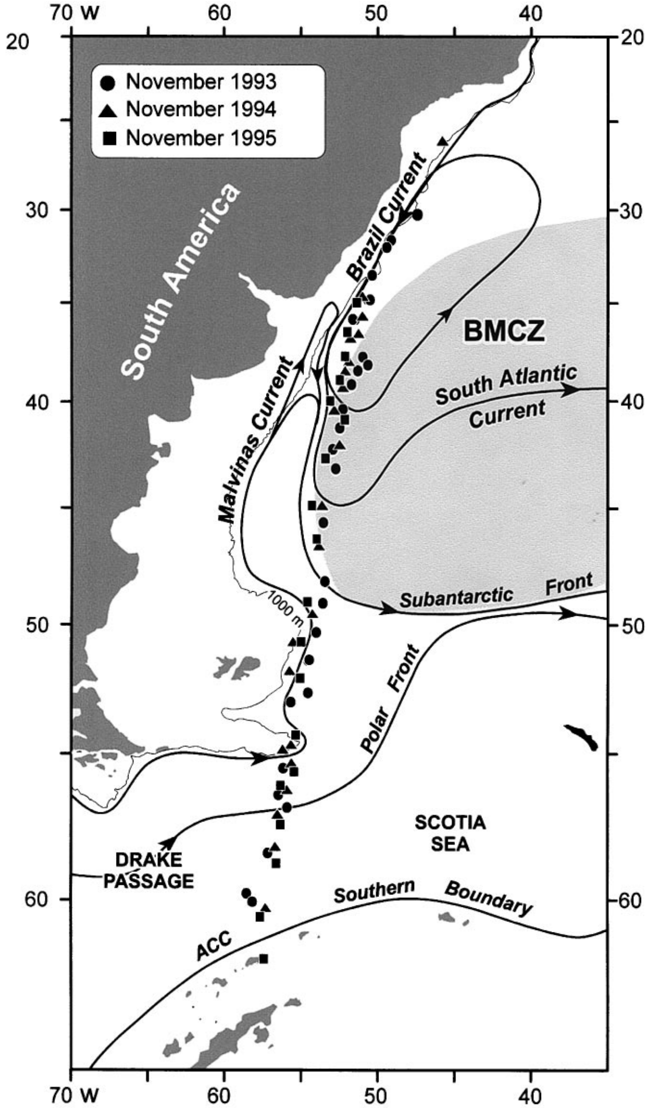

Fig. 1. Station locations and schematic diagram of major upper-level currents and fronts (partly adapted from Peterson and Stramma, 1991). The shaded area denotes the region where waters of subtropical and subantarctic origin may coexist at different times of the year, as indicated by the presence of typically subtropical or subantarctic planktonic organisms, i.e, the Brazil–Malvinas Confluence Zone (chiefly from Boltovskoy, 1970).

The influence of these physical processes on the horizontal structure and geographic distributions in the composition of planktonic assemblages has been long recognized, especially in analyses based on the use of indicator species of the provenance of a given patch of water (e.g., Balech, 1986; Boltovskoy, 1970). On the other hand, data on changes in biological richness associated with these dissimilar physico-chemical settings, as well as vertical profiles including both qualitative and quantitative information, are extremely scarce for this area. For example, vertical chlorophyll and nutrient data have never been reported off the continental margins of the shelves of Brazil, Uruguay and Argentina, an area of important fishing grounds. Meanwhile, as will be shown below, we hypothesize that the processes that determine the vertical structure of the water column are of utmost importance in determining the horizontal distribution of phytoplankton in the various hydrographic domains of the southern southwest Atlantic.

2. Material and methods

Field work was conducted from the support and research vessels "Barão de Teffé" and "Ary Rongel", Brazilian Navy, as part of the Brazilian Antarctic Program. A series of stations was occupied during the southbound track of the ships, between 30 and 62°S, along 47–57°W, in November 1993 (20 stations), November 1994 (22 stations) and November 1995 (19 stations) (Fig. 1). All transects covered subtropical, subantarctic and Antarctic waters. Stations were usually spaced approximately 120 nm apart, but in several instances the spacing was reduced to less than 15 nm in order to achieve a finer spatial resolution in frontal areas.

At each station, water samples were retrieved with Van Dorn bottles at standard depths from the surface down to 125–200 m. Data for chlorophyll and nutrients covered slightly different latitudinal ranges in the three cruises, which must be taken into account when comparing the annual distributions of these parameters. Secchi disk readings were also performed at diurnal stations.

Immediately after collection, 200 ml of water was filtered through 25 mm Whatmann GF/C filters for assessment of total chlorophyll. Filters were stored dried and frozen for subsequent analyses by fluorometry after extraction with 90% acetone (Evans and O'Reilly, 1983) in the laboratory. Fluorometric readings excluded the errors due to phaeophytin using appropriate excitation and emission filters (Welschmeyer, 1994). Aliquots of the filtrates were preserved with a few drops of a saturated solution of $HgCl_2$ and kept frozen for subsequent analyses of nitrate-N, phosphate-P and silicate-Si (except in 1995) at the University of Buenos Aires with a Technicon Autoanalyzer (Strickland and Parsons, 1972). Vertical temperature profiles were obtained with Sippican Ocean Systems XBT probes at regular intervals along the cruise tracks.

