

ENVIRONMENTAL FACTORS

Luciano Felício Fernandes¹ & Frederico Pereira Brandini²

¹Universidade Federal do Paraná, Departamento de Botânica
Setor de Ciências Biológicas, Centro Politécnico
(Caixa Postal 19031 Jardim das Américas, 81531-970, Curitiba, Paraná, Brasil)
E-mail: lff@ufpr.br

²Centro de Estudos do Mar, Universidade Federal do Paraná
(Av. Beira-mar, s.n., 83255-000, Pontal do Paraná, PR, Brasil)

ABSTRACT

The seasonal variation of diatoms in the inshore waters off Paraná State, Southern Brazil was investigated to analyse their temporal dynamics and to detect the main environmental constraints of the planktonic community. Biomass peaks occurred from May to August and from December to March. Among the microplanktonic diatoms, *Cerataulina pelagica*, *Chaetoceros* spp., *Dactyliosolen fragilissimus*, *Guinardia striata*, *Lauderia annulata*, *Leptocylindrus* spp., *Pseudo-nitzschia cf. delicatissima*, *P. australis*, *Rhizosolenia* spp., *Skeletonema costatum* and *Thalassionema nitzschioides* were dominant species. Nanoplanktonic diatoms were dominated by Naviculaceae, *Nitzschia* spp., *Thalassiosira* spp. and *Chaetoceros cf. tenuissimus*. Concentrations of most of the species decreased during and just after the blooms of *Phaeocystis pouchetii* in September and of *Coscinodiscus wailesii* in April. Based on cluster analysis and interpretations of the environmental parameters monitored, six diatom associations were discerned. Four main environmental factors were attributed as the determinants for the grouping: (a) the stronger influence of the tropical oligotrophic waters of the Brazil Current in spring/summer, (b) the alternation between dry and rainy (nutrient-richer) seasons, (c) the influence of subantarctic waters mixed with coastal ones in fall/winter, bringing cold species and promoting the growth of autochthonous species, and (d) the blooms of nanoplanktonic (*Phaeocystis*) and microplanktonic (*C. wailesii*) species.

RESUMO

A variação sazonal das diatomáceas em águas neríticas do estado do Paraná, Sul do Brasil, foi investigada para analisar sua dinâmica temporal e detectar as principais forças ambientais da comunidade planctônica. Picos de biomassa ocorreram de Maio a Agosto e de Dezembro a Março. As espécies dominantes foram *Cerataulina pelagica*, *Chaetoceros* spp., *Dactyliosolen fragilissimus*, *Guinardia striata*, *Lauderia annulata*, *Leptocylindrus* spp., *Pseudo-nitzschia cf. delicatissima*, *P. australis*, *Rhizosolenia* spp., *Skeletonema costatum* e *Thalassionema nitzschioides*. Representantes de Naviculaceae, *Nitzschia* spp., *Thalassiosira* spp. e *Chaetoceros cf. tenuissimus* dominaram as diatomáceas nanoplanctônicas. As concentrações da maioria das espécies decresceram durante e logo após as florações de *Phaeocystis pouchetii* em Setembro, e de *Coscinodiscus wailesii* em Abril. Com base na análise de cluster e interpretações dos parâmetros ambientais monitorados, seis associações de diatomáceas foram discernidas. Quatro fatores ambientais principais foram atribuídos como determinantes para o agrupamento: (a) influência mais forte de águas oligotróficas da Corrente do Brasil na Primavera/Verão, (b) alternância entre as estações chuvosa (rica em nutrientes) e seca, (c) influência de águas subantárticas enriquecidas misturadas às costeiras no Outono e Inverno, trazendo espécies de águas frias, além de promover o crescimento de autóctones, e (d) florações de espécies nanoplanctônicas (*Phaeocystis*) e microplanctônicas (*C. wailesii*).

Descriptors: Bacillariophyta, Diatoms, Phytoplankton, Southern Brazil, Southwestern Atlantic.

Descritores: Bacillariophyta, Diatomáceas, Fitoplâncton, Taxonomia, Ecologia, Sul do Brasil.

INTRODUCTION

Phytoplankton studies of South Brazilian waters have documented its composition, distribution, biomass and primary productivity in relation to hydrographic conditions (see review of Brandini *et al.*, 1997 and references therein; Fernandes & Brandini, 1999). As for other investigations carried out in different marine ecosystems around the world, these works have found that diatoms (Bacillariophyta) are responsible for high cell densities and most of the primary productivity. They dominate the phytoplankton community in mid-shelf and coastal regions of southeastern Brazil, gradually diminishing oceanwards, where the relative contribution of dinoflagellates and nanoplankton increases (Brandini & Fernandes, 1996; Brandini *et al.*, 1997). The environmental factors determining the changes in the structure of diatom associations in coastal areas off South Brazil appear to be seasonal fluctuations in the hydrographic regime and land drainage, which affect temperature, salinity and nutrient concentrations (Brandini, 1990). The study region also exhibits a distinctive seasonal oceanographic pattern due to the proximity of the northern limits of the Brazil-Malvinas Confluence Zone, making ecological studies on diatoms more interesting. The Brazil Current transports warm, oligotrophic tropical waters southwards, dominating oceanic and shelf areas. Off Rio Grande State (38-42°S), the tropical waters meet the colder, nutrient-rich waters of the Malvinas Current flowing northwards over the shelf and continental slope of Argentina and Uruguay, which are also greatly affected by freshwater discharges from the La Plata river and the Patos Lagoon (Boltovskoy, 1981; Hubold 1980, 1980a). The influence of the Malvinas Current is stronger in the winter, when the penetration of a tongue of subantarctic waters is regularly detected along the south Brazilian continental shelf (Campos *et al.*, 1996).

The papers on plankton ecology in Brazilian waters describe annual variations in several dominant diatom taxa at the generic level (e. g. *Chaetoceros* spp., *Nitzschia* spp., *Thalassiosira* spp.), or they are referred to as "centric" and "pennate" diatoms. Few works follow the annual variation of dominant diatoms and discuss the environmental conditions influencing their specific composition (e.g. Valentin *et al.*, 1986). As a result, the published textbooks on phytoplankton (e. g. Harris, 1986; Smayda, 1980; Werner, 1977) provide limited information on the ecology and biogeography of diatoms over the extensive Brazilian continental shelf.

Many floristic and taxonomic works have been published on the coastal waters off Paraná State, but again not including enough ecological information (see Moreira Filho *et al.*, 1990 for review and list of species). Brandini (1985, 1985a, 1990) described the spatio-temporal dynamics of phytoplankton groups, chlorophyll-a and primary production in oceanic and shelf waters, discussing their association with hydrographic and climatologic regimes.

The present work describes the annual variation of diatom associations at a coastal station off Paraná State, South Brazil, searching for a better understanding of their peak occurrence in relation to the environmental conditions throughout the year.

MATERIAL AND METHODS

The sampling station was located at 48°15'30"W and 25°37'30"S, 5.4 nautical miles off the entrance of the Bay of Paranaguá, Paraná State, Southern Brazil (Fig. 1). Local depths ranged from 16 to 18 meters, depending on the tidal variation. Water samples were collected every 7-15 days for one year from May 1990 to April 1991, at 0, 2.5, 5, 10 and 15 meters depth, using a 3.5 liters Van Dorn bottle.

Water samples (100 ml) were preserved with buffered formaldehyde solution (0,4%) for diatoms and thecate dinoflagellates; and with Lugol's acetic solution for athecate dinoflagellates and nanoflagellates (Thronsen, 1978). Cell counts were made by allowing 25ml of subsample to settle over 24hs in Utermöhl chambers for inverted microscope analysis (Hasle, 1978). At least 500 individuals of all dominant diatoms were counted, reducing the counting error to 10% (Venrick, 1978). Microplankton and nanoplankton cells were observed at magnifications of 160x and 400x, respectively. Results show average density values of the five depths sampled, except when absolute values for each depth were required. Spectrophotometric measurements of chlorophyll-a were estimated by means of extractions with 90% acetone according to Strickland & Parsons (1972).

A quantitative cluster analysis of diatom taxa (and interpretations from the field data) was performed to detect groups and their environmental constraints, according to Krebs (1989). Selection of species for analysis was based on abundance (>4000 cells.l⁻¹), frequency of species (at least 10%) in the samples, or ecologically relevant characteristics such as biovolume, thermal preferences, etc. The Pearson correlation coefficient complement was used as a measure of distance for the delimitation of diatom groups, and the Euclidean distances of cell densities

for the sampling dates (Digby & Kempton, 1987; Krebs, 1989).

Samples for taxonomic analysis of diatoms were obtained by vertical net towing (20 μm mesh) from bottom to surface. Permanent slides were prepared according to Hasle & Fryxell (1970) for species identification with optical (Olympus BX40) and scanning electron (Phillips LX30) microscopes.

