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Seasonal diatom cycle in Anegada Bay, El Rincón estuarine system, Argentina

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Seasonal variations in the composition and carbon biomass of diatoms and other phytoplankton groups were analyzed over two years, from December 1996 to January 1999, at a fixed station in Anegada Bay, within the El Rincón estuarine system (38–41°S). Phytoplankton communities characterizing the different seasons were identified by classification and detrended correspondence analyses. Diatom communities were highly speciose, with 117 species recorded during the two-year study. Three diatom species are new records for the Argentinean Sea (i.e., *Minidiscus trioculatus* (F.J.R. Taylor) Hasle, *M. decoratus* Chrétiennot-Dinet & Quiroga and *Thalassiosira tealata* Takano). Phytoplankton taxonomic composition and carbon biomass showed a strong seasonality, with two carbon (C) biomass maxima occurring in summer and winter (maximum concentration: 193 μg C L^{-1}). Summer blooms were mainly dominated by tychoplanktonic diatom species (*Paralia sulcata* (Ehrenberg) Cleve, *Rhaphoneis amphiceros* (Ehrenberg) Ehrenberg and *Delphineis surirella* (Ehrenberg) Andrews), probably resuspended from the sediments, and by the pelagic diatom *T. hendeyi* Hasle & Fryxell. The winter phytoplankton community was characterized by a high number of diatom species and a high carbon biomass of diatom resting spores. The occurrence of the winter bloom seems to be closely associated with the inoculation of the water column by diatom resting spores. Maximum diatom carbon biomass corresponded to periods of increased freshwater inflow, whereas seasonal variations in diatom taxonomic composition may be explained by the life-cycle strategies of the species. The taxonomic composition and temporal succession of phytoplankton communities in Anegada Bay are comparable with previous studies in Blanca Bay, suggesting relatively uniform phytoplankton seasonality over shoals in the El Rincón estuarine system.

Keywords: *Argentina, diatoms, estuary, phytoplankton, seasonal succession, taxonomy*

Introduction

The taxonomic composition of marine phytoplankton, and more precisely its size structure, plays a key role in controlling the trophic network through the dominance of a microbial loop versus large grazers and, consequently, carbon cycling through the pelagic system (Legendre & Rassoulzadegan 1995, 1996). In addition, phytoplankton is important in nutrient cycling, influencing biogeochemical cycles in the water column (Arrigo 2005). Therefore, there is increasing concern in understanding the dynamics of phytoplankton taxonomic composition and standing stock, which constitute important information in environmental monitoring, food-web studies, ecosystem modeling and planning the sustainable exploitation of natural resources (Karlson et al. 2010).

Estuaries are semi-enclosed coastal water bodies with a free connection to the open sea and within which seawater is mixed with freshwater from the land (Pritchard 1967). Freshwater discharge and stratification of the water column, which affect the availability of light and nutrients for phytoplankton growth, are the main processes shaping phytoplankton variability in estuarine ecosystems (Rothenberger et al. 2009, Barbosa et al. 2010, Gameiro & Brotas 2010, O'Boyle & Silke 2010). However, phytoplankton patterns in estuaries show high variability, reflecting the site-specific relative importance of disturbance due to human activities, annual climatology and nutrient enrichment (Cloern & Jassby 2010).

There are two major estuarine systems along the Argentinean coast: the Río de la Plata estuary (35–36°S), which represents an extensive and shallow coastal plain estuary, and the El Rincón estuary, located between 39 and 41°S (Acha et al. 2004, Lucas et al. 2005). These two estuaries are characterized by high biological production linked to the presence of frontal areas (Acha et al. 2004) and they sustain important commercial fisheries and mariculture shellfish farmings (Pascual & Zampatti 1998, Cousseau et al. 2004).

Although several studies have been performed in the Río de la Plata estuary, showing spring phytoplankton communities dominated by diatoms or dinoflagellates in the outer (mixohaline) zone (Carreto et al. 2003, Gómez et al. 2004, Licursi et al. 2006), little is known about the ecosystem dynamics in El Rincón (see Acha et al. 2004 and references therein). The El Rincón is of particular ecological relevance