On the first cruise, 50 ml of water was obtained from each sampling depth and fixed with lugol solution for quantitative diatom analysis with the Utermöhl (1958) sedimentation technique. Cell numbers and dimensions were used to convert densities and volumes into carbon biomass per water volume, according to Edler (1979).

3. Results

3.1. November 1993

Temperatures above 20°C were recorded in the upper 100 m of the northernmost subtropical region between 30 and 32°S (Fig. 2) and decreased with depth until the colder (15–19°C) South Atlantic Central Water was reached at >150 m (not indicated in Fig. 2). Temperature dropped gradually toward the south until 37°S, where the Brazil Current Front (BCF, Ikeda et al., 1989) was detected as the northern limit of the BMCZ. At 38°S, isotherms indicated upwelling of deeper waters and a strong drop in SST. Within the BMCZ, surface temperatures decreased sharply southwards from 18 to 7°C at ca. 50°S, where another well-defined front, the Falkland Escarpment Front (FEF, Ikeda et al., 1989), delineated the southernmost boundary of the BMCZ. At various locations in the BMCZ, deepening of isotherms suggested convergence of cold surface waters. Here temperatures were slightly higher at the surface (0–5 m) than below. In subantarctic waters of the Malvinas Current temperatures were homogeneous both horizontally and vertically, ranging between 7 and 5°C. The Polar Front (PF) was detected around 56°S with temperatures decreasing sharply from 5 to 2°C and isotherms deepening to 200 m. Antarctic waters south of the PF were below 2°C at the surface, usually ranging between -1 and 0°C, with negative values uniform throughout most of the water column.

Maximum chlorophyll concentrations were found in the BMCZ, with 3.6 μg/l at 25 m at Stn 6 (37°15′S; 51°23′W). Peaks of >1 μg/l occurred frequently, but in general values ranged between 0.4 and 1.0 μg/l between 37 and 41°S (Fig. 2). The second chlorophyll-rich zone along the transect was found in surface and subsurface layers of the Antarctic Surface Water, between the Polar Front and 61°S, with concentrations up to 0.62 μg/l in the upper 25 m at Stn 20 (59°14′S; 56°47′W). Concentrations in the upper 100 m of subtropical, subantarctic and Polar Front waters were much lower, usually between 0.2 and 0.4 μg/l. In the aphotic layers (<100 m) of all regions, chlorophyll concentrations were always below 0.2 μg/l, except for isolated spots of enhanced accumulation within the BMCZ. The distribution of diatom carbon agreed well with that of chlorophyll: peak values of 8–10 μg C/l were recorded in areas of enhanced chlorophyll concentration in the BMCZ and south of the Polar Front, whereas elsewhere it was generally below 4 μg C/l. Also the vertical distribution of diatom carbon matched chlorophyll patterns well, with minimum values (<1 μgC/l) in the aphotic layer below 100 m.

Nutrient concentrations along the transect increased gradually from north to south. Lowest values for nitrate, phosphate and silicate (Fig. 3) were measured in the upper layers of the euphotic zone in the subtropical region that is dominated by the oligotrophic waters of the Brazil Current. Low-nutrient conditions (particularly silicate) extended further south throughout almost all of the BMCZ, most likely due to phytoplankton consumption in these chlorophyll-rich layers (compare with Fig. 2). In the aphotic zone, latitudinal patterns of nutrient concentration were more conservative. Highest overall nutrient concentrations were found in polar waters south of 56°S

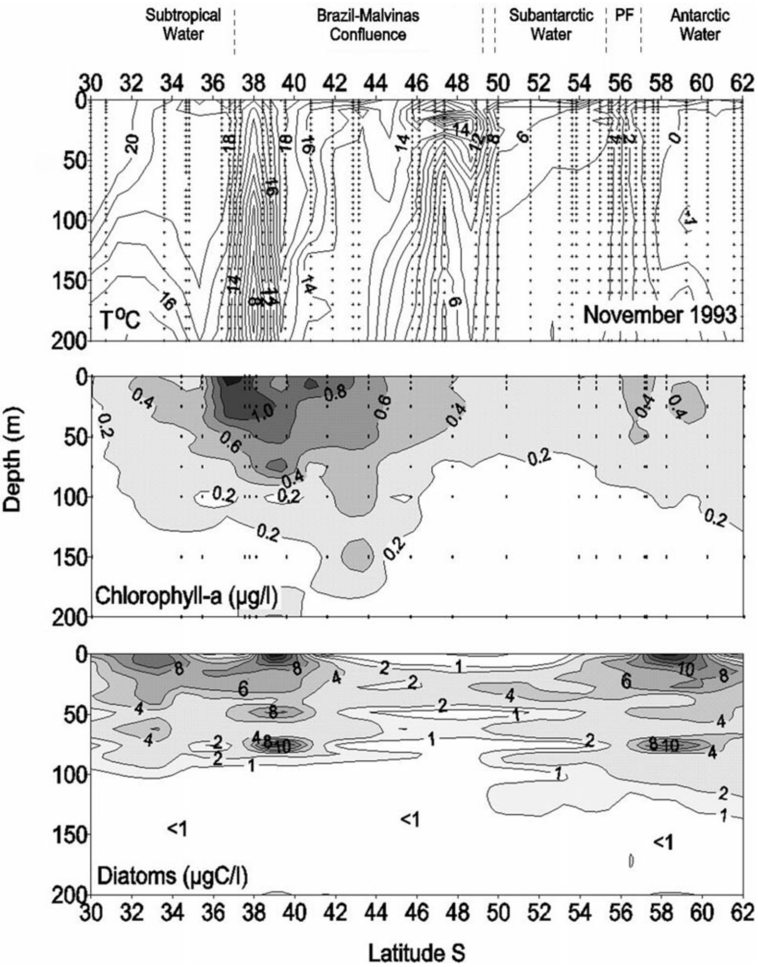

Fig. 2. Vertical profiles of temperature, chlorophyll and diatom biomass in terms of cell carbon in November 1993.

where silicate varied from 20 to 74 µM, nitrate from 25 to 37 µM and phosphate from 2 to 2.6 µM.