Water temperature and salinity, as well as major inorganic nutrients, were measured according to Strickland & Parsons (1972). Water transparency was measured with Secchi disc, and the equation of Holmes (1970) was used to calculate the extension of the euphotic zone. Rainfall and wind data were provided by the meteorological station of the National Institute of Meteorology, Paranaguá City, located about 10 km from our sampling station.

RESULTS

Environmental Conditions

The seasonal pattern of precipitation (Fig. 2) was similar to previous years, with rainy periods from January to March, decreasing over the rest of the year, especially in winter, although July also had high values. Wind regime was frequently dominated by moderate ($2.1\text{-}4.0\text{ m.s}^{-1}$) northeast winds, and by moderate to strong ($4.0\text{-}8.3\text{ m.s}^{-1}$) southeast and east winds. The latter are the main determinants of the sea and weather conditions over the region. During the period, frequent intrusions of polar air masses invaded the region, sometimes accompanied by strong winds ($4.5\text{-}7.3\text{ m.s}^{-1}$). North and west winds were rarely dominant ($< 10\%$) over the study period, at low intensity (less than 2.1 m.s^{-1}).

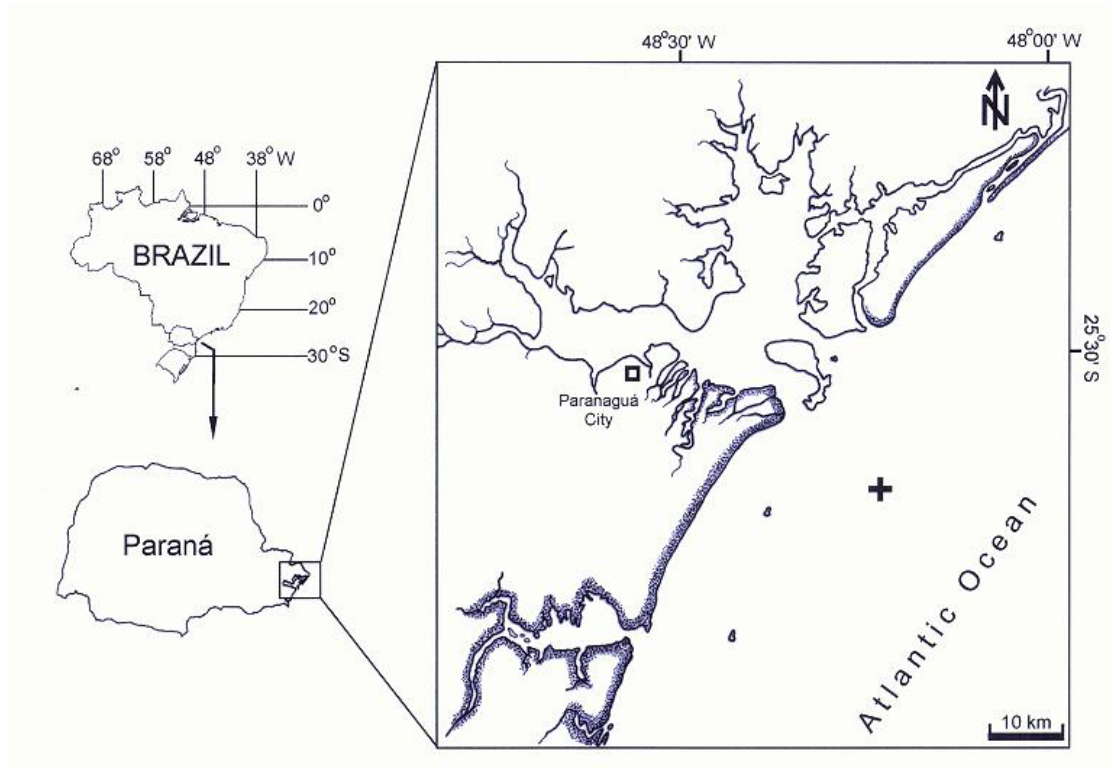


Fig. 1. Map of the study area, showing the sampling station (+).

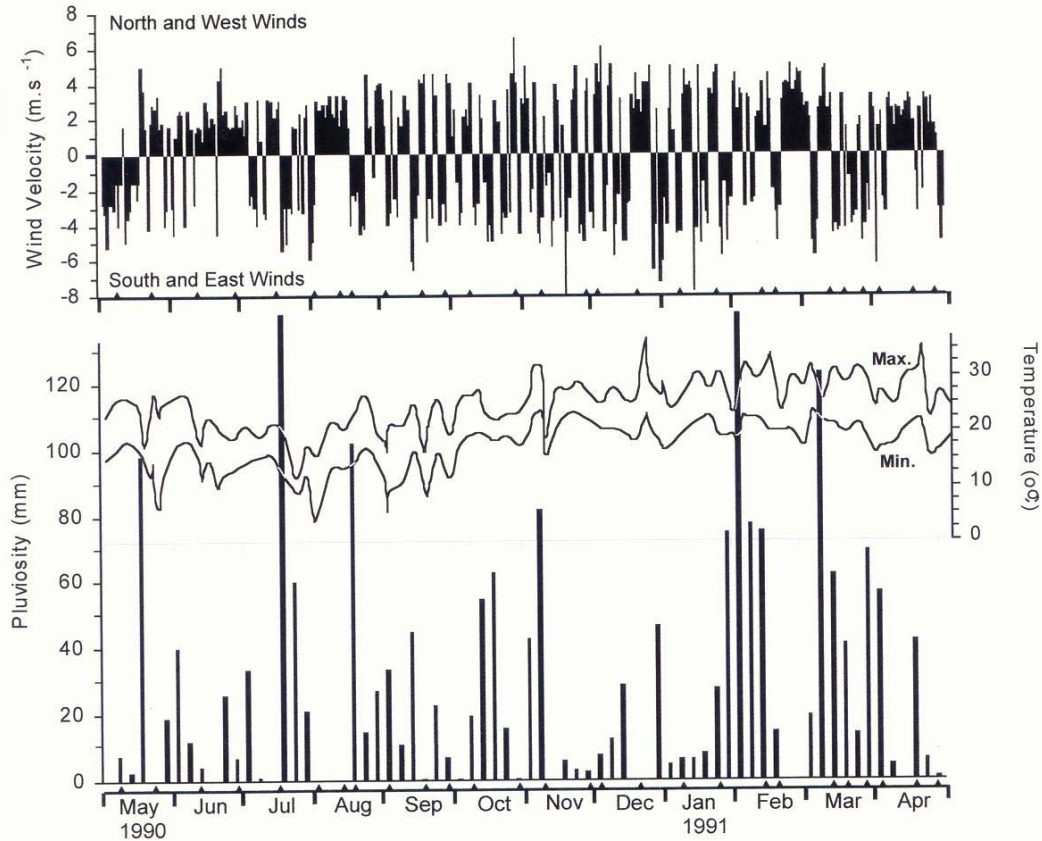


Fig. 2. Climatological parameters recorded from May/1990 to April/1991 in the study region. Wind velocity (upper panel) is expressed as daily values. North and west wind components were plotted on the positive axis, south and east components on the negative axis. In the graph for rainfall, values represent the sum of five days.

Water temperature (Fig. 3) was usually homogeneous throughout the water column, except from January to March, when thermal stratification occurred near the surface. During winter, temperature varied from less than 17°C to 20°C, gradually increasing to 27°C in summer.

The lowest salinities (Fig. 3) were always recorded at the surface, ranging from 29.5 to 33.5, and increasing to 36.5 near the bottom. From August to December and February to April, salinity stratification was observed in the water column, oscillating between 33.0 and 36.5. In other months, the water column maintained homogeneous, with lower values near the surface.

Nitrate concentrations (Fig. 3) varied from less than 0.20 to 1.02 μM , with higher surface values (>0.50 μM) from May to June, and in the whole water column in January. Nitrite concentrations were very

low, usually below 0.10 μM . Phosphate varied from 0.23 to 1.18 μM , with highest values from May to July (0.39-1.18 μM), in January (0.48-0.81 μM) and in April (0.48-0.68 μM), usually near the bottom. Values were below 0.40 μM from August to early November. Concentrations of silicate varied from 5.5 to 51.9 μM , with highest values occurring from August to early October (20.1-47.3 μM) at the surface, and November to January (23.04-51.9 μM) near the bottom. The lowest values were detected from May to July in the upper 10 meters (5.4-24.2 μM), and in April (12.5-29.2 μM).

Light extinction coefficient (k) varied between 0.58 and 0.32, calculated from Secchi disk readings ranging from 2.5 to 4.5 meters. From these values, the estimated 1% light penetration varied from 6.5-12.0 meters (Fig. 4), indicating permanently aphotic conditions below 8.0-9.0 meters.