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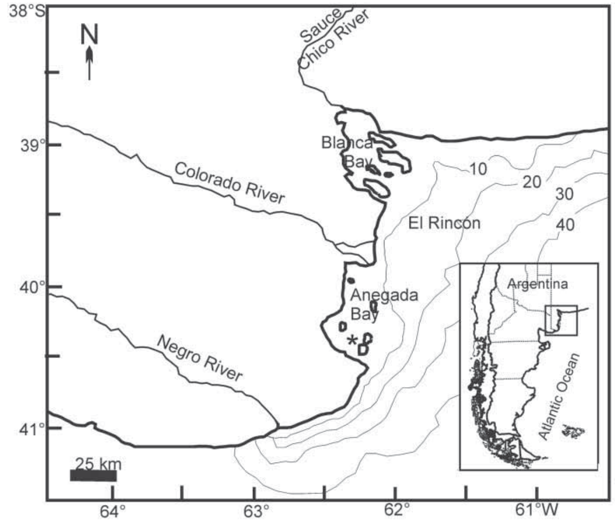


Fig. 1. Map of El Rincón estuarine system showing the position of the sampling station (*) in Anegada Bay. Depth contour in meters, as in Lucas et al. (2005). The 40 m isobath corresponds to the position of the salinity front separating the estuarine waters from the shelf waters.

because it represents an important habitat for fish, squid and bird feeding and reproduction, and is a wintering area for migratory species, as well as sustaining South American sea lion colonies (Macchi & Acha 1998, Yorio et al. 1998a, Esteves et al. 2000, Lucifora et al. 2005). In addition, Anegada Bay, located within El Rincón (Fig. 1), is a Natural Reserve of special interest because it supports very diverse biological communities that develop through a high variety of environments such as sand banks, intertidal mudflats, small islands and lagoons (Yorio et al. 1998b, Boltovskoy 2008).

Previous investigations have studied the phytoplankton dynamics in Blanca Bay in the northern sector of the El Rincón estuarine system (Fig. 1). These studies showed a stable phytoplankton seasonal pattern characterized by a recurrent winter–early spring diatom bloom (Gayoso 1999). This bloom event has been related to an enhanced nutrient supply, a reduction in herbivory and a period of clear waters (Popovich & Marcovecchio 2008, Popovich et al. 2008, Guinder et al. 2009). All these previous studies were performed in the innermost sector of Blanca Bay, and considered local-scale conditions to explain the phytoplankton bloom, but they did not address system-wide processes that may also affect phytoplankton seasonality in the El Rincón estuary. Therefore, it is unknown whether the described pattern is characteristic of Blanca Bay or of other shallow, nearshore areas of El Rincón, like Anegada Bay.

There is increasing interest in studying the phytoplankton community in Anegada Bay, because an incipient mariculture exploitation of the non-indigenous Pacific oyster (*Crassostrea gigas* Thunberg) has developed in the area, representing a new commercial resource for local populations (Pascual & Castaños 2000). Since its introduction into the area in 1982, this oyster species has expanded ca. 90 km to the south (Castaños et al. 2009). Regulations for shellfish exploitation require the ongoing monitoring of phytoplankton communities in order to detect the presence of toxic microalgal species in the area. However, the phytoplankton taxonomic composition in Anegada Bay has still not been analyzed.

The aim of this study is to examine the seasonal variability in the phytoplankton taxonomic composition and carbon biomass in Anegada Bay. Particular attention is being paid to diatoms, which are a major component of the phytoplankton in estuaries, generally accounting for the bulk of the autotrophic biomass and producing periodic biomass maxima which are especially relevant to herbivorous grazers (Cloern & Dufford 2005). In addition, we compare the diatom taxonomic composition and temporal succession with results from Blanca Bay, and we identify distinctive and common patterns in phytoplankton seasonality. Finally, possible mechanisms determining diatom blooms and changes in taxonomic composition are hypothesized.

Materials and methods

Study area

The El Rincón estuarine system comprises the inner zone, between 39° and 41°S, of the Argentine Continental Shelf in the southwest Atlantic Ocean (Fig. 1). Freshwater enters the estuary through the Colorado River in the north and the Negro River in the south, which represent the main rivers in northern Patagonia flowing from the Andes Mountains (Acha et al. 2004). The Negro River contributes ca. 90% of the freshwater input to El Rincón estuary, with two periods of maximum flow: one in winter (1130 $m^3\ s^{-1}$) due to heavy rainfall, and one in spring (1210 $m^3\ s^{-1}$) corresponding to snow melting in the Andes Mountains (Guerrero 1998, Lucas et al. 2005). The minimum flow discharge in the Negro River occurs in autumn (395 $m^3\ s^{-1}$). The Colorado River monthly averaged flow discharge ranged from 70 $m^3\ s^{-1}$ in autumn to 215 $m^3\ s^{-1}$ in late spring (Fig. 2a). In the northern, inner part of El Rincón basin, freshwater inflow from the Sauce Chico River forms the Blanca Bay estuary (Fig. 1) (Piccolo & Perillo 1990). However, freshwater run-off from the Sauce Chico River is low (mean annual discharge 1.9 $m^3\ s^{-1}$), and the mouth of the Blanca Bay is under the influence of the El Rincón estuarine system (Lucas et al. 2005).