3.2. November 1994

Temperature data for November 1994 indicated the same hydrographic domains with limits similar to those recorded the previous year (Fig. 4). The BCF, the northernmost boundary of the BMCZ, occurred around 36°S (i.e., 1° north of its 1993 position). Notably, again a conspicuous upwelling was present at 36–39°S; in 1993 this feature was centered on 38°S. The FEF, the southern limit of the BMCZ, was located

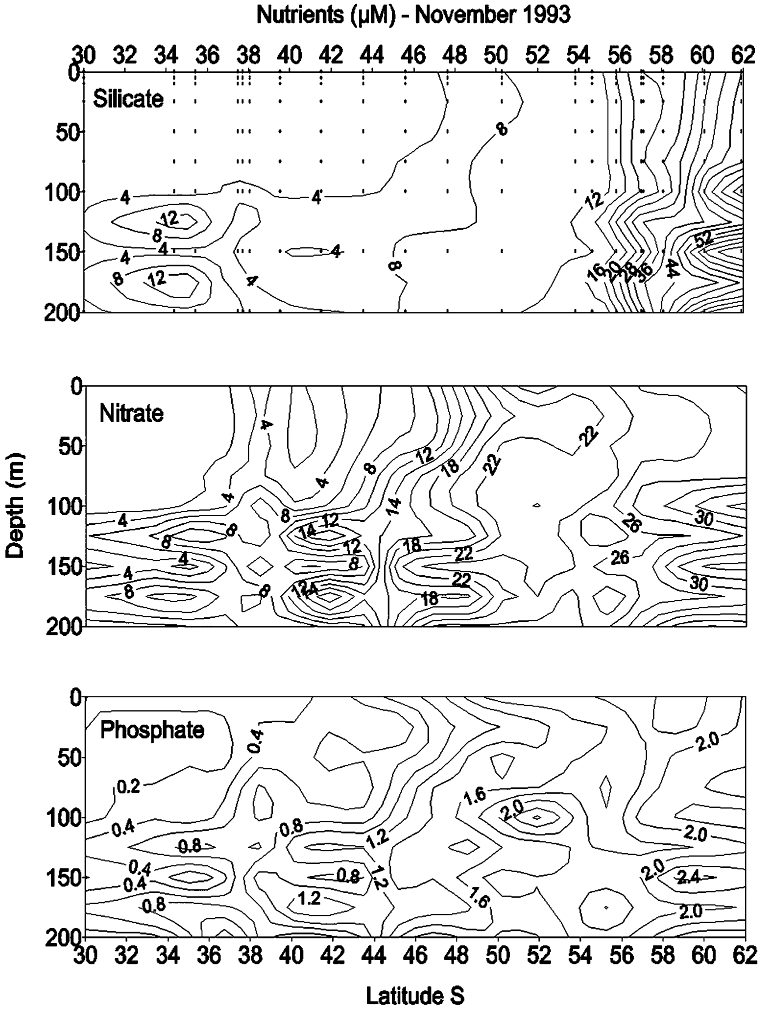

Fig. 3. Vertical profiles of silicate, nitrate and phosphate concentrations (µM) in November 1993. Dots in silicate distribution represent data points for all nutrients.

at 48–49°S, and the Polar Front around 56°S. Horizontal and vertical temperature patterns were similar to those recorded the previous year.

The vertical distribution of chlorophyll again indicated higher concentrations in the BMCZ (Fig. 4). However, maximum concentrations of 2.2 µg/l were found in the subsurface layers of the AASW at 50 m, between the Polar Front and 60°S, rather than in the BMCZ as observed in November 1993. BMCZ values were between 0.4 and >1 µg/l, with peak concentrations occurring at various sites, either at surface or at subsurface depths. In subantarctic waters concentrations were within the same

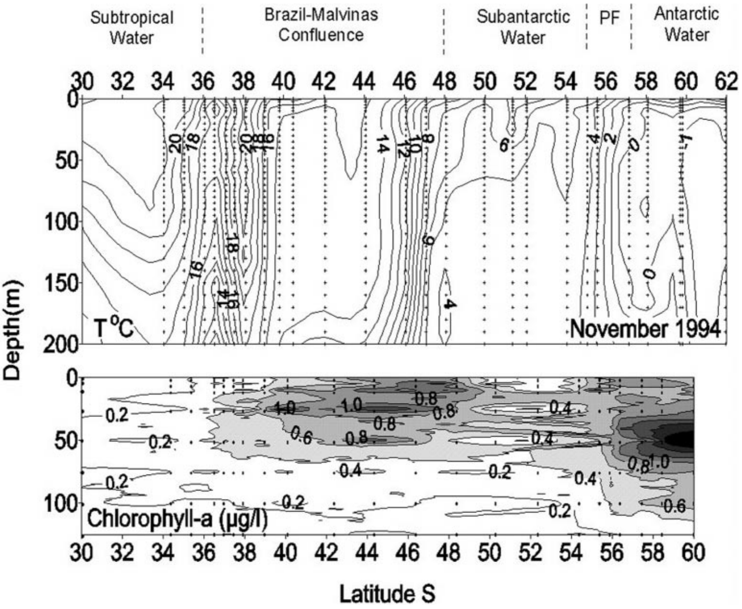

Fig. 4. Vertical profiles of temperature and chlorophyll in November 1994.