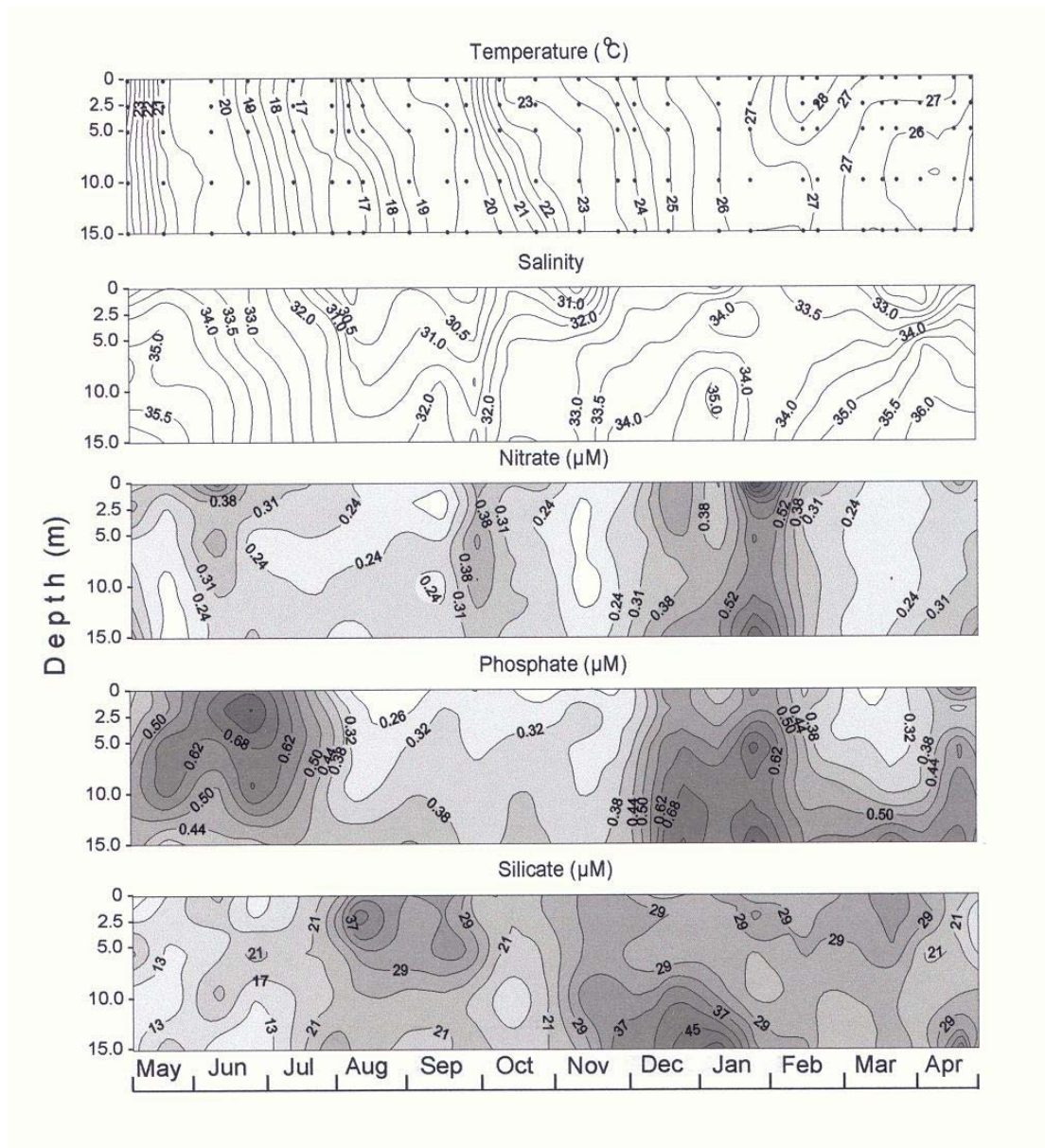


Fig. 3. Vertical distributions of hydrographic parameters from May/1990 to April/1991 at the sampling station off Paranaguá, Paraná, Brazil. Points (●) on graph of water temperature represent the sampling depths.

Vertical distributions of chlorophyll-a and diatom densities in depth and time

Figure 4 shows the vertical distributions of chlorophyll-a and diatom abundances in the >10 µm size fraction. As a general pattern, chlorophyll-a tended to increase from surface to bottom. High values of chlorophyll were observed throughout the water column during the diatom blooms in May and June (up to 1.2×10^6 cells.l⁻¹). In August, diatoms were abundant near the bottom. In September, both

chlorophyll and cell densities decreased, maintaining low densities until early January (except for November). Abundances and chlorophyll-a were high from January to March. In April, when a bloom of *C. walesii* occurred, cell densities were low but chlorophyll values were high (> 3.78-4.72 mg.m⁻³ at bottom depths), due to the large biovolume and the chlorophyll content of *C. walesii*.

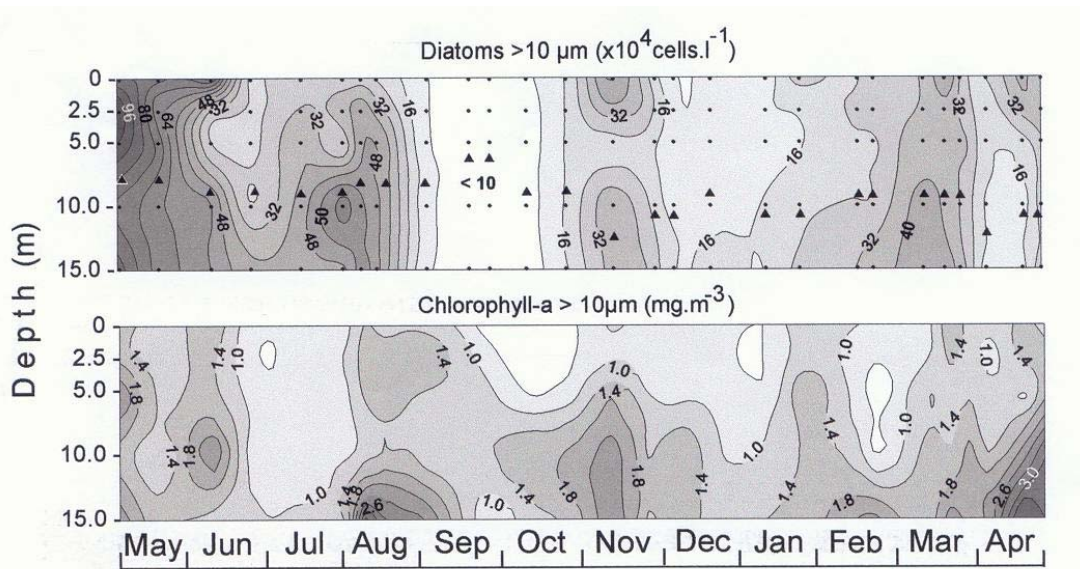


Fig. 4. Vertical distributions of microplanktonic diatoms and chlorophyll-a from May/1990 to April/1991 at the sampling station off Paranaguá, Paraná, Brazil. Depth of euphotic zone (1%) is indicated by (▲).

Annual variation of diatoms and other phytoplankton groups in different size classes

Average densities of microplankton (>20 µm) cells ranged from 6.0×10^4 to 9.6×10^5 cells.l⁻¹ (Figs 5 and 6) with diatoms as the dominant group (5.4×10^4 - 9.6×10^5 cells.l⁻¹). They accounted for most of the phytoplankton cells, and should be responsible for the bulk of chlorophyll-a (> 10 µm) concentrations. Diatoms were very abundant

from May to August (2.6×10^5 - 9.6×10^5 cells.l⁻¹), decreasing from September to January (5.5×10^4 - 3.7×10^5 cells.l⁻¹). From January 23 to March cell densities varied between 1.1×10^5 cells.l⁻¹ and 4.1×10^5 cells.l⁻¹. Abundances were low again in April (1.1×10^5 - 2.9×10^5 cells.l⁻¹). In this month, a bloom of *Coscinodiscus wailesii* (with 290 µm-410 µm valvar diameter and 180 µm-240 µm pervalvar axis) occurred, reaching densities up to 5.6×10^3 cells.l⁻¹.

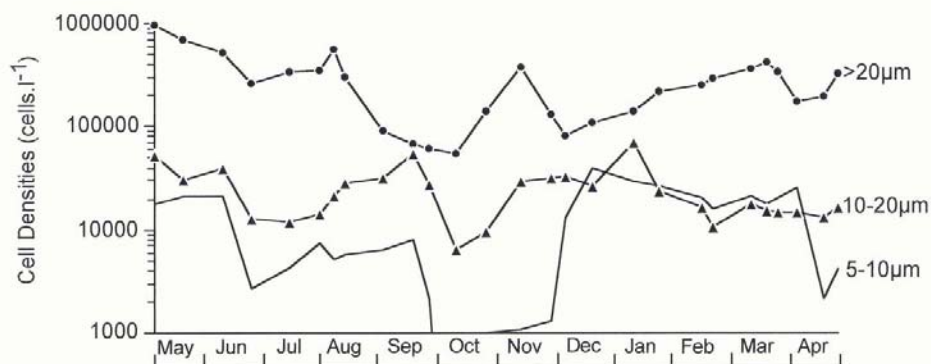


Fig. 5. Annual variation of diatoms in different size classes at the sampling station, expressed as cell densities. Note logarithmic scale on the axis for cell densities. Values are averages from the five depths sampled.

