

Offshore Distribution Patterns of the Cyanobacterium *Trichodesmium erythraeum* Ehrenberg and Associated Phyto- and Bacterioplankton in the Southern Atlantic Coast (Paraná, Brazil)

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ABSTRACT

Studies were carried out on *Trichodesmium erythraeum* occurring on the inner shelf in the state of Paraná, Brazil. Temperature, salinity, rainfall, wind velocity, total bacteria, bacterial biomass, chlorophyll-*a*, phytoplankton, *Anabaena* sp., *Merismopedia* sp. and *T. erythraeum* densities were measured in surface water. Centric and pennate diatoms, *Anabaena* sp. and *Merismopedia* sp. were most abundant at 15 m isobath, while dinoflagellate abundance was relatively constant among stations. Similarly, total bacterial densities were relatively homogeneous throughout the sampling area, suggesting that blooms of *T. erythraeum* were not yet in the senescent phase. Results showed that *T. erythraeum* was capable of surviving in relatively inhospitable environmental conditions, due to its ability to fix nitrogen and to photosynthesis at high light intensities.

Key words: *Trichodesmium erythraeum*, bloom, cyanobacteria, phytoplankton, south Brazil

INTRODUCTION

Cyanobacteria are prokaryotes, gram-negative, photosynthetic microorganisms. Species with the ability to fix nitrogen are included in the Eubacteria group (Barbrook et al., 1998; Doyle, 1998). Cyanobacteria are distributed globally in soils, freshwater and marine environments. In marine environments, cyanobacteria may form blooms, similar to those of microalgae, which are often toxic to other organisms. Blooms are usually associated with eutrophication caused by the discharge of untreated domestic sewage and so primarily occur in estuaries and coastal waters. Yet, bloom complexity cause some authors to view the anthropogenic nutrient sources as

secondary triggering factors (Richardson, 1997). The genus *Trichodesmium* is known to bloom frequently in calm tropical and sub-tropical waters (Bidandda, 1997).

The dynamics of *Trichodesmium* and dinoflagellates blooms occurring along the Brazilian shelves have been studied by Satô et al. (1963) in Pernambuco (northeastern state of Brazil), Rosa and Buelato (1981) in Rio Grande do Sul (southern state of Brazil) and a few other studies in the state of São Paulo (southern Brazil; Ganesella-Galvão et al., 1995; Kutner and Sassi, 1978).

The first large-scale descriptions of the distribution of *Trichodesmium* in southeastern Brazilian shelves demonstrated that relatively high

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concentrations of *Trichodesmium* occur in areas dominated by tropical waters and that concentrations decline greatly in winter, when sub-Antarctic waters reach the region (Brandini, 1988). On the shelf in the state of Paraná, large concentrations of cyanobacteria, mostly *Trichodesmium* sp., were recorded in November (late southern spring) 1987 at the water surface between the 25 and 60 m isobaths, and in the subsurface layers between the 100 and 300 m isobaths (Brandini et al., 1988). Also, blooms of *T. erythraeum* were observed in the states of São Paulo and Paraná (southern Brazil), which were affected by the tropical waters of the Brazil Current (Fernandes and Brandini, 1999).

In February 2000, a bloom of *T. erythraeum* with ca. 100 km of extension was observed at about 80 km from the coast, between the Superagüi Island (Paraná) and southern Cardoso Island (São Paulo) (CETESB, 2000). Due to the scarcity of studies of southern cyanobacterial blooms and the ecological importance of these nitrogen-fixing organisms, we initiated the study described herein. Our objective

was to investigate the distribution and seasonal dynamics of *T. erythraeum* blooms and the associated phytoplankton groups, and attempt to associate these dynamics with variations in the biotic and abiotic environment.

STUDY AREA

The coast of Paraná is 105 km in length, between 25°12'44"S - 48°01'15"W, and 25°58'38"S - 48°35'26"W (Fig. 1). Paranaguá and Guaratuba Bays are two large estuarine systems that include large freshwater inputs and relatively large quantities of both natural and anthropogenic organic and inorganic nutrients, which are then carried to the inner shelf, mainly during the rainy season (summer) (Noernberg, 2001). The continental shelf of Paraná is part of the South Brazil Bight (S.B.B.) and is relatively-broad, with a maximum width of 180 km off the Mel Island.

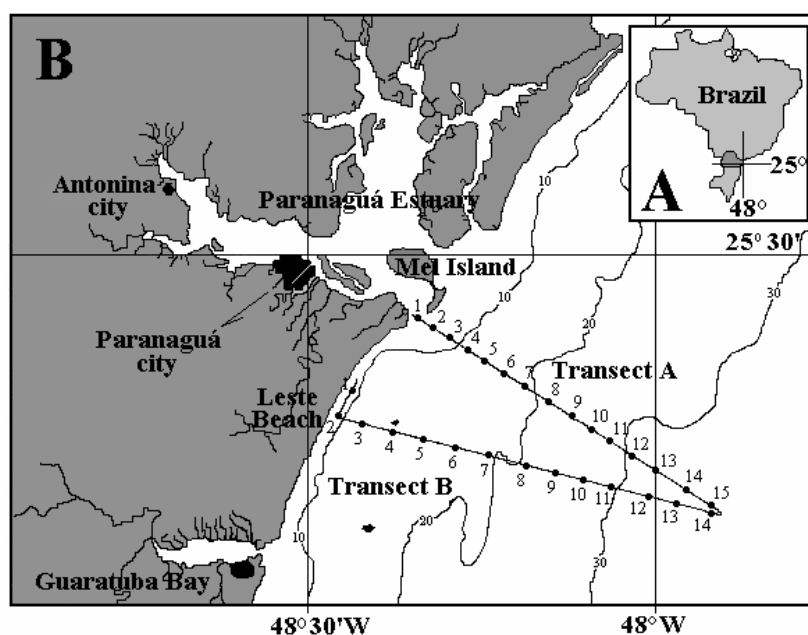


Figure 1 - Map of the study area. A) location of the study region in Brazil; B) organization of transects A and B on the coastal shelf.

Three water masses characterize the local hydrographic system: Coastal Waters (CW), Tropical Waters (TW) and South Atlantic Central Waters (SACW) (Castro Filho et al., 1987; Emilsson, 1961). TW are generally warm,

oligotrophic surface waters, while SACW are cold but rich and found in the lower water column (Brandini et al., 1988; Brandini, 1990; Emilsson, 1961; Matsuura, 1986; Matsuura, 1996). Consequently, primary production in the pelagic

ecosystem is relatively low in the upper layers, but may increase greatly in deeper waters at the nutricline level, where maximum levels of chlorophyll *a* have been recorded in austral Summer (Brandini et al., 1988; Brandini, 1990).