range as in November 1993, usually between 0.2 and 0.6 µg/l. In subtropical waters, chlorophyll concentrations in the upper 100 m varied between 0.2 and 0.4 µg/l as in November 1993. Below 100 m, concentrations along the transect were always below 0.2 µg/l.

Although the sampling differed between 1993 and 1994, the overall geographic and vertical patterns were similar for the two years (Fig. 5). Nitrate and phosphate concentrations were again lowest (< 4 and < 0.4 µM, respectively) in the shallow subtropical waters, increasing with depth, and to the south, reaching maxima in the polar waters with nitrate at 20–32 µM and phosphate at 1.5–2.3 µM. Concentrations of silicate were below 8 µM along most of the transect, increasing sharply up to 52 µM in the Antarctic waters below 100 m.

3.3. November 1995

The thermal structure in November 1995 is not resolved due to an insufficient number of XBT profiles. The rather scarce nutrient data available for the subtropical domain (silicate was not measured) generally agree with the 1993 and 1994 patterns: these permanently stratified subtropical waters again showed the lowest nitrate (< 4 µM) and phosphate (< 1 µM) concentrations (Fig. 6). Concentrations increased with depth towards the layers dominated by the SACW. Concentrations again increased southwards, as in the previous two cruises, up to 30 µM of nitrate and 2.4 µM of phosphate south of 58°S, mainly at depths below 100 m.

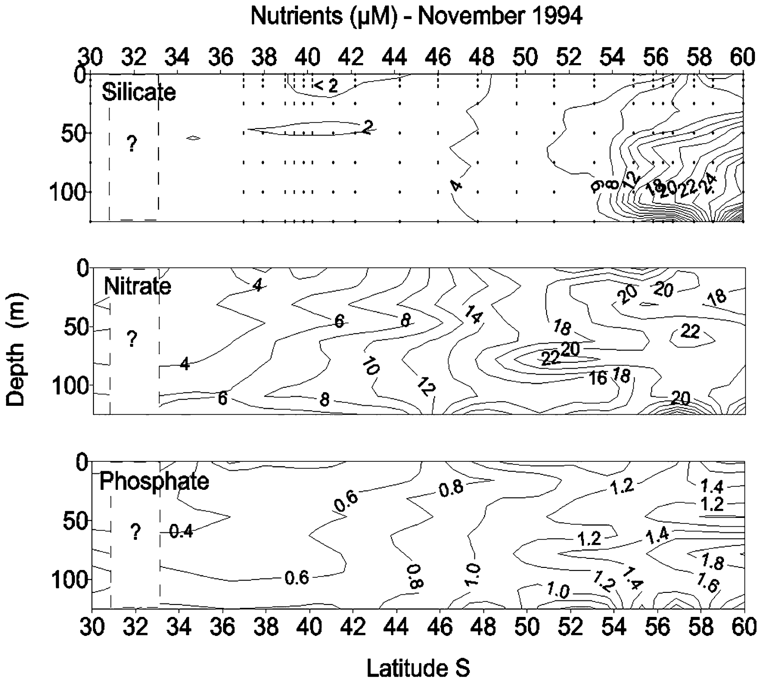

Fig. 5. Vertical profiles of silicate, nitrate and phosphate concentrations (μM) in November 1994. Dots in silicate distribution represent data points for all nutrients.

The distribution of chlorophyll also was similar to the 1993 and 1994 patterns, with highest phytoplankton biomass in the BMCZ and in subsurface waters (around 50 m) of the AASW south of 58°S (Fig. 6). Peak concentrations above 1 μg/l were found between 39 and 48°S in the upper 25 m, with maxima of 2.6 and 2.4 μg/l at 42°S (10 m) and at 44°S (5 m), respectively. Concentrations in the subtropical region were slightly higher than those in 1993 and 1994, varying from < 0.2 to 0.6 μg/l, with maxima around 75–100 m. The upper layer of subantarctic waters also yielded from 0.2 to 0.6 μg/l. As in previous years, concentrations below 100 m were usually < 0.2 μg/l throughout the transect. Peak concentrations in antarctic waters (up to 1.34 μg/l) were in the subsurface layers.