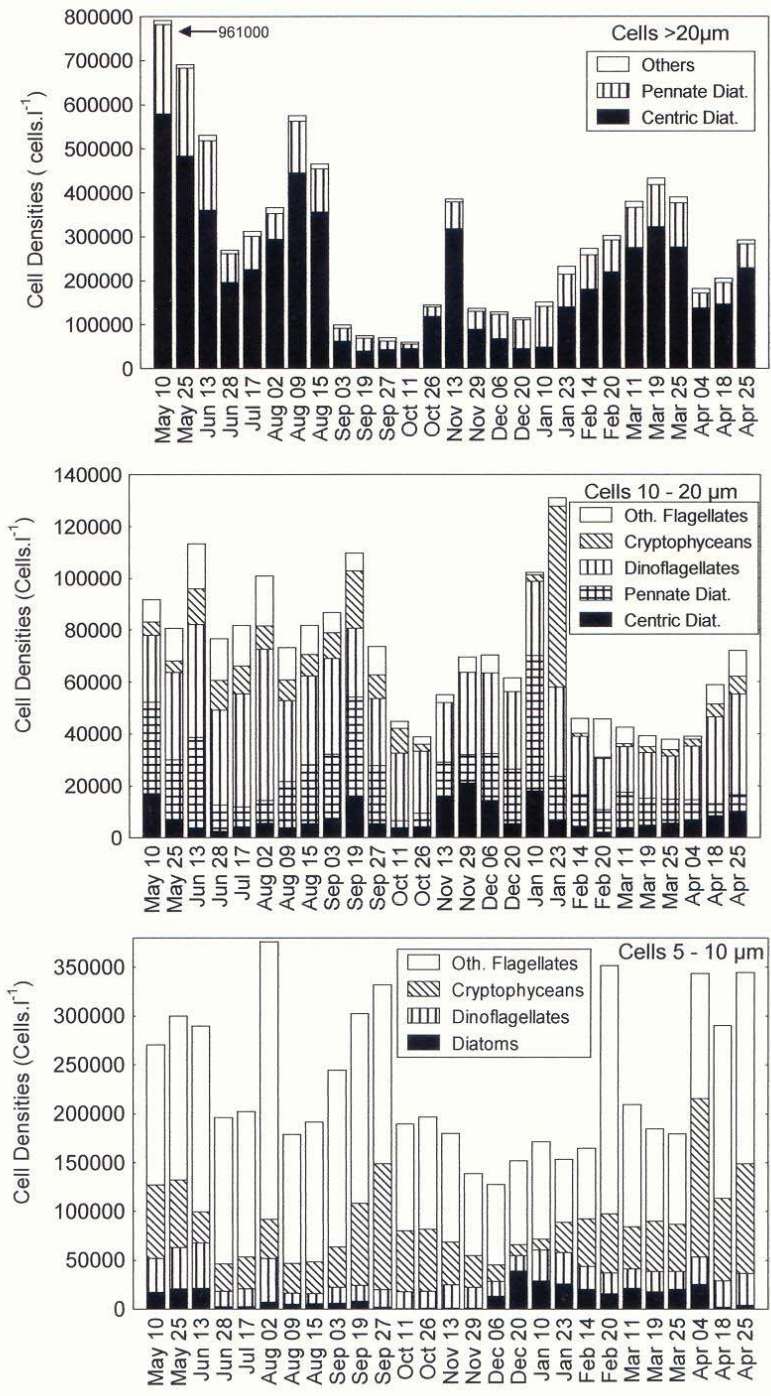


Fig. 6. Annual variation of diatoms and other groups of the phytoplankton in different size classes, expressed as cell densities. Values are averages from the five depths sampled.

The nanoplankton (2-20 μm) was studied in three size classes. In the 10-20 μm size class (Figs 5 and 6) diatoms were also important (9.4×10^3 - 7.4×10^4 cells.l⁻¹), the highest values being detected on May 10, September 19, and January 10. Centric diatoms varied from 2.1×10^3 to 3.8×10^4 cells.l⁻¹, and pennate diatoms from 5.2×10^3 to 5.2×10^4 cells.l⁻¹, mainly epiphytic on chain-forming species of *Bacteriastrum* spp. and *Chaetoceros* spp.. *Thalassiosira* spp. (4 species), *Nitzschia* spp. (3 species) and two non-identified species of Naviculaceae were often present. In the 5-10 μm size class (Figs 5 and 6), diatoms were poorly represented ranging from less than 1.0×10^3 to 3.9×10^4 cells.l⁻¹, with peaks in May, June, December and January. Identification of species with light microscopy was difficult, but pennate diatoms resembling *Nitzschia* and *Fragilaria*, and the small species *Chaetoceros cf. tenuissimus* (4-6 μm) were frequently observed. Phytoflagellates and gymnodiniaceans were dominant, occurring at densities between 1.4×10^5 and 3.7×10^5 cells.l⁻¹. In the 2-5 μm size class (Fig. 5), the contribution of diatoms was low (less than 4.0×10^4 cells.l⁻¹). Phytoflagellates dominated, with 8.7×10^4 to 8.6×10^5 cells.l⁻¹. From August to September, a bloom of *Phaeocystis pouchetii* in gelatinous colonies (up to 6.1×10^5 to 1.0×10^6 cells.l⁻¹ near the surface) occurred. From October to April, flagellate densities tended to diminish, varying between 8.7×10^4 cells.l⁻¹ and 3.1×10^5 cells.l⁻¹, and the lowest values were detected in April, during the bloom of *C. wailesii*.

Annual variation of abundant species and groups of diatoms

The bulk of the diatom biomass was made up of chain-forming species. Figure 7 shows the annual variation of cell densities (averaged from the five depths sampled) of 27 abundant species or higher taxonomic groups. Two prominent growth episodes (May-August and January-March) were detected (confirmed by Cluster analysis), when *Cerataulina pelagica*, *Chaetoceros* spp., *Dactylosolen fragilissimus*, *G. striata*, *Lauderia annulata*, *Leptocylindrus* spp., *Pseudo-nitzschia* spp. and *Rhizosolenia* spp. (mainly *R. hebetata* followed by *R. calcaravis*, *R. setigera* and *R. styliformis*) dominated. Between these periods, total cell densities tended to decrease, mainly in September, October, January and April. *Skeletonema costatum* and *Thalassionema nitzschioides* showed irregular peaks along the study period. In some months, *Thalassiosira* spp. (May to

August), *Hemiaulus* spp. (June to August and October to November), *Eucampia* spp. (November and December) and *Coscinodiscus* spp. (May, August and October) were important. Large species of *Coscinodiscus* were abundant in October and November (*C. oculus-iridis* and *C. centralis*) and in April (*C. wailesii*).

Some additional comments about the dominant species within the taxonomic categories represented in the Figure 7 are given. Within *Chaetoceros*, the most abundant species were *C. affinis*, *C. compressus*, *C. curvisetus*, *C. debilis* and *C. didymus*. The genus *Guinardia* was composed of *G. delicatissima* and *G. striata*. *B. delicatulum* and *B. hyalinum* composed the genus *Bacteriastrum*. In "Naviculaceae", a broader taxon composed of many species; *Navicula* spp. and *Mastogloia* spp. were abundant, as planktonic and benthic forms.

CLUSTER ANALYSIS

The dendrogram produced for temporal patterns of diatoms (Fig. 8a) generated six groups (A - F). The warm species *Hemiaulus hauckii* and *H. sinensis* and *Coscinodiscus* spp. comprised Group A. Their maximal abundances occurred not only in October and November, but also in June and July, when water temperatures recorded were the lowest. In Group B, *Detonula pumila* and *T. mediterranea* were usually scarce, but with sharp peaks in July and August. The position of *S. costatum* in this group could not be explained, since its occurrence pattern was distinct, being abundant throughout the year, and with peaks in July, August and November. Group C contained two subtropical species (*E. cornuta* and *E. zoodiacus*) but with density peaks from October to November, but at low concentrations for most of the year. The first three groups are related to the influence of warm waters, carrying species to coastal waters, after the late fall/winter diatom bloom. Groups D, E, and F were formed by abundant neritic species from May to July and February to March. They were associated with periods of nutrient enrichment in the water column due to the higher rainfall, and the influence of coastal subantarctic waters. Group D was composed of *Bacteriastrum* spp. and *L. annulata*, and their clustering was based on evident peaks in May, June and April. Diatoms in Group E showed peaks in February and March. Group F was influenced by the higher abundances recorded from May to July and from February to March.