MATERIAL AND METHODS

From November 1998 to March 1999, monthly sampling surveys were conducted using a S/V "Formalhaut" boat from the Brazilian Navy. Surface water was collected with a bucket, once per station per sample. Stations were sampled every 15 minutes along two transects established on the inner shelf, from the coast to 40 miles offshore (25°41'33"S - 48°23'49"W; Fig. 1). Due to climatic conditions of each trip, a minimum of 21 (in December) to a maximum of 25 (in November) locations were sampled.

Temperature was measured with a mercury thermometer and salinity was measured by refractometer (ATAGO, S/Mill, Japan). Rainfall and wind velocity were provided by the Marine Physics Laboratory of the Federal University of Paraná. Statistical analysis used the averages for rainfall and wind velocity calculated over a 4 day interval (i.e. the sampling day and the prior 3 days).

A random, 100 ml, sub-sample of the surface water was fixed with neutralized formalin solution (0.4%) with Bengal Rose stain (18 to 20 drops of a 1 mg/100 ml solution) for future phytoplankton and cyanobacteria counts. Samples were then kept in a sedimentation chamber for 24 hours after which they were examined with an inverted Zeiss microscope (Axiovert 100), following settling count technique (Utermöhl, 1958).

To count the number of filament groups, each sample was filtered through a 100 µm mesh, collected in a square Petri dish and viewed with an Olympus (SZH) stereomicroscope. Average number of cells within a filament and average cell length were calculated from a random sample of 50 filaments selected among the total samples. The identification of *T. erythraeum* was made by the kind collaboration of Dr. Luciano Fernandes of the Federal University of Paraná. Chlorophyll-*a* concentration was determined by fluorimetry, following Strickland and Parsons (1972). Due to technical problems, no chlorophyll-*a* data were available for February 24, 1999, and thus average

values were substituted on that day in the analyses to avoid missing values.

For the quantification of total bacteria, 15 ml of water samples were immediately upon collection preserved in 4% formaldehyde p.A. Bacterial count and biomass quantification was done following Parsons et al. (1984), using the fluorochrome acridine orange. A conversion factor 0.4 pgC µm⁻³ was used, following Bjørnsen and Kuparinen (1991). Cluster Analysis was conducted using original, centered and square-root transformed data (Clark and Warwick, 1994). The Bray-Curtis index of similarity was used for distance estimation and clusters were formed using the "unweighed pair-group average" method (UPGMA) (Legendre and Legendre, 1983; Ludwig and Reynolds, 1988; Clark and Warwick, 1994).

Main tendencies of variation were detected through Principal Component Analysis (PCA). Original data were natural log (ln x) transformed and standardized. Linear correlation matrices of the biotic and abiotic variables with the plankton abundance were performed (Bouroche and Saporta, 1982; Ludwig and Reynolds, 1988). First, all stations were analyzed (PCA 1A and B - of the transects A and B); then, only distant stations (Cluster II to IV in transect A and II to VI in transect B) from the coast were analyzed (PCA 2A and B - of both transects). Missing data for stations located near the coast were replaced by the average value collected during all other months at the given station, while in the case of offshore stations, missing data were replaced by the value obtained at the prior station, in order to avoid missing data in the analyses. Since cells of *T. erythraeum* were extremely abundant, and hence difficult to count, the number of filaments was used instead of the number of cells as an estimation of abundance.

RESULTS

Water temperature varied from 24°C (Transect A: Stations 1, 2, 3 and 4 on November 25, 1998) to 30°C (Transect B: Stations 8 and 9 on January 22, 1999). For both transects, lower temperatures were registered for the stations located between the infra-littoral and the 10 m isobath. The salinity varied from 25 (Transect A: Station 1 on March 24, 1999) to 40 (Transect A: Stations 11, 12, 13 and 14; Transect B: station 9, all on February 24,

1999). Generally, salinity increased, mainly in and 40 m isobaths. transect A, for the stations located between the 15

Table 1 - Daily arithmetical average of rainfall (mm) and wind velocity (m/s) registered in the three days prior to sample (from Nov/98 to Mar/99), and during the sampled days.

Parameter		Nov./98	Dec./98	Jan./99	Feb./99	Mar./99
Rainfall	Absolute values	1.8	0.0	0.0	16.0	4.1
		0.0	0.0	3.0	2.4	151.9
		0.1	0.1	4.2	8.6	53.9
		0.0	2.0	0.0	0.0	0.0
	Mean	0.48	0.53	1.80	6.75	52.48
Wind	Absolute values	5.15	3.44	2.08	2.62	2.44
		4.41	4.76	3.27	2.49	3.36
		6.09	5.85	3.13	2.96	2.40
		3.04	3.85	3.14	2.62	2.42
	Mean	4.67	4.48	2.91	2.67	2.66