El Rincón is a relatively shallow basin (depth <40 m) separated from the outer shelf waters by a steep coastal front at the 40 m isobath (Fig. 1) (Acha et al. 2004, Lucas et al. 2005). Sea surface salinity varies from 30.0 to 33.3, while sea surface temperature gradually decreases from nearshore to offshore open waters, from 15.5 to 13°C during summer and from 11.5 to 10.5°C during winter (Martos & Piccolo 1988, Lucas et al. 2005). The main current in El Rincón is from the southwest to the northeast (Lucas et al. 2005). The

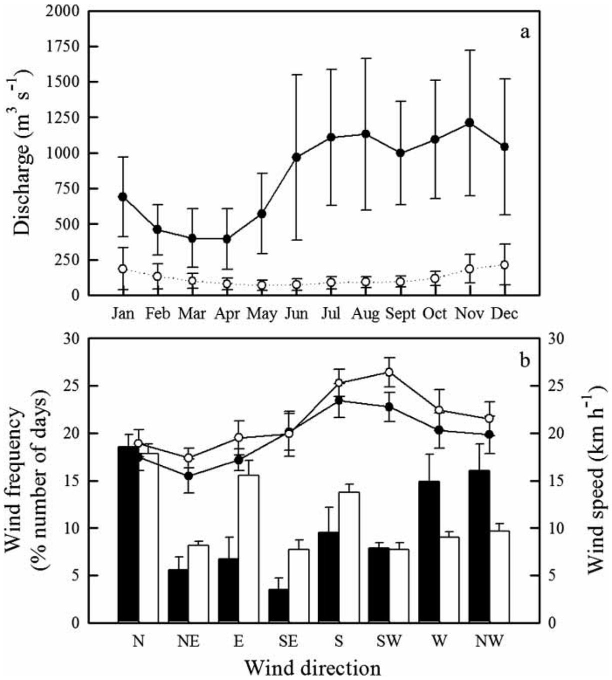


Fig. 2. Variations in (a) the mean monthly discharge of the Negro (full circle) and Colorado (open circle) rivers between 1927 and 1999, and 1982 and 2006, respectively, and (b) the mean wind frequency and speed for the autumn–winter (black bar and full circle) and spring–summer (white bar and open circle) periods as a function of wind direction from 1971 to 1990 in the El Rincón estuarine system. Error bars correspond to one standard deviation. Data provided by the Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina. N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west; NW, northwest.

water column is characterized by a vertical homogeneity due to wind and tidal mixing. In El Rincón estuary between 1971 and 1990, the wind showed an autumn–winter period of predominantly offshore winds and a spring–summer period dominated by onshore winds. Wind speed is higher during spring and summer than during autumn and winter (Fig. 2b) (Lucas et al. 2005).

The study site is among small islands in Anegada Bay, a relatively large (2371 km^2) and shallow (depth <10 m) semi-enclosed bay located in the southern sector of El Rincón estuary (Fig. 1). The bay is covered by unstable sandy sediments, with some exposed rock outcrops and mudflats in the intertidal zone (Aliotta et al. 1999). Sand and mud banks <2 m deep at high tide are abundant in the bay. The water column in the bay is vertically homogeneous throughout the year due to the turbulent wind mixing. Turbidity is high due to suspended sediment (Martos & Piccolo 1988, Guerrero 1998).

Sampling and analyses

A sampling location in Anegada Bay (40°28′S, 62°22′W) was monitored monthly from a boat between December 1996 and January 1999 (Fig. 1). Surface water temperature and salinity were measured with a surface thermometer and a Beckman salinometer, respectively. Surface water samples for phytoplankton analyses were collected using 2.5-L Van Dorn bottles. In addition, a 20-μm mesh net-tow was used to collect phytoplankton samples for specific taxonomic identifications. Phytoplankton samples were preserved with 2% acidic Lugol's solution (Strickland & Parsons 1984). Surface water nitrite (NO_2), nitrate (NO_3), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations were obtained for the same sampling period from Borges (2006).