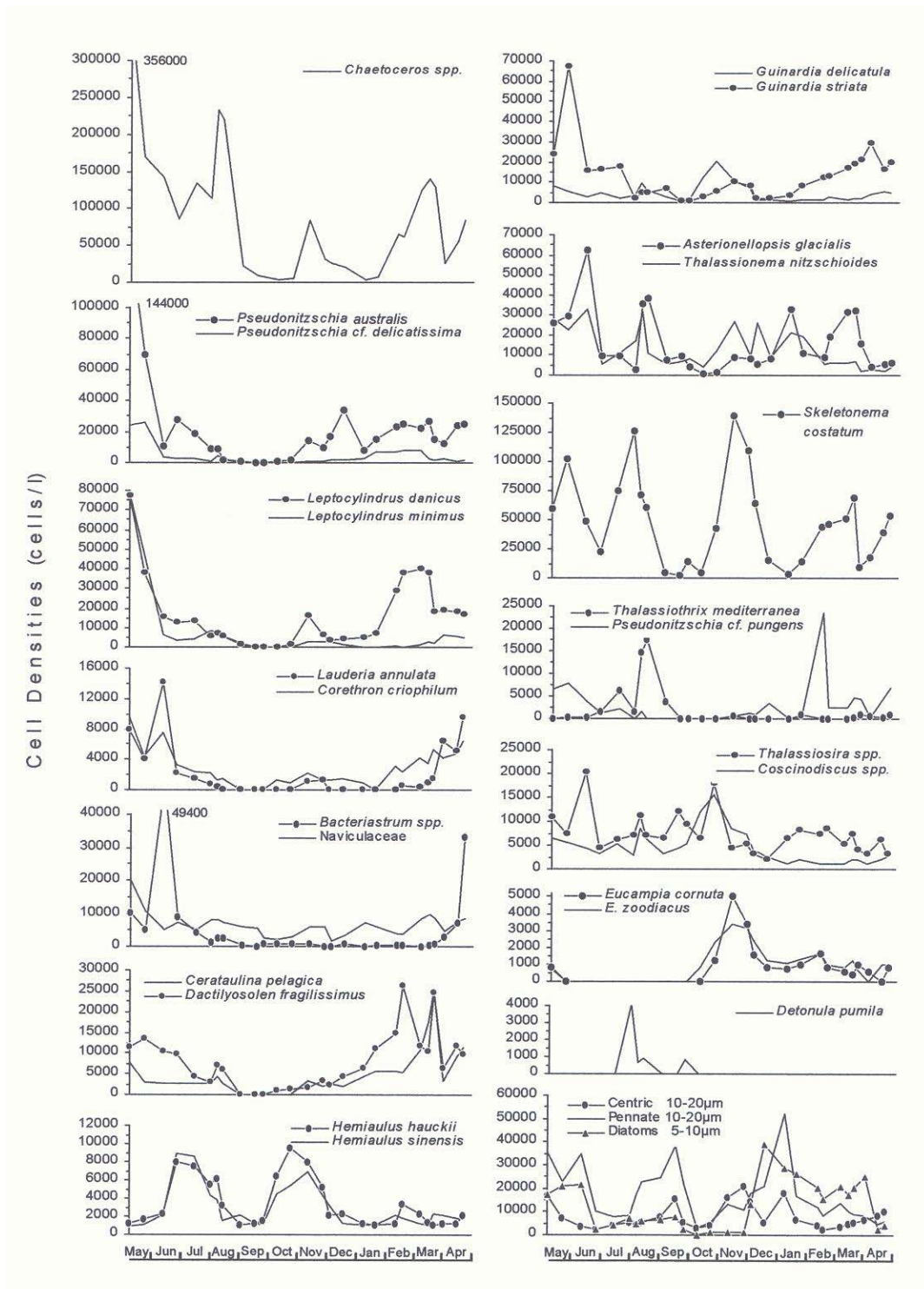


Fig. 7. Annual variation of most important diatom taxa from May/1990 to April/1991 in the sampling station. Note different scales of cell densities in the graphs. Values are averages from the five depths sampled.

The cluster analysis of sampling dates/cell densities (Fig. 8b) indicated the main environmental factors acting over the region. Group I represented periods of low diatom densities under low nutrient levels due to the stronger influence of oligotrophic waters of the Brazil Current, and when the blooms of *Phaeocystis* and *C. wailesii* occurred. Group II

probably represents periods of intermediate or diverse environmental conditions, when different stages of diatom growth took place. Groups III and IV were influenced by the higher abundance of dominant species, resulting from the presence of enriched subantarctic waters from May to early August, and the more intense land drainage in March.

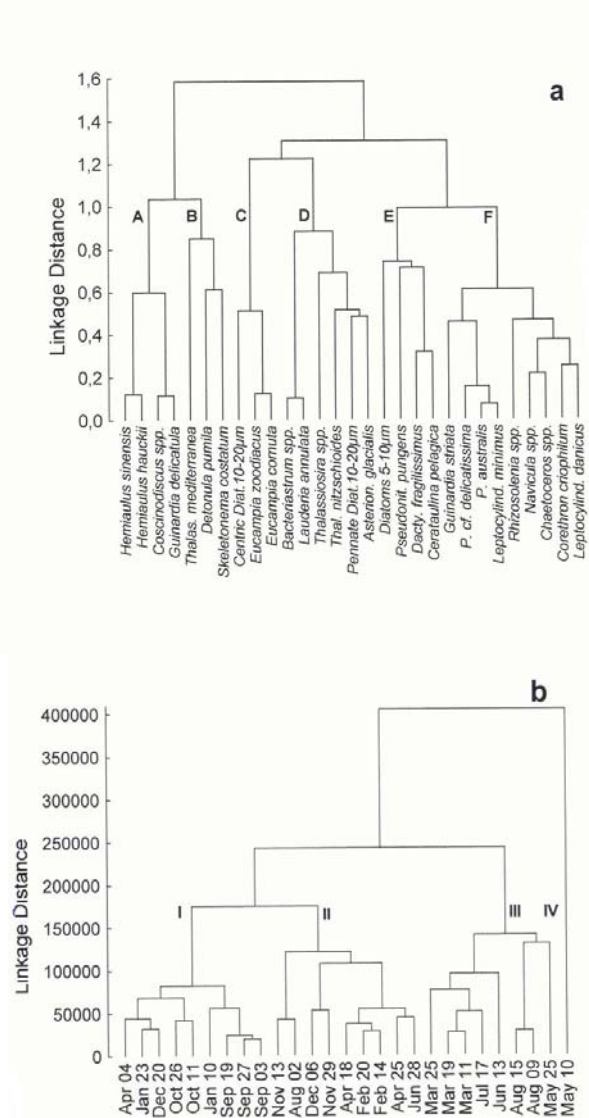


Fig. 8. Quantitative dendrograms for classification of diatom taxa (a) and of sampling dates (b) in the sampling station. Six diatom groups (A-F) were considered as true biological associations. For details, see the text.

NET PLANKTON

Some observations were made on the composition of net plankton diatoms, and Appendix I shows the species found in the present study. A mixed flora of warm and temperate planktonic neritic species formed the majority of the community, and their abundance varied depending upon water mass. During spring and summer, species typical of warm waters appeared frequently, e. g. *Climacodium frauenfeldianum*, *Coscinodiscus centralis*, *C. gigas*, *Eucampia* spp., *Hemiaulus membranaceus*, *Stephanopyxis turris* and, rarely, *Gossleriella tropica* and *Planktoniella sol*. In addition, the coccolithophorid *Umbilicosphaera sibogae* and other tropical/subtropical species of dinoflagellates such as *Ceratium azoricum*, *C. vultur*, *Corithodinium tessellatum*, *Podolampas bipes*, *P. elegans*, and *Schuttiella mitra* were recorded. In winter, cold water species such as *Asteromphalus hookerii*, *Lauderia annulata*, *Rhisozolenia setigera*, *Detonula pumila*, *Thalassiothrix frauenfeldii*, *Thalassiosira nodulolineata*, *T. poroseriata* and *T. tumida* were frequent. Uncommon diatoms in Brazilian waters were *Anorthoneis eurystoma*, *Asteromphalus arachnae*, *Asteromphalus sarcophagus*, *Bacteriastrum comosum*, *Minidiscus chilensis* and *Porosira pentaportula*.