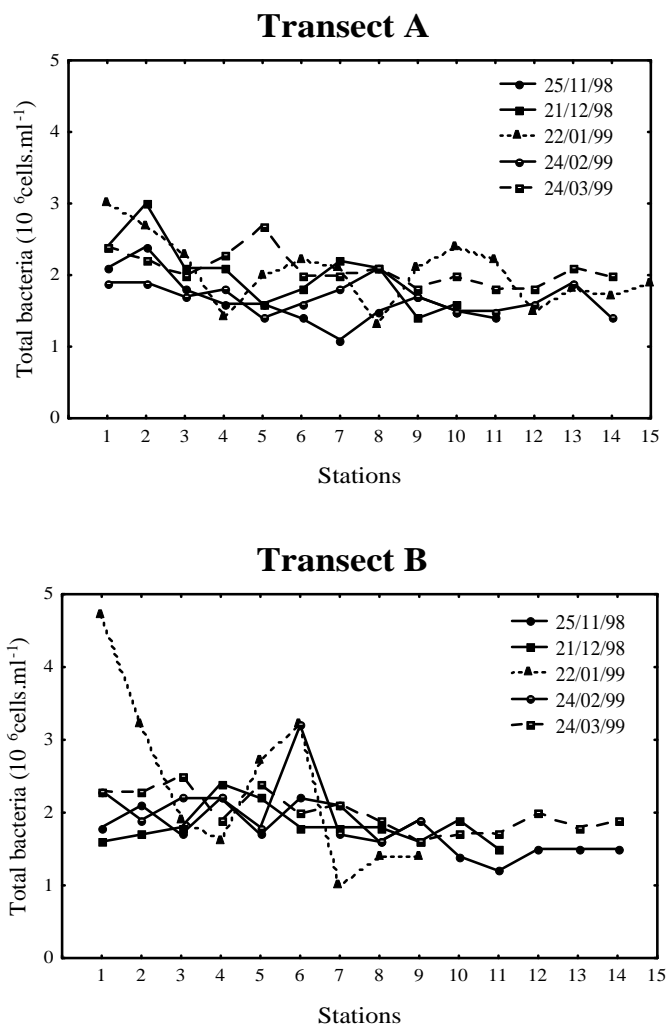
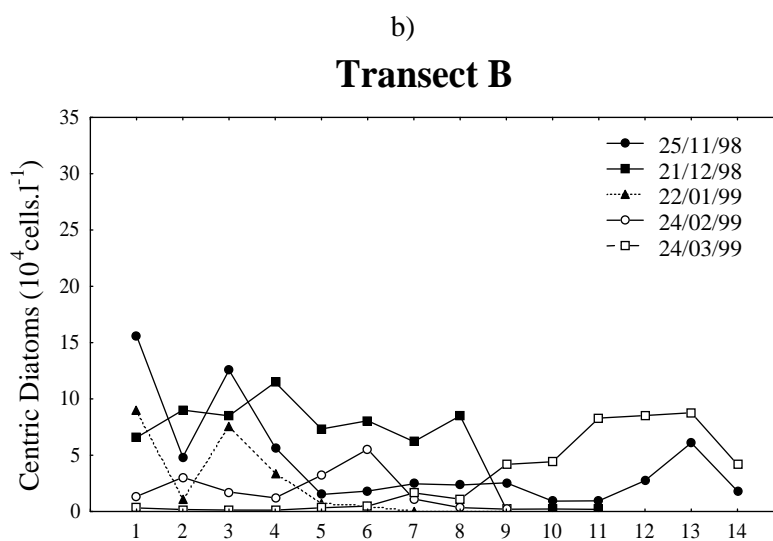
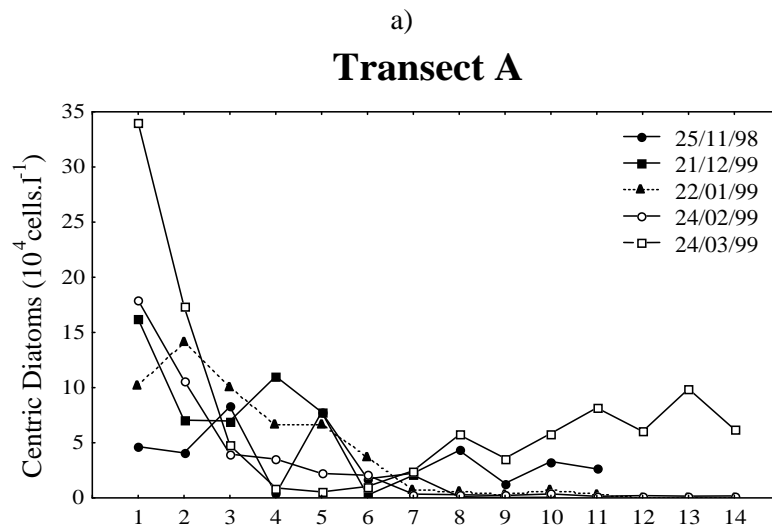


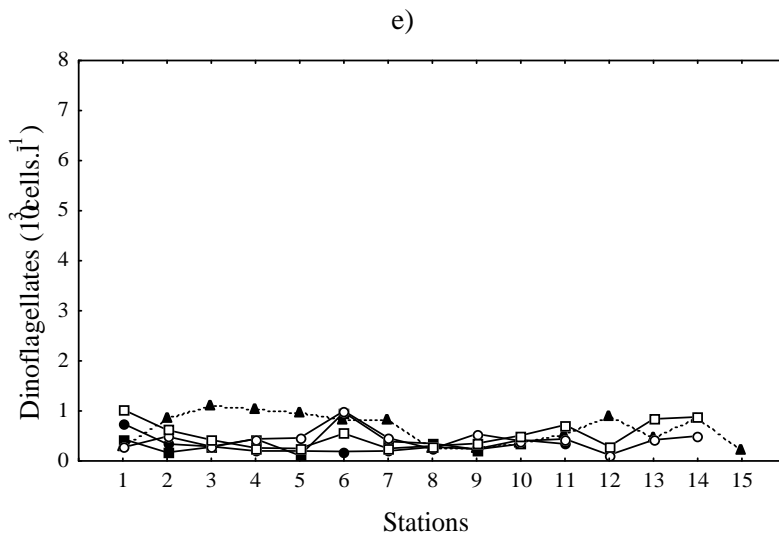
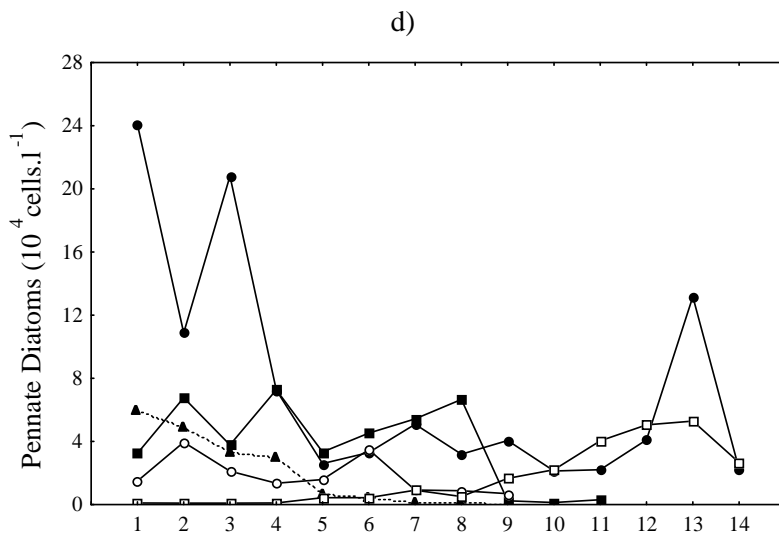
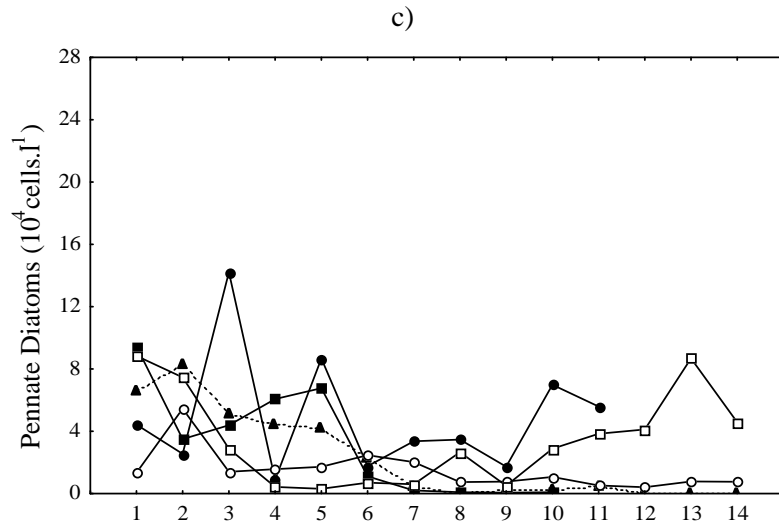
Figure 2 - Absolute values of cell density of total bacteria in the transects A and B.