Net-tow samples were used to identify diatom species more accurately and to determine species richness. Samples were cleaned of organic matter following the method of Hasle & Fryxell (1970) and prepared for microscopical analyses following the protocols recommended by Ferrario et al. (1995). Specimens were examined in light (Wild M20, Heerbrugg, Switzerland) and scanning electron microscopy (JEOL JSMT 100, Tokyo, Japan). Diatom terminology follows Round et al. (1990) and Hasle & Syvertsen (1997).

Owing to unforeseeable logistical problems during the study, phytoplankton samples were collected over only 18 months between December 1996 and September 1998, including at least two samples for each season. Phytoplankton cells were counted using an inverted microscope (Iroscope SI-PH, Mexico City, Mexico) according to Utermöhl (1958). Cell enumeration was performed in random fields according to Villafañe & Reid (1995). Cell biovolumes were estimated using the geometric shapes and equations proposed by Hillebrand et al. (1999) with corrections for cell shrinkage due to sample fixation (Montagnes et al. 1994). Cell carbon content was calculated from cell biovolumes using carbon:volume ratios published by Montagnes et al. (1994) and Montagnes & Franklin (2001). The conversion factors are:

$$C = 0.380\text{cellvol}^{0.850} \text{ for diatoms} \tag{1}$$

$$C = 0.109\text{cellvol}^{0.991} \text{ for other phytoplankton groups} \tag{2}$$

where C is the carbon biomass ($\mu g\ L^{-1}$) and cellvol is the cell biovolume (μm^{-3}). These carbon:volume ratios are considered to be the best proxy to estimate phytoplankton C biomass (Garibotti et al. 2003).

Statistical analyses

Analyses of simple linear correlation were use to relate changes in diatom carbon biomass to nutrient concentrations (Zar 1996). A two-way indicator species analysis (TWINSPAN) was run to classify species into phytoplankton groups co-occurring during certain sampling periods. The data matrix used for the analysis comprised carbon biomass data of 35 species or phytoplankton groups from 18 quantitative phytoplankton samples. TWINSPAN works with qualitative data (i.e., presence/absence), so quantitative species' carbon biomass data were transformed to qualitative variables called pseudospecies, which are defined by cut-levels of species carbon biomass concentrations (Lepš & Šmilauer 1999). In our analysis, pseudospecies cut-levels were set at 0, 2, 5, 10, 20 and 100 μg C L^{-1}, representing the whole range of species carbon biomass values.

A detrended correspondence analysis (DCA) was applied to ordinate samples according to the species composition and carbon biomass in their phytoplankton communities, allowing to assess overall seasonal patterns in phytoplankton. The ordination axes are weighted sums of the phytoplankton species, which are used to calculate the position of the stations in the ordination diagram according to their species composition and carbon biomass. Thus, the distances between stations in the ordination diagram reflect the similarity in their phytoplankton communities (Jongman et al. 1995). Detrending was performed by segments and rare species were not down-weighted. The length of the first axis was over three standard deviation units, supporting the use of an ordination method based on the unimodal model of species response to the underlying environmental gradient (Hill & Gauch 1980).

Results

Environmental conditions

Sea surface temperatures varied in Anegada Bay from 9°C in winter to 22.5°C in summer, while sea surface salinity varied between 26.2 and 34.8, with two minima in the seasonal cycle (Fig. 3a). Sea surface nutrient concentrations showed large seasonal and interannual variation (Fig. 3b, Table 1). Mean seasonal concentrations for nitrite reached a maximum in summer 1997, whereas nitrate concentrations reached a maximum in winter 1997; both nitrite and nitrate concentrations were higher during 1997 than during 1998 (Table 1). The highest mean seasonal phosphate concentration was recorded in autumn 1998. Silicic acid concentrations reached a maximum usually during the summer months, but a second annual maximum was recorded during the winter 1997 (Fig. 3b).

Phytoplankton community structure

The phytoplankton community was composed of diatom vegetative cells and resting spores, cryptophytes, prasinophytes, dinoflagellates and unidentified phytoflagellates. Monthly phytoplankton cell abundance and carbon biomass are presented in Fig. 4, while these monthly values were averaged into season in Table 2. The interannual variability in phytoplankton cell abundance and carbon biomass was high, with maximum values recorded in 1997. Phytoplankton cell abundance and carbon biomass were four and two times higher in winter 1997 than in winter 1998, respectively (Table 2). A similar trend was observed in phytoplankton seasonal patterns during the two-year study, with maximum cell abundance and carbon biomass in summer and in late autumn–early winter (Fig. 4).