4. Discussion

4.1. Hydrography

Our data set shows that the Southwestern Atlantic can be partitioned into four hydrologically distinct domains: subtropical, mixing zone, subAntarctic and Antarctic, characterized rather clearly by decreasing (from north to south) surface

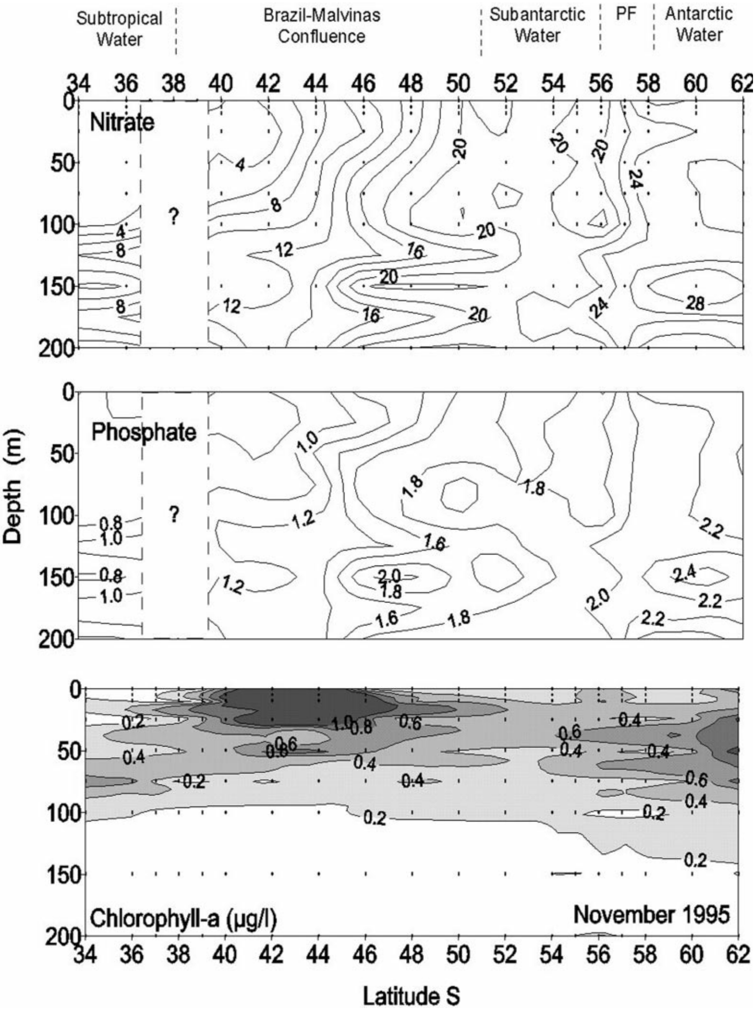

Fig. 6. Vertical profiles of nitrate, phosphate and chlorophyll in November 1995. Dots in nitrate distribution also represent data points for phosphate distribution. Concentrations of nutrients are in μM.

temperature (Boltovskoy, 1986). All four zones were detected during the first two cruises discussed here:

(1) the northernmost area (usually north of 36°S) dominated by warm subtropical waters of the Brazil Current (mean SST around 22–23°C);
(2) the Brazil–Malvinas Confluence Zone — BMCZ, roughly between 36 and 50°S. Surface temperatures here vary widely, dropping from ca. 19–20°C in the north to below 8–9°C in the south;

(3) the subantarctic waters transported by the Malvinas Current from 50 to 55°S (mean SST ca. 6°C); and
(4) the colder (mean SST below 2°C) Antarctic Surface Water (AAASW), south of the Polar Front, which was detected around 56°S in 1993 and 1994.

A rising of isotherms around 38–39°S was detected, presumably associated with the cyclonic retroflexion of the Malvinas Current (Gordon and Greengrove, 1986). The Brazil Current Front described by Ikeda et al. (1989), and detected here in the first two cruises, coincided with the outer margin of this large-scale meander and is probably responsible for the upwelling of deep water observed in November 1993 and 1994. In this area, the distribution of nutrients did not match the isotherms (Figs. 2–5), probably because they were being consumed by phytoplanktonic growth, therefore masking the upward transport. The only clear indication of upwelling of nutrients is the narrow strip of enhanced nitrate concentrations at 38°S observed mainly in November 1993, but also visible in November 1994, extending from 100 m upwards. The dynamic topography of this area was reported by Mata and Garcia (1996) using altimetry data obtained by the TOPEX/POSEIDON satellite. They noticed that the area between 35–50°S and 45–52°W is the most variable in terms of sea surface topography, due to local interactions between the Brazil and the Malvinas Currents.

4.2. Chlorophyll distribution in the BMCZ

In the area of our survey, generally the most productive waters are those within the broad frontal system of the BMCZ, and the subsurface waters (around 50 m) of the Antarctic Surface Water in the Drake Passage south of the Polar Front. These contrast with the overall warm oligotrophic waters of the Brazil Current (N/P between 2 and 4), where phytoplankton growth is strongly nutrient-limited, and the nutrient-rich (N/P usually between 12 and 14) but strongly turbulent Malvinas Current waters. Here permanent wind-stress generates a deep mixing layer, as in the Antarctic Circumpolar Current, thus limiting phytoplanktonic production according to Sverdrup's Critical Depth condition (Mitchel and Holm-Hansen, 1991).

High phytoplankton production in the BMCZ is of special interest due to the large area. As opposed to most oceanic fronts, where phytoplankton accumulation occurs along narrow bands (Laubsher et al., 1993; Olson et al., 1994), the BMCZ is a unique frontal system in that it is generated by the confluence and mixing of the Brazil and the Malvinas currents, which flow in opposite directions. In the BMCZ, enhanced chlorophyll concentrations are associated not only with the well-defined fronts (e.g., BCF, FEF), but are also found in the more homogeneous areas between them. N/P ratios in this area were usually between 8 and 12, which seems adequate for supporting fast growing diatoms, the dominant phytoplankton during November 1993 (Fig. 2).