The lowest average rainfall was 0.48 mm (November 25, 1998) while the highest was 52.5 mm (March 24, 1999). The highest average wind velocity during the study period was 4.67 m/s (November 25, 1998) and the lowest was 2.66 m/s (March 24, 1999) (Table 1). The maximum point wind velocity never exceeded 6 m/s, and can therefore be considered weak winds [Marone, pers. com].

Average total bacterial density was 1.9×10^6 cells. ml^{-1} in transect A, and 2.0×10^6 cells. ml^{-1} in transect B. The maximum density (4.7×10^6 cells. ml^{-1}) was observed on January 22, 1999 at station 1, transect B, and the maximum (1.0×10^6 cells. ml^{-1}) was observed on January 22, 1999 at

station 7, transect B (Fig. 2). The common pattern during the study period comprised relatively high densities between the infra-littoral and the 10 m isobath, mainly in transect A (stations 1 to 3). Overall average bacterial biomass was $80.4 \mu\text{gC.l}^{-1}$ (Transect A), and $83.17 \mu\text{gC.l}^{-1}$ (Transect B). The maximum was $217 \mu\text{gC.l}^{-1}$ (Transect B: Station 1 on January 22, 1999) and the minimum was $49.1 \mu\text{gC.l}^{-1}$ (Transect A: Station 7 on November 25, 1998). Bacterial biomass was higher at all stations located between the infra-littoral and the 10 m isobath, mainly in transect A, as was the case for total bacteria. Average chlorophyll-*a* concentration was $2.47 \mu\text{g.l}^{-1}$ in transect A and $1.96 \mu\text{g.l}^{-1}$ in transect B.





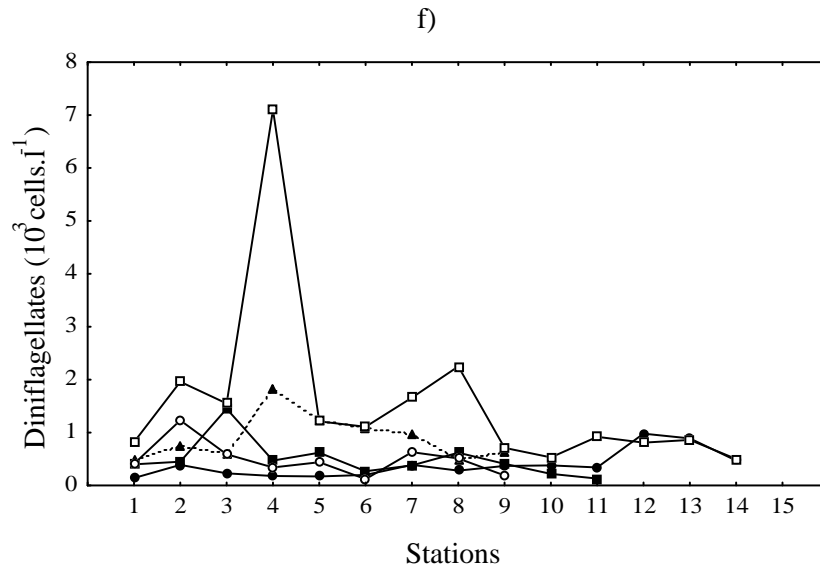
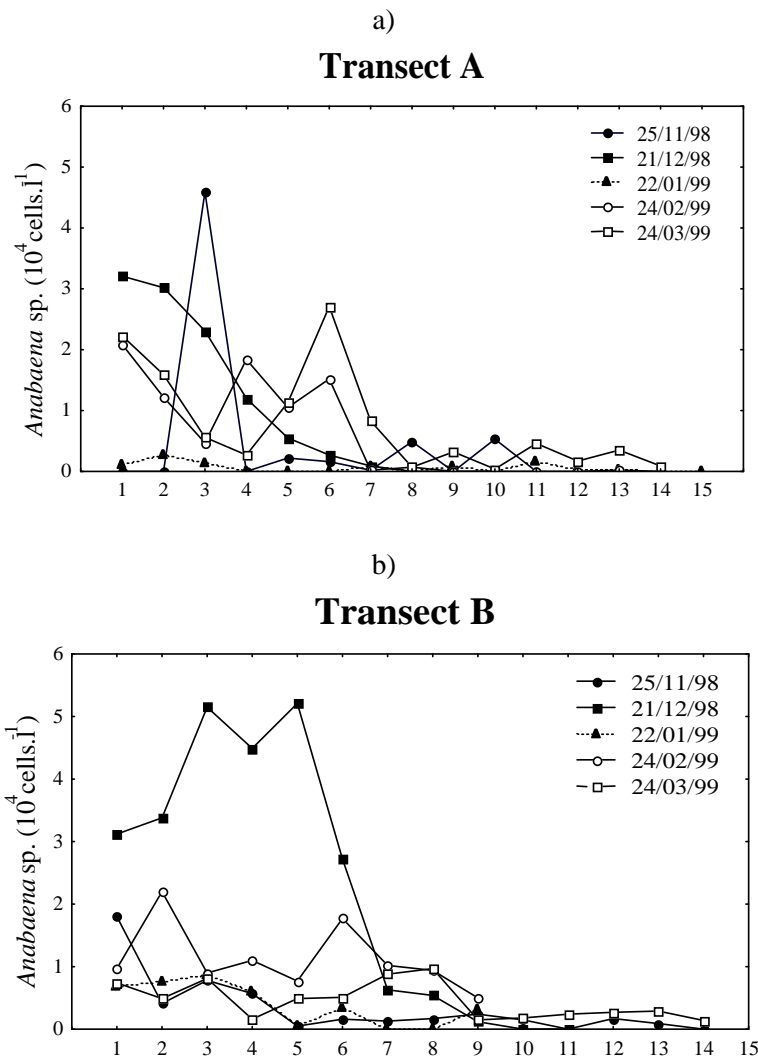
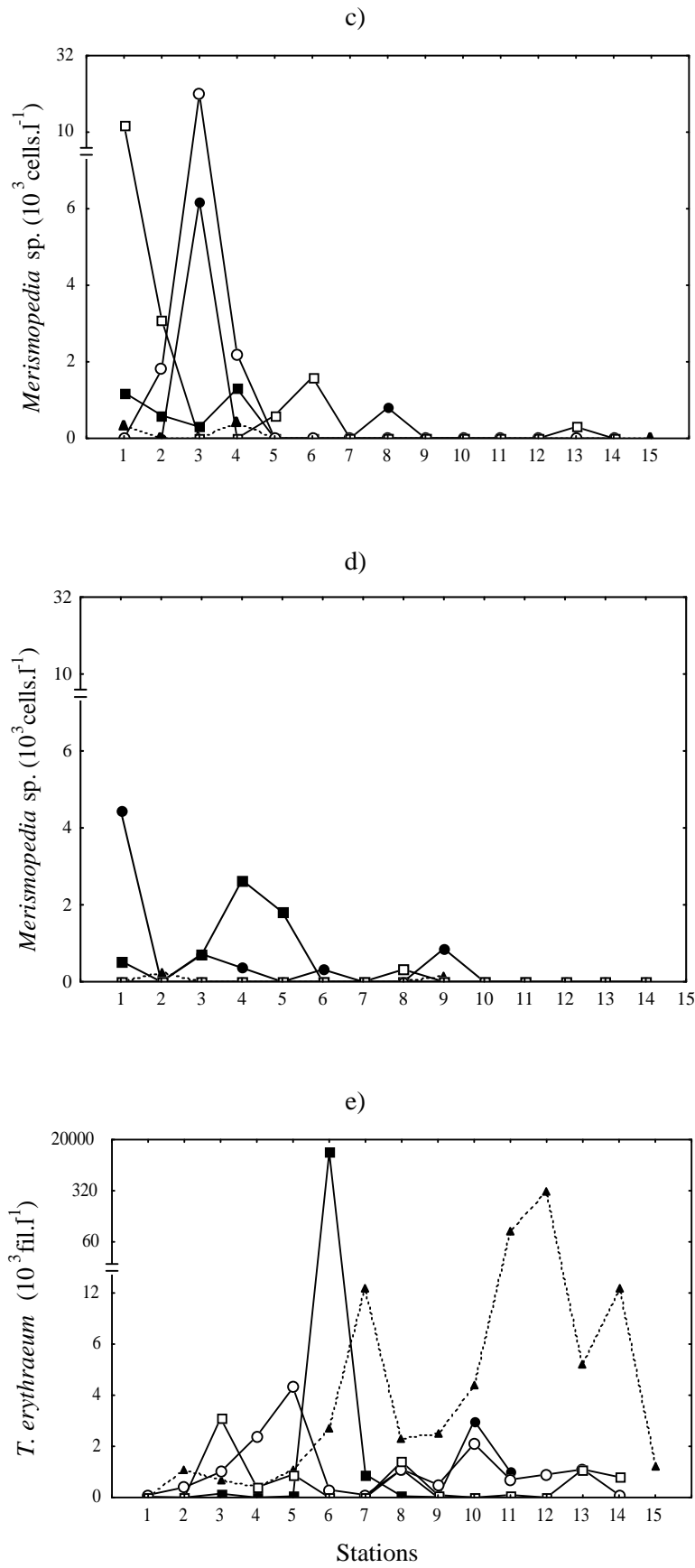