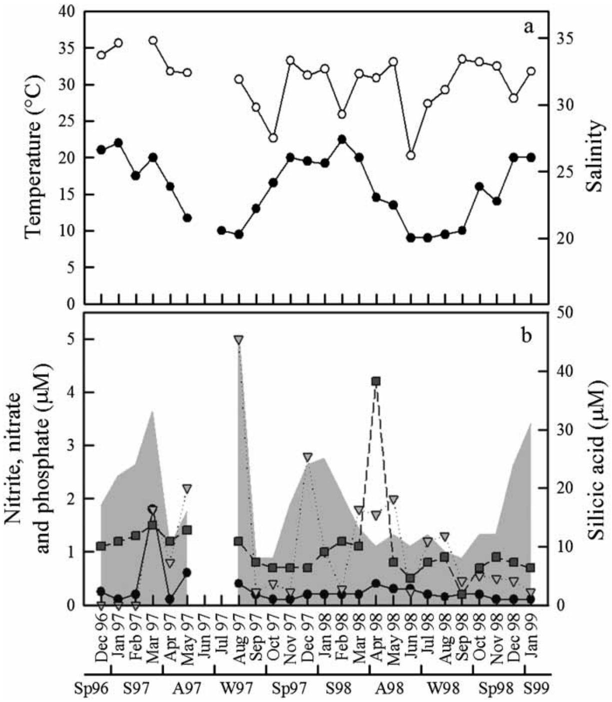


Fig. 3. Seasonal variations in surface water (a) temperature (full circle) and salinity (open circle), and (b) nitrite (circle), nitrate (triangle), phosphate (square) and silicic acid (shaded area) concentrations in Anegada Bay, El Rincón estuary, Argentina, during a two-year study from December 1996 to January 1999. Modified from Borges (2006). Sp, spring; S, summer; A, autumn; W, winter.

Unidentified phytoflagellates contributed between 68 and 93% of the total phytoplankton cell abundance throughout the year, whereas diatom cells contributed between 60 and 88% of the total phytoplankton carbon biomass. Diatom vegetative cells accounted for >70% of the total phytoplankton carbon biomass in summer, whereas both diatom vegetative cells and resting spores prevailed in winter, and represented >80% of the total phytoplankton carbon biomass (Fig. 4 and Table 2). Unidentified phytoflagellates and cryptophytes attained maximum cell abundances in summer. *Pyramimonas* spp. and dinoflagellates were relatively scarce during the two-year study, being present in low numbers in autumn and winter of 1998.

The annual phytoplankton dynamics from DCA and TWINSPAN analyses in Anegada Bay during the two-year study is presented in Fig. 5. Ordination of the samples according to the composition and carbon biomass of phytoplankton clearly differentiate summer and winter samples along the first axis, indicating a strong seasonality in phytoplankton communities. However, autumn and spring samples overlap in the middle part of the diagram, which indicates transitional phytoplankton communities (Fig. 5a). The classification of taxonomic composition and

Table 1. Sea surface physico-chemical variables (mean seasonal values ± standard deviation) from Anegada Bay, El Rincón estuary, Argentina.

	Spring 1996	Summer 1997	Autumn 1997	Winter 1997	Spring 1997	Summer 1998	Autumn 1998	Winter 1998	Spring 1998	Summer 1999
Temperature (°C)	21.0	19.8 ± 2.3	13.9 ± 3.0	10.8 ± 1.9	18.7 ± 1.9	20.6 ± 1.7	12.3 ± 2.9	9.5 ± 0.5	16.7 ± 3.1	20.0
Salinity	33.7	34.7 ± 0.1	32.5 ± 0.1	30.9 ± 1.5	31.0 ± 3.1	31.4 ± 1.9	30.5 ± 3.7	31.5 ± 1.7	32.2 ± 1.5	32.5
Nitrite (µM)	0.3	0.7 ± 1.0	0.4 ± 0.4	0.3 ± 0.1	0.1 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	0.1
Nitrate (µM)	0.0	0.6 ± 1.0	1.5 ± 1.0	2.6 ± 3.4	1.2 ± 1.4	1.0 ± 0.8	1.3 ± 0.9	1.0 ± 0.5	0.5 ± 0.1	0.3
Phosphate (µM)	1.1	1.3 ± 0.2	1.3 ± 0.1	1.0 ± 0.3	0.7 ± 0.0	1.1 ± 0.1	1.8 ± 2.1	0.6 ± 0.4	0.8 ± 0.1	0.7
Silicic acid (µM)	17.0	26.3 ± 5.9	13.0 ± 4.2	27.0 ± 26.9	16.3 ± 8.0	19.0 ± 6.0	10.7 ± 1.2	9.7 ± 2.1	16.0 ± 6.9	31.0