We contend that the mixing between the nutrient-rich but vertically unstable subantarctic waters and the nutrient-poor warm subtropical waters is responsible for environmental conditions that allow enhanced phytoplanktonic growth in the BMCZ. Thus, the physical stability required for biomass buildup in nutrient-rich

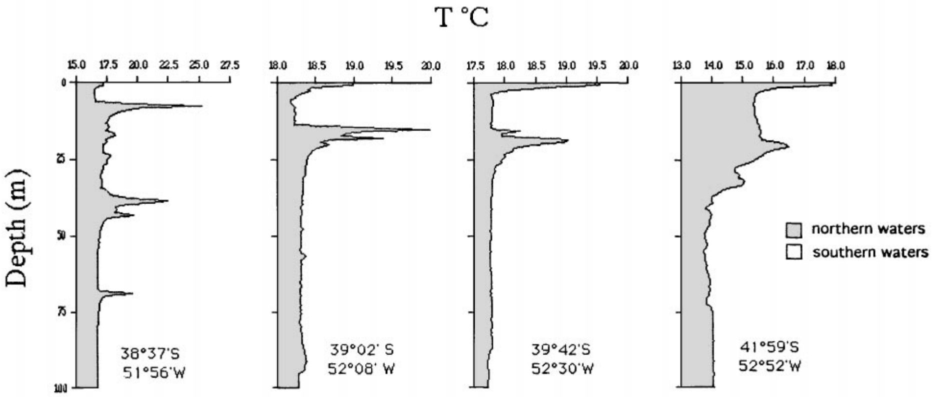

Fig. 7. Examples of typical fine-scale vertical profiles of temperature in the upper 100 m of the Brazil/Malvinas Confluence Zone, as obtained by XBT probes between 38 and 42°S, where chlorophyll peak concentrations were common.

(cool) waters is provided by intrusions of warm subtropical waters. XBT profiles in the BMCZ show extremely complex and variable temperature profiles, indicating several small- and medium-scale intrusions of warm and cold waters from opposite directions. Fig. 7 shows examples of fine-scale temperature profiles obtained in the euphotic layers roughly between 38 and 42°S, where maximum chlorophyll concentrations were measured in November 1993 (see Fig. 2). The figure shows that the vertical homogeneity of the cold subantarctic water is bounded by several layers of northern waters intruding southwards at various depths. Thus, while there is no single shallow upper mixed layer, warm water lenses are interspersed along the profile, producing several density discontinuity layers in the upper 100 m and precluding sinking of the phytoplanktonic cells. The intervening colder, nutrient-rich Malvinas waters, in turn, supply the nutrients needed for biomass buildup. These features have already been noticed by Bianchi et al. (1993), who reported higher flux of salts (obviously including nutrients) and heat in the BMCZ as compared with other frontal systems. A similar interleaving of waters of different densities was described by Veth et al. (1997) for the Polar Front, albeit at much larger spatial scales.

Since salinity data were not collected, we have inspected several quasi-continuous conductivity–temperature–depth (CTD) profiles collected in November 1988 (PD-88), September 1989 (PD-89, Charo et al., 1991) and October 1992 (EA-92, Osiroff et al., 1993) in order to determine the relation between medium-scale vertical temperature variability and physical stratification in the vicinity of the Brazil/Malvinas Confluence. For the upper 100 m of each profile, the density gradient over 5-m-depth intervals has been calculated. Several cases in which the vertical temperature variability enhances vertical stratification and may provide the buoyancy required to support the phytoplankton growth in the euphotic layer within subantarctic waters were identified. Station PD88021 serves to illustrate two layers with enhanced stability (Fig. 8).

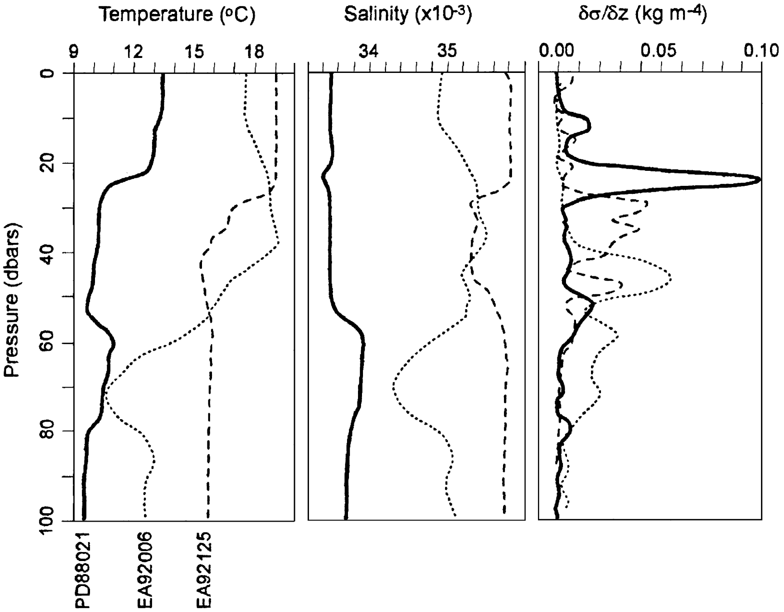

Fig. 8. Vertical temperature, salinity and density gradient profiles from the Brazil/Malvinas Confluence collected in November 1989, PD88021 (solid line), and October 1992, EA92006 (dashed line) and EA92125 (dashed–dotted line).