Besides planktonic species, many benthic diatoms were identified in the water column, and were even abundant occasionally. These included *Achnanthes* sp., *Anorthoneis eurystoma*, *Cyclotella stylorum*, *Delphineis surirella*, *Mastogloia* spp., *Paralia sulcata*, *Rhaphoneis amphiceros* and *Thalassiosira* spp. (valvar diameters ranging from 10 to 20 μm). The latter are quite similar to those found in groups of three to eight cells aggregating small sand grains (Ernissee & Abbott, 1975). These benthic species and other dominant tychoplanktonic species as *Chaetoceros* spp. and *T. nitzschoides* clearly indicate the bottom influence.

DISCUSSION

The dominance of diatoms within coastal phytoplankton assemblages reflects the physical instability of shallow coastal environments. Turbulence tends to maintain the vertical homogeneity of physical and chemical parameters, maintaining high nutrient concentrations in the euphotic zone due to the resuspension of sediments (Smetacek, 1985; 1988). In addition, turbulence tends to retard the sinking of species out of the euphotic zone, while land drainage continuously enriches the

neritic region and decreases salinity, favoring diatom growth (Margalef, 1978; Smayda, 1980).

In the present study, microplanktonic diatoms were always the dominant autotrophs, occurring at 4-10 fold higher densities than other groups during the period, except during the period of low biomass in September and October, when nanoplankton dominated. Diatoms also tended to contribute more with chlorophyll-a biomass than the nanoplankton fraction, except in September and October, when a bloom of *Phaeocystis pouchetii* dominated the phytoplankton, and under the stronger influence of tropical waters carried in the region by the Brazil Current from November to February. Diatoms were also the main primary producers in adjacent areas near our sampling station (Brandini, 1990; 1990a). Their dominance is also reflected in the higher trophic levels, as they represent the principal diet of the dominant copepods (*Acartia lilljeborgii*, *Corycaeus* spp., *Oncaea* spp., *Paracalanus quasimodo*, *Temora turbinata*) in the region, which are large omnivorous or herbivorous grazing on microsize particles (Lopes *et al.*, 1998).

As a general pattern, neritic subtropical diatoms dominated throughout the year, under the influence of the Brazil Current and land drainage. However, colder subantarctic waters and blooms of different algal groups also affected the composition and the overall densities of microphytoplankton. May to August comprised the largest diatom pulses, representing Groups E and F from the cluster analysis, dominated by *Asterionellopsis glacialis*, *Chaetoceros* spp., *Guinardia striata*, *Leptocylindrus* spp. and *Pseudo-nitzschia* spp. Such blooms might be caused by traces of nutrient-rich subantarctic waters mixed with coastal waters, as indicated by the elevated nitrate and phosphate concentrations and the presence of cold-water diatom species. The influence of the freshwater discharges of the La Plata River, as pointed out by Boltovskoy (1981) and Ciotti *et al.* (1995), must also be taken into account as important factors enriching the Paraná coast during autumn and winter. Coastward intrusion of subantarctic waters over the Brazilian shelf is a common feature of the local hydrographic regime during winter (Boltovskoy, 1981; Brandini, 1990; Campos *et al.*, 1996). Brandini (*op. cit.*) also observed higher phytoplankton biomass during the winter, associated with the presence of subantarctic waters. Lange (1985) noted a greater influence of the subantarctic flora over the Argentinian shelf in winter. The typical warm species *Hemiaulus hauckii* and *H. sinensis* also responded to the nutrient enrichment, increasing in abundance in late fall.

The decrease in diatoms between September and early January (except for the isolated peak in November 13) could be associated with the lower availability of silicate due to uptake during fall/winter blooms. Moreover, precipitation was low compared to other months, diminishing the input of nutrients via land runoff. Cell densities decreased and only *Guinardia delicatula*, *Detonula pumila*, *Thalassionema nitzschioides* and some Naviculaceae were abundant. In contrast, a bloom of *Phaeocystis pouchetii* took place in September, just after the diatom bloom. As for the seasonal phytoplankton succession observed in the North Sea over the last decades, *Phaeocystis* becomes dominant after silica depletion and aging of the diatom blooms (Lancelot *et al.*, 1991). In the North Sea such community replacement has been associated with increasing organic pollution, resulting in changes of nutrients and N/P ratios (Riegmann *et al.*, 1992). However, this is not the case on the Paraná coast, where pollution is of minor importance as a factor regulating phytoplankton succession.

Diatom abundance again increased from January 23 to March, when nutrient concentrations near the surface were elevated, due to higher precipitation and concomitant land drainage. In this period, *Asterionellopsis glacialis*, *Cerataulina pelagica*, *Chaetoceros* spp., *Dactylosolen fragilissimus*, *Guinardia striata*, *Leptocylindrus danicus*, *Pseudo-nitzschia* spp. and *Skeletonema costatum* dominated the diatom community. The less pronounced development of diatoms in summer/early fall compared to late fall/winter could be due to the stronger coastward displacement of the oligotrophic Brazil Current waters, mixing with shelf waters (Emilsson, 1960; Brandini, 1990) and diluting nutrients to some extent. The presence of warm-species and higher salinities (up to 35.0) compared to other periods, confirm the influence of tropical waters in the study area. For comparison, near our sampling station in the mesohaline estuarine waters of Paranaguá Bay, the highest phytoplankton biomass occurred during the rainy period from January to March, when nutrient input via land runoff increased. In contrast to our findings, *Skeletonema costatum* dominated the community (up to 4.7×10^6 cells.l⁻¹) in the Bay, accounting for more than 90% of total densities (Brandini, 1985; 1985a).

The bloom of *Coscinodiscus wailesii* was another important event affecting phytoplankton community structure during April 1991, when densities of diatoms and other phytoplankton groups had fallen, and even zooplankton was almost absent (L. F. Fernandes and R. M. Lopes, unpublished data). Chlorophyll-a concentration was high, due to the large volume of *C. wailesii* cell, associated to its

chlorophyll-a content. This bloom persisted until November 1991, and the species became common at Paranaguá Bay in the following years (Fernandes *et al.*, 2001). Despite its large size, this species is fast growing, highly competitive for nutrients, euryhaline and inefficiently grazed or even avoided by copepods (Rick & Dürselen, 1995; Roy *et al.*, 1989). All these factors help to explain why *C. wailesii* has been successful worldwide after invading turbulent coastal waters.

High nutrient concentrations were frequently recorded at 10-15 meters in association with the occurrence of large populations of benthic and tychoplanktonic diatoms. Based on indirect evidence, it seems reasonable that resuspension of bottom sediments through tidal mixing and wind driven turbulence is responsible for the contribution of benthic diatoms and nutrient regeneration. Studies in coastal areas with similar characteristics have shown that the benthic community is responsible for the regeneration of nutrients to the water column through turbulence (Doering, 1989; Flint & Kamiakowski, 1983; Zeitschel, 1980). Other positive effects of turbulence on the diatom communities inhabiting the study region are: (i) the maintenance of abundant species in the water column, avoiding their sinking to a permanently aphotic zone; and (ii) the resuspension of resting cysts and of tychoplanktonic forms such as *Chaetoceros* (Margalef, 1978; Smetacek, 1985) that are frequently dominant in the study region, allowing completion of their life-cycles.

ACKNOWLEDGEMENTS

We thank CNPq (research grant to L.F.F.) and Centro de Estudos do Mar/UFPR for providing financial support and laboratory facilities. Jaqueline Rebello analyzed most of nutrient samples. We are indebted to Dr. Daura R. Stofella (Centro de Microscopia Eletrônica/UFPR) and Paulo Brixel (LACTEC/Paraná) for the assistance with the scanning electron microscope. This work is part of a MSc. Thesis in Botany, UFPR.

REFERENCES

- Boltovskoy, E. 1981. Masas de água en el Atlantico Sudoccidental. In: Boltovskoy, D. ed. Atlas del Zooplancton del Atlántico Sudoccidental y metodos de trabajo con el zooplancton marino. Mar del Plata, Publ esp INIDEP. p. 227-238.
- Brandini, F. P. 1985. Seasonal succession of the phytoplankton in the bay of Paranaguá (Paraná state - Brazil). Rev. brasil. Biol., 45(4):687-694.
- Brandini, F. P. 1985a. Ecological studies in the bay of Paranaguá. I. Horizontal distribution and seasonal dynamics of the phytoplankton. Bolm. Inst. oceanogr. São Paulo, 33(2):139-147.