Figure 3 - Absolute values of cell density of: centric diatoms (a and b); pennate diatoms (c and d) and dinoflagellates (e and f) in the transects A and B.





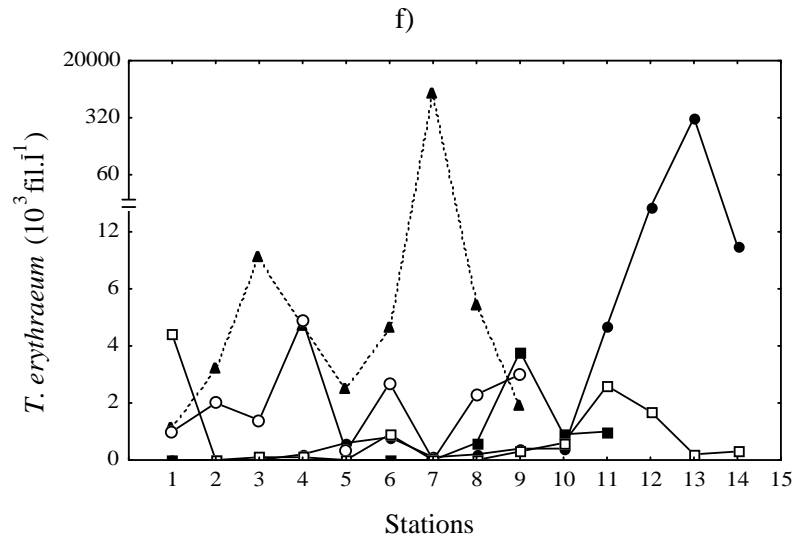


Figure 4 - Absolute values of cell density of: *Anabaena* sp. (a and b); *Merismopedia* sp. (c and d) and *T. erythraeum* (e and f) in the transects A and B.

The highest concentration ($65.1 \mu\text{g.l}^{-1}$) was observed at station 6, transect A, during a bloom of *T. erythraeum* on December 21, 1998. The lowest value ($0.29 \mu\text{g.l}^{-1}$) was at station 9, transect A, on January 22, 1999. In both transects, high values of chlorophyll-*a* occurred at stations with blooms of *T. erythraeum*. Otherwise, values were relatively high from the coast to the 10 m isobath, mainly in transect A.

Centric and pennate diatom, and dinoflagellate abundances (maxima and minima) are described in Fig. 3. Average diatom densities were much higher extending from the coast to the 15 m isobath, after which they decreased towards the 40 m isobath. In contrast, dinoflagellate densities were relatively constant throughout the stations of transect A, while in transect B they were more abundant at stations 4 and 8 on March 24, 1999 and at stations with *Trichodesmium* blooms (Transect A: station 6 on December 21, 1998 and Stations 11 and 12 on January 22, 1999; Transect B: Stations 12 and 13 on November 25, 1998 and Station 7 on January 22, 1999).

Anabaena sp. and *Merismopedia* sp. (cyanobacteria) were abundant in both transects up to the 15 m isobath, then decreased with the distance from the shore. Maximum values were $52 \times 10^3 \text{ cells.l}^{-1}$ at station 5, transect B, on December 21, 1998, and $29 \times 10^3 \text{ cells.l}^{-1}$ on February 24, 1999, at station 3, transect A, respectively (Fig. 4 a, b, c, d). Both were often absent between the 20 and 40 m isobaths. None or few filaments of *T.*

erythraeum were found in coastal stations (to the 15 m isobath), in late autumn and early spring. Blooms of these species were registered in late spring (November 25, 1998) and early summer (December 21, 1998 and January 22, 1999), between the 15 m and 40 m isobaths. A maximum of $19 \times 10^6 \text{ fil.l}^{-1}$ was registered at station 6 of transect A on December 21, 1998 (Fig. 4 e, f). Average length and average cell numbers of 50 randomly chosen filaments were 263 μm and 52 cells, respectively.