First, between 20 and 25 m depth there is a sharp temperature decrease of about 3°C, which induces a sharp increase in the vertical density gradient beyond 0.05 kg/m^4. The warm upper layer is likely to be produced by the warming associated with the net heat gained from the atmosphere in mid-spring. Second, a 25 m-thick warm-salty intrusion located near 60 m induces a moderate increase in stratification (0.02 kg/m^4). In this case the salinity increase (0.5×10^{-3}) observed between 55 and 60 m dominates over the temperature increase (1.5°C), leading to the enhanced stability in the water column.

Intrusions and vertical temperature and salinity variability induced by mixtures of subantarctic water may also act to enhance the vertical stability within subtropical waters. Near the Brazil/Malvinas Confluence a relatively thin layer of low temperature and salinity frequently caps the subtropical water. It is found that the vertical stability increases substantially at the base of the surface layer, where relative temperature and salinity maxima are observed. For example, large vertical density gradients > 0.5 kg/m^4 are estimated at the base of the low-salinity surface layer at station EA92006, occupied in October 1992 (Fig. 8). In addition, station EA92006 shows a large-amplitude subantarctic water intrusion (T 3°C and S 0.8×10^{-3}) near 70 m. At the top of this layer (60 m) the stability grows to 0.03 kg/m^4 and decreases with depth, suggesting temperature and salinity compensation at the base of the intrusion. Further inspection of additional profiles at near-frontal locations within subtropical waters reveal a large increase of vertical stability, $> 0.04\,\mathrm{kg/m^4}$ (e.g., EA92125), associated with subantarctic water intrusions, indicating that the variations in temperature and salinity are not exactly density compensating.

The horizontal extent and persistence of intrusions are also relevant to the maintenance of the stability maxima required to support the phytoplankton growth. Based on existing estimates of the lateral heat flux associated with Confluence intrusions ($1.2 \times 10^{-2}\,^{\circ}\mathrm{C\,m/s}$, Bianchi et al., 1993) and an aspect ratio of 10^{-2}, a 30-m-thick intrusion with a 3°C temperature anomaly, such as the one observed at 70 m in station EA92006, will dissipate in 4 d. Individual intrusions and the associated vertical structure embedded within the front will be advected downstream tens of kilometers per day and will dissipate in a few days. However, thermohaline intrusions are an ubiquitous feature of oceanic fronts (Joyce, 1977), and observations suggest that stability maxima, induced by intrusions, are likely to occur at any time in the vicinity of the Confluence.

Due to the significant role played by the vertical salinity structure in the density distribution, a simple relationship between vertical stability and temperature variability cannot be derived, preventing the detection of stability maxima based only on temperature observations. However, the analysis of quasi-continuous CTD data collected in the vicinity of the Brazil/Malvinas Confluence reveals several situations where the small-scale variations of temperature and salinity lead to increased vertical stability. Thus, by enhancing cross-frontal nutrient fluxes down-gradient and by inducing relatively high stability layers, the small-scale vertical structures may contribute to the maintenance of the high primary productivity near the Confluence.

A relevant question regarding this interpretation is the provenance and ecologic affinities of the species responsible for the high chlorophyll values recorded. Indeed, it is conceivable that:

(1) warm-water species are supported by the supply of Malvinas Current nutrients;
(2) the subantarctic innoculum, favored by enhanced stability due to the warm-water intrusions, reproduces more actively, engendering local chlorophyll accumulations; and
(3) both warm- and cold-water taxa benefit from these conditions and produce a mixed bloom.

The above scenarios have been investigated before, with evidence supporting either hypothesis. For example, Gayoso and Podesta (1996) speculated that the high diatom densities observed at three sites along 37°S, between 52°13′W and 53°34′W, in the Malvinas retroflexion, were due to subtropical assemblages enriched with nutrients from the Malvinas Current. On the other hand, Furuya et al. (1986) reported shallow pycnoclines in the Subtropical Convergence of the Pacific Ocean along 150°E, confining subantarctic phytoplankton species (mostly diatoms subjected to good nutrient conditions) within the euphotic zone. Plancke (1977) also ascribed high phytoplankton production in the Subtropical Convergence south of the African Continent to enhanced stability of the surface layers.