- Brandini, F. P. 1990. Hydrography and characteristics of the phytoplankton in shelf and oceanic waters off southeastern Brazil during winter (july/august-1982) and summer (February/March-1984). *Hydrobiol.*, 196(2):111-148.
- Brandini, F. P. 1990a. Produção primária e características fotossintéticas do fitoplâncton na região Sueste do Brasil. *Bolm. Inst. oceanogr.*, S Paulo, 38(2):147-159.
- Brandini, F. P. & Fernandes, L. F. 1996. Microalgae of the continental shelf of Paraná State, southern Brazil: review of studies. *Bolm. Inst. oceanogr.*, S. Paulo, 44(1):69-80.
- Brandini, F. P.; Lopes, R. M.; Gutseit, K. S.; Spach, H. L. & Sassi, R. 1997. Planctonologia na plataforma continental do Brasil. *Diagnose e revisão bibliográfica*. Brasília, Ministério do Meio Ambiente/CIRM/FEMAR. 196p.
- Campos, E. J. D.; Lorenzetti, J. A.; Stevenson, M. R.; Stech, J. L. & Souza, R. B. 1996. Penetration of waters from the Brazil-Malvinas Confluence region along the South American continental shelf up to 23°S. *An. Acad. Bras. Ci.*, 68 (Suppl. 1):49-58.
- Ciotti, A. M.; Odebrecht, C.; Fillmann, G. & Möller Jr, O. 1995. Freshwater outflow and Subtropical Convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. *Continent. Shelf Res.*, 15(14):1737-1756.
- Digby, P. G. N. & Kempton, R. A. 1987. *Multivariate analysis of ecological communities*. London, Chapman and Hall. 450p.
- Doering, E. G. 1989. On the contribution of the benthos to pelagic production. *J. Mar. Res.*, 47(2):371-383.
- Emilsson, I. 1960. The shelf and coastal waters off the Southern Brazil. *Bolm. Inst. oceanogr.*, S Paulo, 11(único):101-112.
- Ernissee, J. J. & Abbott, W. H. 1975. Binding of mineral grains by a species of *Thalassiosira*. *Nova Hedwigia, Beih.*, 53:241-252.
- Fernandes, L.F. & Brandini, F.P. 1999. Microplankton communities in Southwestern Atlantic Ocean: biomass and distribution in November 1992. *Rev. bras. oceanogr.*, 47(2):189-205.
- Fernandes, L. F.; Zehnder-Alves, L. & Bassfeld, J. C. 2001. The recently established diatom *Coscinodiscus wailesii* (Coscinodiscales, Bacillariophyta) in Brazilian waters. I. Remarks on morphology and distribution. *Phycological Res.*, 49:89-96.
- Flint, R. W. & Kamiakowski, D. 1984. Benthic nutrient regeneration in South Texas coastal waters. *Estuar. Coast. Shelf Sci.*, 18(2):221-230.
- Harris, G. P. 1986. *Phytoplankton ecology: structure, function and fluctuation*. New York, Chapman and Hall. 384p.
- Hasle, G. R. 1978. Using the inverted microscopy. In: Sournia, A., ed. *Phytoplankton manual*. Monogr. Oceanogr. Methodol, U.N. 6:191-196.
- Hasle, G. R. & Fryxell, G. A. 1970. Diatoms: cleaning and mounting for light and electron microscopy. *Trans. Am. Microsc. Soc.*, 89:469-474.
- Holmes, R. W. 1970. The Secchi disk in turbid coastal waters. *Limnol. Oceanogr.*, 15:688-694.
- Hubold, G. 1980. Hydrography and plankton off Southern Brazil and Rio de la Plata: august-november 1977. *Atlantica*, 4:1-21.
- Hubold, G. 1980a. Second report on Hydrography and plankton off Southern Brazil and Rio de la Plata: autumn cruise: april-june 1978. *Atlantica*, 4:23-42.
- Krebs, C. J. 1989. *Ecological methodology*. New York, Harper Collins Publ. 850p.
- Lancelot, C.; Billen, G. & Barth, H. 1991. The dynamics of *Phaeocystis* blooms in nutrient enriched coastal zones. *Water Pollut., Res. Rep.*, 23:1-116.
- Lange, C.B. 1985. Spatial and seasonal variations of diatom assemblages off the argentinian coast (South Western Atlantic). *Oceanol. Acta*, 8:361-369.
- Lopes, R. M.; Vale, R. & Brandini, F. P. 1998. Composição, abundância e distribuição espacial do zooplâncton no complexo estuarino de Paranaguá durante o inverno de 1993 e o verão de 1994. *Rev. bras. oceanogr.* 46(2):195-211.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in unstable environments. *Oceanol. Acta*, 1:493-509.
- Moreira-Filho, H.; Valente-Moreira, I. M.; Souza-Mosimann, R. M. & Cunha, J.A. 1990. Avaliação florística e ecológica das diatomáceas (Chrysophyta-Bacillariophyceae) marinhas e estuarinas nos estados do Paraná, Santa Catarina e Rio Grande do Sul. *Est. Biologia (PUC)*, 25:5-48.
- Rick, H. J. & Dürselen, C. D. 1995. Importance and abundance of the recently established species *Coscinodiscus wailesii* Gran et Angst in the German Bight. *Helgolander Meeresunters.*, 49: 355-74.
- Riegmann, R.; Noordeloos, A. A. M. & Cadée, G. C. 1992. *Phaeocystis* blooms and eutrophication of the coastal zones of the North Sea. *Mar. Biol.*, 112(3):479-484.
- Roy, S.; Harris, R. P. & Puleo, S. A. 1989. Inefficient feeding by *Calanus helgolandicus* and *Temora longicornis* on *Coscinodiscus wailesii*: quantitative estimation using chlorophyll-type pigment and effects on dissolved free amino acids. *Mar. Ecol. Prog. Ser.*, 52:145-53.
- Smayda, T. 1980. Phytoplankton species succession. In: Morris, I. ed. *The physiological ecology of phytoplankton*. Studies in ecology 7. Oxford Blackwell Scient. Publ. p. 493-570.
- Smetacek, V. S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.*, 84:239-251.
- Smetacek, V. S. 1988. Plankton characteristics. In: Postma, H. & Zijlstra, J. J. eds. *Ecosystems of the world, Continental shelves*, v. 27 Amsterdam, Elsevier. p. 93-130.
- Strickland, J. D. H. & Parsons, T. R. 1972. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Can.*, 122:1-172.
- Thronsen, J. 1978. Preservation and storage. In: Sournia, A., ed. *Phytoplankton manual*. Monogr oceanogr. Methodol., V.N., 6: 69-74.

- Valentin, J. L.; Lins da Silva, N. M.; Monteiro-Ribas, W. M.; Mureb, M. A.; Bastos, C. T. B. T.; Tenenbaum, D. R.; André, D. L.; Jacob, S. A. & Pessotti, E. 1986. Le plancton dans l'upwelling de Cabo Frio (Brésil): microrépartition spatio-temporale à une station fixe. Ann. Inst. océanogr., Paris, Nouv. Serv., 62:117-135.
- Venrick, E.L. 1978. How many cells to count? In: Sournia, A. ed. Phytoplankton manual. Monogr. oceanogr. Methodol., V.N., 6:167-180.
- Werner, D. ed. 1977. The biology of diatoms. Ecolog. Monogr., 13. Los Angeles, University of California Press. 498p.
- Zeitschel, B. 1980. Sediment-water interactions. In: Tenore, K. R. & Coull, B. C. eds. Marine benthic dynamics. South Carolina, University of South Carolina Press. p. 195-218.

*(Manuscript received 07 May 2003; revised
15 September 2003; accepted 06 October 2003)*

Appendix 1. Diatom taxa recorded during the sampling period in the coastal station off Paranaguá, Paraná, Southern Brazil.