The first component of the PCA related to transect A explained 27% of the total variation of the abiotic and biotic variables and showed a strong tendency for higher salinity at stations 8, 9 and 10 on December 21, 1998 at stations 8, 9, 13 and 15 on January 22, 1999 and stations 5, 7, 8, 9, 10, 11, 12, 13 and 14 on February 24, 1999. Centric and pennate diatoms, *Anabaena* sp., total bacteria, bacterial biomass, and chlorophyll-*a* were higher at stations 1, 2, and 3 on December 21, 1998, January 22, February 24, and March 24, 1999, station 4 on December 21, 1998 and station 13 on March 24, 1999 (Fig. 5 - PCA 1A).

The second principal component explained 17% of the variation. Rainfall, temperature, dinoflagellates, and *T. erythraeum* were higher at station 6 on December 21, 1998 and stations 11 and 12 on January 22, 1999, and *Merismopedia* sp. was higher at all sampled stations in late autumn (November 25, 1998) (Fig. 5 - PCA 1A).

The first component of the PCA related to transect B explained 29% of the variation. *T. erythraeum* abundance was higher at stations 7, 8, and 9 on January 22, 1999, and bacterial biomass, centric and pennate diatoms, and *Merismopedia* sp. were higher at stations 1, 2, 3, 4, 6, and 7 on November 25, 1998, at stations 1, 2, 3, 4, 5, 6, and 7 in December 21, 1998, and at station 6 in February 24, 1999 (Fig. 5 - PCA 1B).

The second component from the PCA explained 22% of the variation, and associated temperature, rainfall, total bacteria, and dinoflagellates being higher at stations 1, 2, 3, 4, 5, and 6 on January 22, 1999, and all stations on March 24, 1999 (autumn). Salinity and chlorophyll-*a* were higher at stations 5, 8, 10, 11, 12, 13, and 14 on November 25, 1998 (spring), and at stations 9, 10, and 11 on December 21, 1998 (early summer) (Fig. 5 - PCA 1B).

Cluster Analysis of the biotic variables of transect A formed the stations into four groups with a 10% dissimilarity. The first group of transect B, at 6% dissimilarity, included the four stations between the infralittoral and the 12 m isobath (Fig. 6). It is important to note that for both transects, group I included all stations influenced by the coastal environment and presenting relatively high values of biotic factors. Therefore, those stations (i.e. from 1 to 5 in transect A, and from 1 to 4 in transect B) were excluded from the subsequent statistical analysis (i.e. PCA).

The first two principal components applied only to stations located between 15 and 40 m isobaths of transect A and between 12 and 40 m isobaths of transect B explained 48% of data variation in transect A (stations 6 to 14), and 47% of data variation (stations 5 to 14) in transect B.

The first principal component of transect A explained 25% of variability. Correlation was positive for salinity, *T. erythraeum* and, to a lower extent, for bacterial biomass, temperature and chlorophyll *a* in the majority of the stations during the summer and was positive for centric and pennate diatoms, *Merismopedia* sp., and *Anabaena* sp. at station 6 on February 24, 1999, and at all stations on March 24, 1999 (autumn). The second principal component of transect A explained 22% of the variation. Positive relationships between rainfall, total bacteria, dinoflagellates, and for chlorophyll- *a*, temperature, and bacterial biomass

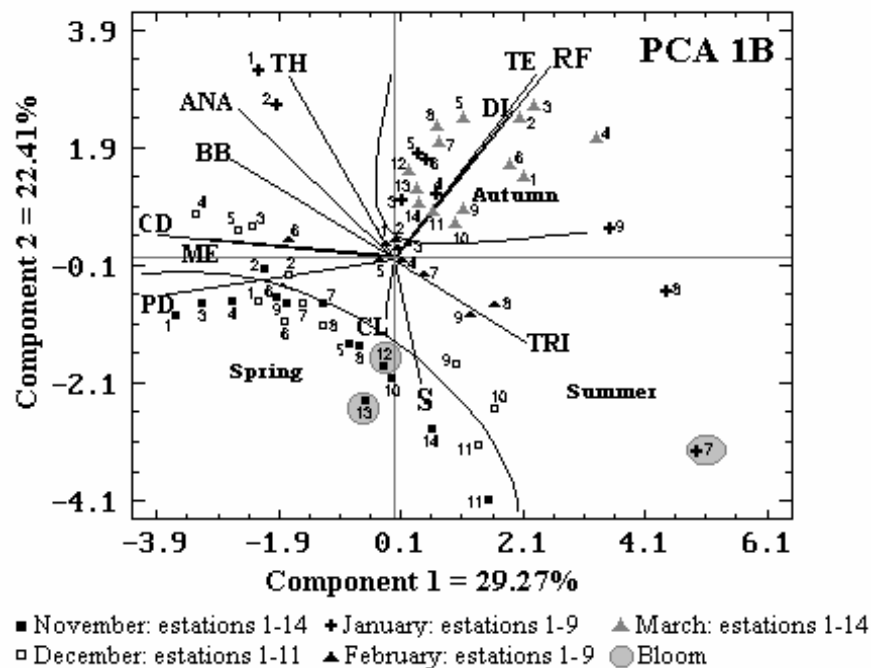
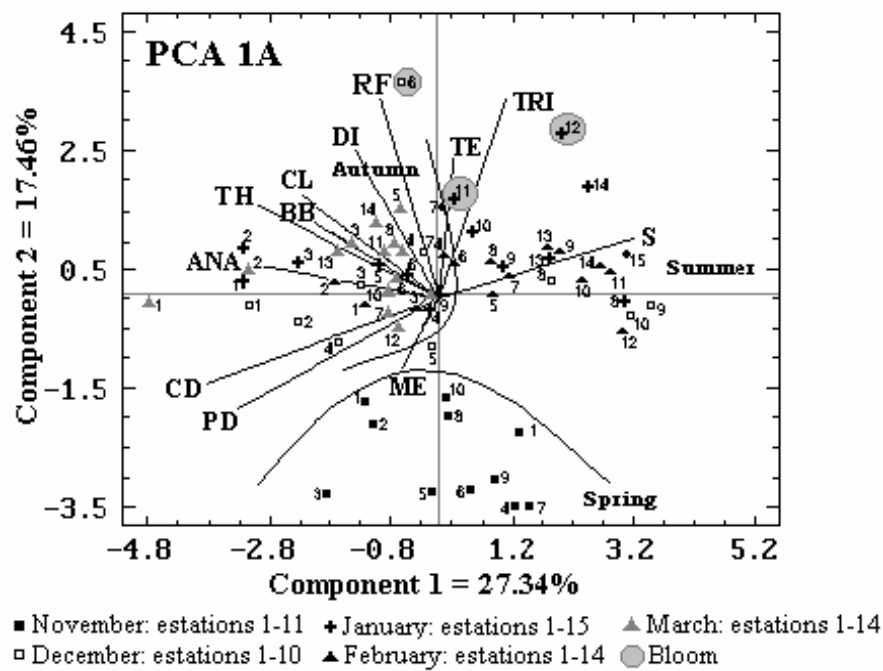
were found at stations 6 and 7 on January 22, 1999 (Fig. 7 - PCA 2A).