Species-specific analyses carried out during the first cruise (Olguin et al., 1997) revealed that in warm waters near the fronts, phytoplankton was largely dominated by flagellates and only few diatoms (*Leptocylindrus* spp. and unidentified pennate cells). Diatom assemblages of the Malvinas Current south of the BMCZ were much more diverse and dominated by colder water species of the genera *Pseudonitszchia, Rhysozolenia, Fragilariopsis, Thalassiosira, Thalassionema* and *Eucampia*. Similarly, Lange (1985) reported Antarctic and subantarctic species dominating the diatom collections in the outershelf regions of the Malvinas Current during spring. The chlorophyll-rich waters of the BMCZ were usually dominated by temperate diatoms of the genera *Leptocylindrus, Pseudonitszchia, Rhizosolenia*, *Fragilariopsis,* small *Chaetoceros* and *Odontella*. They were responsible for reducing silicate concentrations within the BMCZ in November 1993 (Fig. 3). This pattern was also observed by Allanson et al. (1981) and Lutjeharms et al. (1985) south of Africa. Blooms of such micro-sized diatoms could also have been iron-stimulated, since the chlorophyll-rich oceanic waters of the BMCZ are on the downstream side of the shelves of Argentina and the Malvinas (= Falkland) Islands, as discussed by Banse (1996) in relation to subantarctic islands and shelves. Discharge waters of the Río de La Plata estuary can also be a source of iron at certain times of the year, especially west of the area transected (Fig. 1), since their influence can be perceived as far oceanward as 53°W (e.g., by the presence of freshwater chlorophyceae, like *Scenedesmus*, which were identified in samples collected around 38°S; E. Uliana, pers. comm.).

The dinoflagellate populations in the BMCZ in November 1993 and 1994 were formed by mixture of cold and subtropical heterotrophic species (e.g., *Gonyaulax* spp, *Protoperidinium acanthophorum, Dinophysis schroederie*). A few autotrophic forms were also abundant and contributed to localized chlorophyll maxima along the BMCZ. *Ceratium lineatum*, a typical subantarctic species, dominated the dinoflagellate population during November 1993 (E. Balech, pers. comm.). Interestingly, surface waters with highest chlorophyll values (around 38–40°S, see Fig. 2) hosted much higher proportions of cold-water foraminifers (*Globigerina bulloides, G. quinqueloba, Neogloboquadrina pachyderma*) than areas both north and south of this locale (Boltovskoy et al., 1996). These typically subantarctic organisms were most probably brought to the surface by the upwelling at 38°S, within the cyclonic retroflexion of the Malvinas Current. Thus, we favor the hypothesis that the chlorophyll peaks recorded were mainly due to enhanced growth of subantarctic species stimulated by the increased vertical stability provided by warm-water intrusions.

4.3. Chlorophyll distribution in the Antarctic surface waters

South of the Polar Front chlorophyll-rich subsurface layers (50–75 m) were observed during all three cruises, but they were especially noticeable in November 1994 and 1995. This feature was also reported by Watanabe and Nakajima (1982) for the Indian sector along 45°E, and by Fukuchi and Tamura (1982) (though less developed) along 40–43°E, associated with the winter temperature minimum layer.

Franks and Walstad (1997) provided interpretations for the formation of subsurface chlorophyll maximum layers (SCML) in frontal zones. They used a combined physical/biological model to simulate the development of subsurface blooms considering mainly sinking of cells, cross-frontal nutrient gradients, grazing pressure, and historical wind regimes along the frontal zone, in association with Ekman transport. If their model is applied to the Drake Passage section of the Polar Front, the predominantly westerly winds would induce continuous surface Ekman fluxes from the cold (south) to the warm (north) side of the front, causing superficial blooms, as usually observed on the northern side of the Antarctic Polar Front (El-Sayed and Turner, 1977; Fukuchi et al., 1986; Laubsher et al., 1993). This, however, was not the scenario recorded during our three cruises: The SCML were not at the front itself but south of it, as far as 62°S. In November 1993, they were chiefly represented by *Fragilariopsis kerguelensis*, and in lower proportions by different species of *Pseudonitzshia*, *Rhizosolenia* and *Phaeocystis*, with very few dinoflagellates. Holm-Hansen et al. (1994) detected blooms below 50 m in the southern part of the Drake Passage in late spring/summer, suggesting actively growing phytoplankton populations under the sufficient lighting and micronutrient (e.g., Fe) conditions prevailing in the subsurface AASW, rather than due to sedimentation of cells from upper layers. They mentioned the possibility of these SCML extending further north to the Polar Front. Our data support this interpretation, because we found them just south of the Polar Front.

5. Conclusion

The importance of frontal zones for the qualitative and quantitative distribution of plankton in the oceans has been recognized from the pioneering studies of the early 19th Century (see Olson et al., 1994). As far as the distribution of species is concerned, fronts probably constitute the most important barriers to dispersion, thus defining the overall biogeographic patterns of marine organisms. On the other hand, their bearing on biological production seems of no lesser importance, insofar as they are often sites of major phytoplankton concentration (e.g., Lutjeharms et al., 1985; Laubsher et al., 1993; Olson et al., 1994; Froneman et al., 1997). Olson et al. (1994) suggested that pumping of deeper nutrient-rich water into the euphotic zone is responsible for phytoplankton development along meander-associated fronts of the Gulf Stream downstream of Cape Hatteras, along the southeastern coast of the US. A combination of adequate iron availability (either by aeolic or upwelling inputs) and water column stability has been suggested as responsible for phytoplankton biomass accumulation along the Polar Front (de Baar et al., 1995; Banse, 1996; Smetacek et al., 1997). However, despite the extensive literature describing biological enhancements along shelf and oceanic fronts, mechanisms of chlorophyll accumulation in the BMCZ are still poorly understood. The same applies to chlorophyll accumulations along the Polar Front discussed in recent publications (de Baar et al., 1995; Banse, 1996; Smetacek et al., 1997), but not observed in our three consecutive cruises that crossed the Drake Passage.

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