<i>Achnanthes curvirostrum</i> Brun	<i>Cocconeis scutellum</i> Ehrenberg
<i>Achnanthes fimbriata</i> (Grunow) Ross	<i>Corethron criophilum</i> Castracane
<i>Achnanthes</i> sp.	<i>Coscinodiscus asteromphalus</i> Ehrenberg
<i>Actinocyclus ehrenbergii</i> Ralfs	<i>Coscinodiscus centralis</i> Ehrenberg
<i>A. ehrenbergii</i> var. <i>ralfsii</i> (Wm. Smith) Hustedt	<i>Coscinodiscus curvatus</i> Grunow
<i>Actinoptychus campanulifer</i> A. Schmidt	<i>Coscinodiscus gigas</i> Ehrenberg
<i>Actinoptychus undulatus</i> (Bailey) Ralfs	<i>Coscinodiscus granii</i> Gough
<i>Actinoptychus vulgaris</i> Schumann	<i>Coscinodiscus jonesianus</i> (Greville) Ostenfeld
<i>Amphiprora alata</i> (Ehrenberg) Kutzing	<i>Coscinodiscus kutzingii</i> A. Schmidt
<i>Amphiprora gigantea</i> Grunow	<i>Coscinodiscus obscurus</i> A. Schmidt
<i>Amphiprora</i> sp.	<i>Coscinodiscus oculus-iridis</i> Ehrenberg
<i>Amphora arenaria</i> Donkin	<i>Coscinodiscus rothii</i> (Ehrenberg) Grunow
<i>Amphora</i> spp.	<i>Coscinodiscus wailesii</i> Gran and Angst
<i>Anorthoneis eurystoma</i> Cleve	<i>Coscinodiscus</i> spp.
<i>Asterionellopsis glacialis</i> (Castracane) F.E. Round	<i>Cyclotella litorallis</i> Lange & Syvertsen
<i>Asteromphalus arachne</i> (Brébisson) Ralfs	<i>Cyclotella stylorum</i> Brightwell
<i>Asteromphalus heptactis</i> (Brébisson) Ralfs	<i>Cylindrotheca closterium</i> (Ehrenberg) Reimer
<i>Asteromphalus hookeri</i> Ehrenberg	<i>Cymatodiscus planetophorus</i> (Meister) Hendey
<i>Asteromphalus sarchofagus</i> Wallich	<i>Cymatnitzschia marina</i> (Lewis) Simonsen
<i>Bacillaria paradoxa</i> Gmelin	<i>Cymatotheca weissflogii</i> (Grunow) Hendey
<i>Bacteriastrum comosum</i> Pavillard	<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle
<i>Bacteriastrum delicatulum</i> Cleve	<i>Dactyliosolen mediterraneus</i> H. Peragallo
<i>Bacteriastrum hyalinum</i> Lauder	<i>Delphineis surirella</i> (Grunow) Andrews
<i>B. hyalinum</i> var. <i>princeps</i> (Castracane) Ikari	<i>D. surirella</i> var. <i>australis</i> (Grunow) Andrews
<i>Bacteriastrum varians</i> Lauder	<i>Dimerogramma marinum</i> (Gregory) Ralfs
<i>Biddulphia longicuris</i> Greville	<i>Dimerogramma minor</i> (Gregory) Ralfs
<i>Biddulphia rhombus</i> (Ehrenberg) W. Smith	<i>Diploneis bombus</i> Ehrenberg
<i>Biddulphia tridens</i> (Ehrenberg) Ehrenberg	<i>Diploneis crabro</i> (Ehrenberg) Ehrenberg
<i>Campylodiscus ecclesianus</i> Greville	<i>Diploneis smithii</i> (Brébisson) Cleve
<i>Campylosira cymbeliformis</i> (A. Schmidt) Grunow	<i>Diploneis weissflogii</i> (A. Schmidt) Cleve
<i>Cerataulina pelagica</i> H. Peragallo	<i>Diploneis</i> sp.
<i>Chaetoceros affinis</i> Lauder	<i>Ditylum brightwellii</i> (West) Grunow
<i>Chaetoceros coarctatus</i> Lauder	<i>Donkinia reta</i> (Cleve) Cox
<i>Chaetoceros compressus</i> Lauder	<i>Eucampia cornuta</i> (Cleve) Grunow
<i>Chaetoceros costatum</i> Pavillard	<i>Eucampia zodiacus</i> Ehrenberg
<i>Chaetoceros curvisetum</i> Cleve	<i>Fragilariopsis doliolus</i> (Wallich) Medlin and Sims
<i>Chaetoceros danicus</i> Cleve	<i>Grammatophora marina</i> (Lyngbie) Kutzing
<i>Chaetoceros debilis</i> Cleve	<i>Guinardia delicatula</i> (Cleve) Hasle
<i>Chaetoceros decipiens</i> Cleve	<i>Guinardia flaccida</i> (Castracane) Peragallo
<i>Chaetoceros didymus</i> Ehrenberg	<i>Guinardia striata</i> (Stolterfoth) Hasle
<i>Chaetoceros diversus</i> Cleve	<i>Gyrosigma balticum</i> (Ehrenberg) Rabenhorst
<i>Chaetoceros eibenii</i> (Grunow) Meister	<i>Gyrosigma exoticum</i> Cholnoky
<i>Chaetoceros laevis</i> Leuduger-Fortmorel	<i>Gyrosigma scalproides</i> (Rabenhorst) Cleve
<i>Chaetoceros lauderi</i> Ralfs	<i>Hemiaulus hauckii</i> Grunow
<i>Chaetoceros lorenzianus</i> Grunow	<i>Hemiaulus membranaceus</i> Cleve
<i>Chaetoceros messanensis</i> Castracane	<i>Hemiaulus sinensis</i> Greville
<i>Chaetoceros pendulus</i> Karsten	<i>Hemidiscus cuneiformis</i> Wallich
<i>Chaetoceros peruvianus</i> Brightwell	<i>Lauderia annulata</i> Cleve
<i>Chaetoceros socialis</i> Lauder	<i>Leptocylindrus danicus</i> Cleve
<i>Chaetoceros cf. tenuissimus</i> Meunier	<i>Leptocylindrus minimus</i> Gran

Cont. Appendix 1.

- Climacodium frauenfeldianum* Grunow
Licmophora clevei Hustedt
Lithodesmium undulatum Ehrenberg
Lyrella abruptoides (Hustedt) D.G. Mann
Lyrella barbara (Heiden and Kolbe) D.G. Mann
Lyrella hennedyi (Wm. Smith) Stickle and Mann
Lyrella lyra (Ehrenberg) D.G. Mann
Margaritum terebro (Leuduger F.-Morel) H. Moreira
Mastogloia acutiuscula Grunow
Mastogloia angulata Lewis
Mastogloia apiculata Wm. Smith
Mastogloia decussata Grunow
Mastogloia exigua Lewis
Mastogloia meisterii Hustedt
Mastogloia pumilla (Grunow) Cleve
Mastogloia spp.
Minidiscus chilensis Rivera and Koch
Navicula crucicula (Wm. Smith) Donkin
Navicula pennata A. Schmidt
Navicula yarrensii Grunow
Navicula spp. (4 species)
Nitzschia longissima (Brebisson) Ralfs
Nitzschia ventricosa Kitton

Nitzschia spp.
Odontella aurita (Lyngbie) Simonsen
Odontella mobiliensis (Bailey) Simonsen
Odontella sinensis (Greville) Simonsen
Odontella sp.
Palmeria hardmaniana Greville
Paralia sulcata (Ehrenberg) Kutzing
Parlibellus hagelsteinii (Hustedt) E. J. Cox
Parlibellus tubulosus (Grunow) E. J. Cox
Petrodycton gemma (Ehrenberg) D.G. Mann
Petronis marina (Ralfs) D.G. Mann
Plagiogramma staurophorum (Gregory) Hendey
Plagiotropis sp.
Pleurosigma diversistriatum Meister
Pleurosigma formosum Wm. Smith
Pleurosigma intermedium Wm. Smith
Pleurosigma sp.
Podocystis adriatica Kutzing
Podosira stelliger (J.W. Bailey) Mann
Porosira pentaportula Syvertsen and Lange

Licmophora abbreviata Agardh
Proboscia alata (Brightwell) Sündstrom
Psamodycton panduriforme (Grunow) D.G. Mann
Pseudo-nitzschia australis Frenguelli
Pseudo-nitzschia cf. *delicatissima* (Cleve) Heiden
Pseudo-nitzschia pungens (Grunow ex Cleve) Hasle
Pseudosolenia calcar-avis (Schultze) Sündstrom
Rhaphoneis amphiceros (Ehrenberg) Cleve

Rhizosolenia hebetata Gran
Rhizosolenia pungens Cleve-Euler
Rhizosolenia robusta Norman
Rhizosolenia setigera Brightwell
Rhizosolenia styliformis Brightwell
Detonula pumila (Castracane) Gran
Skeletonema costatum (Greville) Cleve
Stauropsis membranacea (Cleve) Meunier
Stephanopyxis palmeriana (Grev.) Grunow
Stephanopyxis turris (Greville) Ralfs
Streptothecca tamensis Schrub
Surirella fastuosa Ehrenberg
Synedra sp.
Thalassionema nitzschioides Grunow
Thalassiosira anguste-lineata (Schmidt) Fryxell and Hasle

Thalassiosira decipiens (Grunow) Jorgensen
Thalassiosira eccentrica (Ehrenberg) Cleve
Thalassiosira gravida Cleve
Thalassiosira leptopus Jouse
Thalassiosira nanolineata (Mann) Fryxell
Thalassiosira nodulolineata (Hasle) Hasle and Fryxell
Thalassiosira oestrupii (Ostenfeld) Hasle
Thalassiosira poroseriata (Ramsf.) Hasle
Thalassiosira punctigera (Castracane) Hasle
Thalassiosira rotula Meunier
Thalassiosira simonsenii Hasle and Fryxell
Thalassiosira subtilis (Ostenfeld) Gran
Thalassiosira tumida (Janisch) Hasle
Thalassiosira spp.
Thalassiothrix frauenfeldii Grunow
Thalassiothrix mediterranea Cupp
Thalassiosira spp.
Thalassiothrix frauenfeldii Grunow
Thalassiothrix mediterranea Cupp
-