In transect B, the first component explained 25% of variability. Positive correlations were detected for *T. erythraeum* and chlorophyll-*a* at: 1) stations 7 and 8 on January 22, 1999; 2) stations 8 and 9 in February 24, 1999 and to a lower extent at 3) stations 11 in November 25, 1998, and 4) stations 9, 10, and 11 in December 21, 1998. On the other hand, positive correlations of centric and pennate diatoms, total bacteria, bacterial biomass and *Anabaena* sp. were found at stations 6, 7, and 9 in November 25, 1998 at stations 5, 6, 7, and 8 in December 21, 1998 and at station 6 in February 24, 1999. The second component explained 22% of the variation and correlating salinity with 1) stations 5, 8, 10, 11, 12, 13, and 14 in November 25, 1998 (spring) and 2) stations 9, 10, and 11 in December 21, 1998. Temperature, rainfall, and dinoflagellates were inversely correlated with 1) stations 5, 6, and 9 in January 22, 1999, and 2) all stations in March 24, 1999 (autumn) (Fig. 7 - PCA 2B).

DISCUSSION

The average drift current velocity off Mel Island was 11 cm/s towards the north [Noernberg, pers. com.], suggesting that, in the absence of cold fronts, a particle could travel approximately 285 km within 30 days. Therefore, it was unlikely that the blooms of *T. erythraeum* observed over two consecutive months were the same. Although, in November 1998 and January 1999, blooms were registered in consecutive stations in transects A and B, that possibly could be isolated groups of *T. erythraeum* that came from a greater bloom that formed previously in the south.

Isolated filaments of *T. erythraeum* were also encountered throughout the study period. In January and February of 1999, they were characterized by relatively large numbers of trichomes, and filamentous cells were recorded in coastal stations, which suggested that warm months were associated with development of the cyanobacterium in this region. Relatively few filaments of *T. erythraeum* were found close to the coast (up to the 15 m isobath), especially during the months of November and December, 1998.



S = Salinity; TE = Temperature; PL = Rainfall; CL = Chlorophyll *a*; CD = Centric Diatoms; PD = Pennate Diatoms DI = Dinoflagellates; ANA = *Anabaena* sp.; ME = *Merismopedia* sp.; TRI = *T. erythraeum*; TH = Total Bacteria; BB = Bacterial Biomass.

Figure 5 - Distribution of sampled points and biotic and abiotic variables during the study period in transect A (PCA 1A) and B (PCA 1B), plotted by the first two Principal Components.

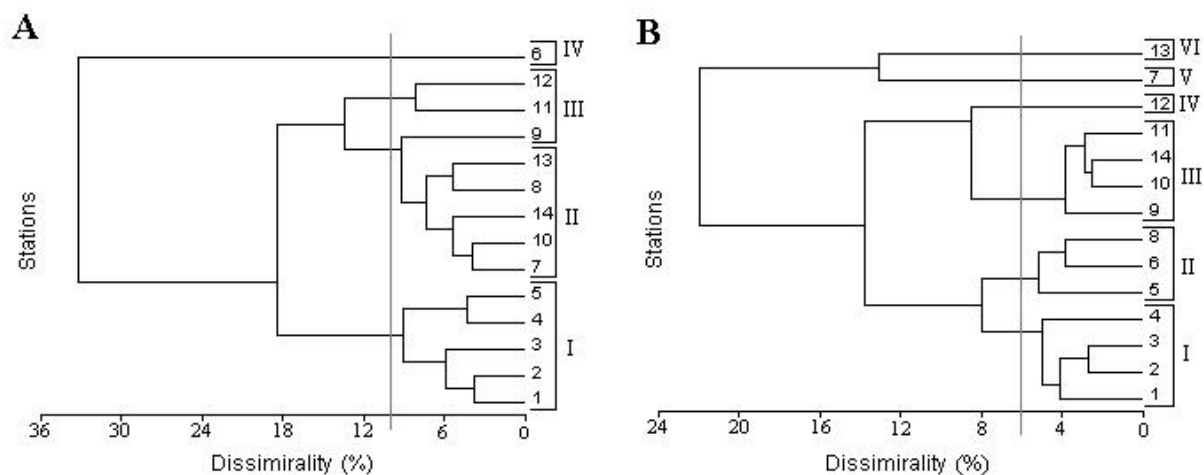


Figure 6 - Clusters from the group analysis of the study stations, based on the biotic measurements obtained between November/98 and March/99 in transects A and B. Numbers I, II, III, IV, V, and VI indicate the station groups.

During the remainder of the study period, filament densities were relatively constant along both transects, except at the station that recorded blooms. However, centric and pennate diatoms, *Anabaena* sp. and *Merismopedia* sp. were common between the infralittoral and the 15 m isobath. This indicates that these phytoplankters and cyanobacteria needed nutrient-rich waters with low salinity to develop, unlike *T. erythraeum* that favored oligotrophic, saline waters (Brandini and Moraes 1986).

Cluster analyses suggested that nutrient-rich waters, originating from the Paranaguá estuarine system, could spread farther at transect A, which was closer to the river mouth. Consequently, abundance of the organisms that relied on dissolved organic nutrients to grow was higher in transect A than in transect B. In stations that did not experience blooms of *T. erythraeum*, concentrations of dinoflagellates were relatively stable, except in March 1999 in transect B where cell densities were highest up to regions contiguous to the 12 m isobath. Dinoflagellates were relatively more abundant in Summer, early Autumn and in the vicinity of *T. erythraeum* blooms. Although results refer to total dinoflagellates, heterotrophic dinoflagellates could also be considered that, according to Strasburger et al. (1983), fed on planktonic bacteria and algae. No data are apparently available that describe whether dinoflagellates feed on *T. erythraeum*. Associations between these organisms and the

blooms suggest that they may consume cyanobacteria, heterotrophic bacteria, or heterotrophic nanoflagellates. Furthermore, similarly to *T. erythraeum*, they found an ideal habitat and multiplied. On the other hand, it was possible that dinoflagellates utilized the nitrogen fixed by the *Trichodesmium* in nitrogen poor waters.