Note: No standard deviation values are given for spring 1996 and summer 1999 because only one month was monitored.

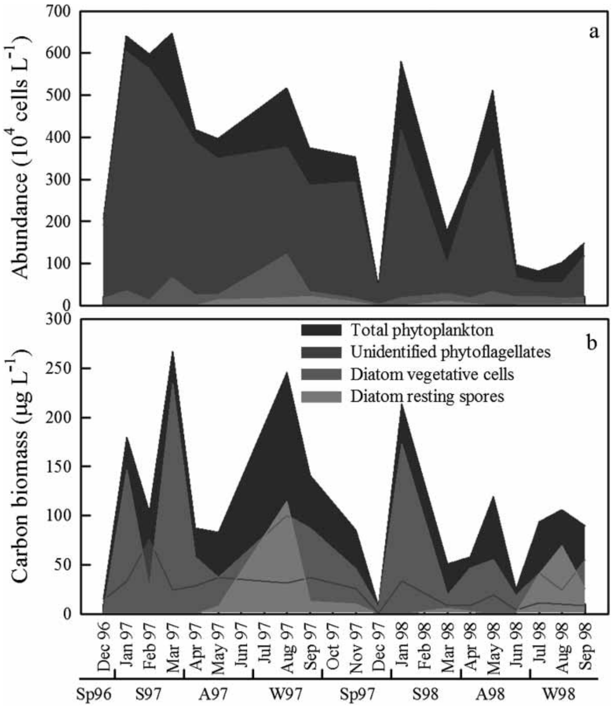


Fig. 4. Seasonal variations in sea surface (a) cell abundance and (b) carbon biomass of total phytoplankton, unidentified phytoflagellates, diatom vegetative cells and resting spores in Anegada Bay, El Rincón estuary, Argentina, during a two-year study from December 1996 to September 1998. Sp, spring; S, summer; A, autumn; W, winter.

carbon biomass data allows establishing six phytoplankton communities which represent taxa with similar distributions between the sampled seasons. Phytoplankton communities correspond to (1) preferential summer species, (2) preferential winter species, and (3) species without any specific season preference (Fig. 5b). These phytoplankton communities reflect the changes in the taxonomic composition that occurs along the annual cycle, as described below.

The summer phytoplankton community was mainly represented, in terms of carbon biomass, by *Thalassiosira hendeyi*, *Paralia sulcata*, *Rhaphoneis amphiceros* and *Delphineis surirella* (Table 3). In addition, *Paralia* cf. *marina*, *T. anguste-lineata* and *T. curviseriata* had high carbon biomass during summer 1997. Most of the dominant summer diatom species share a benthic habitat, except for the pelagic *Thalassiosira* species. In addition, nanophytoflagellates (i.e., unidentified cells and cryptophytes) attained maximum carbon biomass in summer, representing <25% of the total phytoplankton carbon biomass.

The winter phytoplankton community was characterized by high diatom species richness, and high carbon biomass of diatom vegetative cells and resting spores (Fig. 4b and Table 2). The resting spores were mainly identified as *Chaetoceros didymus, C. radicans* and *C. socialis.* Different winter diatom species, mainly represented by *C. socialis, T. curviseriata, P. sulcata, R. amphiceros,*

Table 2. Seasonal average ± standard deviation of phytoplankton cell abundance and carbon (C) biomass during a two-year study from spring 1996 to winter 1998 in Anegada Bay, El Rincón estuary, Argentina.

	Spring 1996	Summer 1997	Autumn 1997	Winter 1997	Spring 1997	Summer 1998	Autumn 1998	Winter 1998
Abundance (10^4 cells L^{-1})								
Diatom vegetative cells	16	38 ± 27	26 ± 10	78 ± 2	10 ± 10	24 ± 7	24 ± 8	19 ± 2
Diatom resting spores	0	0	0	20 ± 2	4 ± 6	5 ± 7	2 ± 2	2 ± 1
Dinoflagellates	0	0	0	0	0	3 ± 5	2 ± 5	0
Cryptophytes	0	39 ± 50	4 ± 6	17 ± 24	18 ± 22	69 ± 66	35 ± 54	11 ± 10
Prasinophytes	0	0	0	0	0	14 ± 20	5 ± 8	2 ± 3
Unidentified phytoflagellates	192	550 ± 61	388 ± 148	331 ± 64	166 ± 181	259 ± 224	237 ± 156	75 ± 38
Total phytoplankton	208	628 ± 27	417 ± 106	446 ± 101	198 ± 219	374 ± 285	306 ± 207	111 ± 35
Biomass (μg C L^{-1})								
Diatom vegetative cells	1.8	135.1 ± 104.7	57.9 ± 23.2	93.5 ± 9.1	26.0 ± 28.0	96.2 ± 109.1	39.7 ± 19.2	39.9 ± 15.3
Diatom resting spores	0	0	0	63.5 ± 72.1	4.7 ± 6.7	2.8 ± 3.9	1.3 ± 1.4	45.0 ± 22.2
Dinoflagellates	0	0	0	0	0	6.4 ± 9.0	12.5 ± 21.6	0
Cryptophytes	0	3.9 ± 4.7	0.5 ± 0.5	2.1 ± 3.0	2.3 ± 2.8	4.2 ± 1.7	3.1 ± 4.0	1.3 ± 1.0
Prasinophytes	0	0	0	0	0	0.8 ± 1.2	0.3 ± 0.5	0.1 ± 0.2
Unidentified phytoflagellates	13.7	44.3 ± 27.4	28.6 ± 15.4	34.2 ± 4.0	13.0 ± 17.4	20.8 ± 17.5	10.4 ± 7.8	9.7 ± 1.7
Total phytoplankton	15.5	183.4 ± 81.8	87.1 ± 64.5	193.4 ± 74.1	46.1 ± 54.8	132.0 ± 115.4	67.3 ± 47.8	96.0 ± 8.5

Note: No standard deviation values are given for spring 1996 because only one month was monitored.