The PCA results applied to off-coast sampling points of transect A showed a positive correlation between blooms of *T. erythraeum* and environmental parameters such as salinity, temperature and chlorophyll-*a*. The PCA analysis also showed a positive correlation between the cyanobacteria bloom and bacterial biomass. According to Mesquita (1993), healthy alive phytoplankton repel bacteria cells, however, when die under situations of nutrient limitation, phytoplankton cells may be attacked by bacteria. Thus, phytoplankton are directly converted in detrite and bacterial biomass. The gas vacuoles present in *T. erythraeum* cells enable them to stay on the surface even in senescence. Statistical analysis did not detect any significant variation on total bacterial population among the blooms detected, neither on transects A and B, nor on the other oceanic sampling stations. These results led to the conclusion that the blooms were at their maximum development stage. The results showed that the *T. erythraeum* blooms occurred in calm periods at the end of spring and summer seasons.

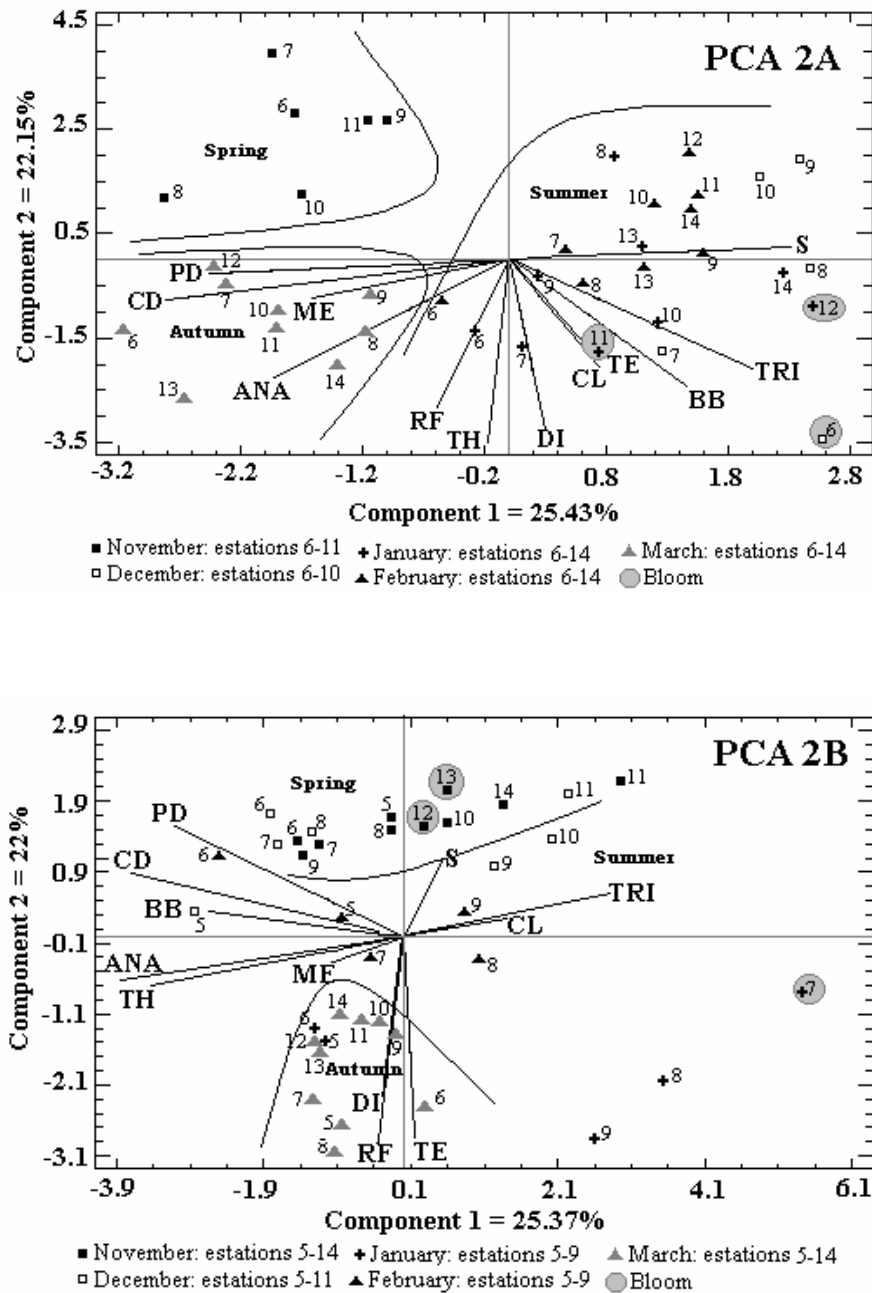


Figure 7 - Distribution of sampled points, and of the biotic and abiotic values of the stations distant from the coast in transect A (PCA 2A) and transect B (PCA 2B) with the axes being the first two principal components.

No cyanobacteria bloom was detected at the end of summer and beginning of autumn.

During the summer period, the Brazilian Current with oligotrophic waters mix-up with the Coastal Continental Shelf Waters (CCSW) of Paraná State,

making them nutrient poor waters and favoring the development of *T. erythraeum* blooms. With the increase of salinity and temperature of surface water masses, the biggest bloom was observed at 10 and 20 m isobath. The present results

confirmed that blooms of *T. erythraeum* formed along Paraná coast and also confirmed the findings of Lee (1989), Bell (1992) and Rörig et al. (1998) that *T. erythraeum* was a nitrogen-fixing and silicate free growing organism; its photosynthesis was performed at high light intensities and it was adapted to survive in areas with low competition, different from other cyanobacteria.

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RESUMO

O propósito principal da presente pesquisa foi investigar as florações de *Trichodesmium erythraeum* na plataforma continental interna do Estado do Paraná, Brasil. Foram medidas, em águas de superfície a temperatura, salinidade, bactérias totais, biomassa bacteriana, clorofila-*a*, densidade fitoplanctônica, densidade das cianobactérias *Anabaena* sp., *Merismopedia* sp. e *T. erythraeum*. Ao contrário dos dinoflagelados, cuja abundância foi relativamente constante em todas as estações, as diatomáceas cêntricas e penadas, *Anabaena* sp. e *Merismopedia* sp. foram mais abundantes até a isóbata dos 15 m. A densidade de bactérias totais também foi relativamente homogênea na área amostrada, o que sugere que as florações de *T. erythraeum* não se encontravam em fase senescente. Os resultados confirmam que *T. erythraeum* é capaz de sobreviver em condições ambientais relativamente inóspitas devido à sua capacidade de fixar nitrogênio e efetuar a fotossíntese em altas intensidades de luz.

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