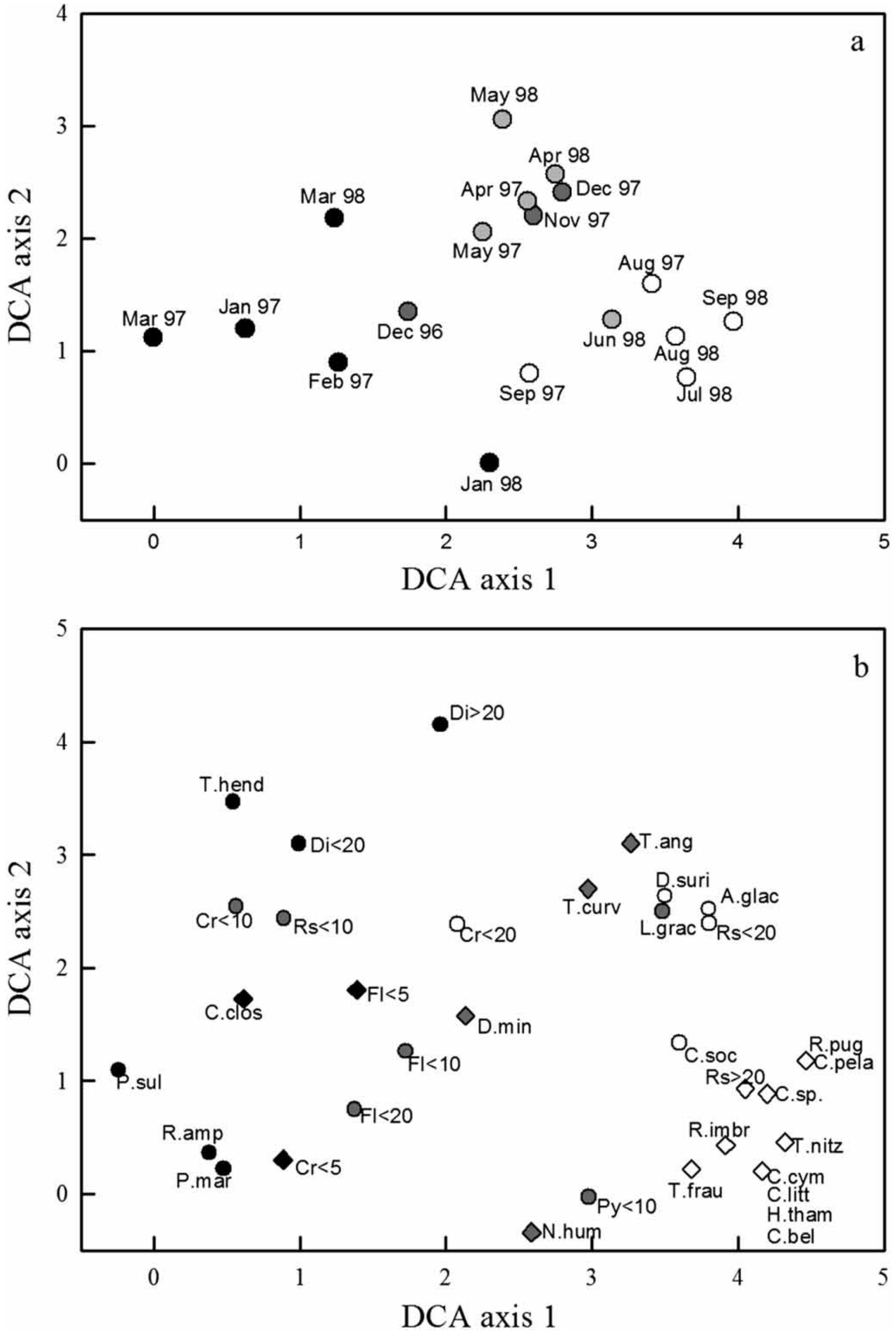


Fig. 5. Ordination (DCA) and classification (TWINSPAN) of phytoplankton taxonomic composition and carbon biomass. (a) Distribution of seasonal samples based on similar phytoplankton taxonomic composition: summer (black), spring (dark gray), autumn (light gray) and winter (white). (b) Distribution of phytoplankton taxa grouped in different seasonal communities using TWINSPAN classification analysis: preferential summer taxa (black), taxa without any specific season's preference (gray) and preferential winter taxa (white). For both graphs, the eigenvalues are 0.75 and 0.51 for the first and second axes, respectively. Taxon abbreviations are given in Table 3.

Asterionellopsis glacialis and *D. surirella* prevailed in 1997 compared with 1998 (Table 3). These species are relatively small (230–3200 μm^3), but were present in high abundance, determining the maximum in total phytoplankton biomass. During winter 1998, the dominant species contributing to phytoplankton carbon biomass were *Cerataulina pelagica, Helicotheca thamensis, Cyclotella littoralis, A. glacialis, Rhizosolenia pungens* and *R. imbricata* (Table 3). These species were present in low abundance ($<$10 000 cells L^{-1}), but showed high carbon biomass due to their relative large size (between 9000 and 30 000 μm^3). Most of the winter diatoms are typically marine planktonic species. In winter, phytoflagellates contributed $<$20% to the total phytoplankton carbon biomass.

Table 3. Seasonal average carbon biomass ($\mu g\,L^{-1}$) of phytoplankton taxa in Anegada Bay, El Rincón estuary, Argentina.

	Abbreviated name	Habitat	Spring 1996	Summer 1997	Autumn 1997	Winter 1997	Spring 1997	Summer 1998	Autumn 1998	Winter 1998
Diatom vegetative cells										
Asterionellopsis glacialis	A. glac	P		1.1		6.6	2.5		1.9	2.9
Campylosira cymbelliformis	C. cym	B								1.4
Cerautaulina pelagica	C. pela	P								12.6
Chaetoceros socialis	C. soc	P				22.3	0.4		2.2	0.5
Chaetoceros spp. $< 20\,\mu m$	C. sp.	P								1.3
Cyclotella littoralis	C. litt	P								3.0
Cylindrotheca closterium	C. clos	P		0.5	0.3			0.3		0.1
Cymatosira belgica	C. bel	B								0.1
Delphineis minutissima	D. min	B	1.8						0.2	
D. surirella	D. suri	B		1.3		5.8		1.8	2.7	1.5
Helicotheca tamensis	H. tham	P								6.2
Licmophora gracilis	L. grac	B							1.1	
Nitzschia humii	N. hum	B				1.6			1.0	
Paralia cf. *marina*	P. mar	B		11.6						1.1
P. sulcata	P. sul	B		72.6		29.0		3.9		
Rhaphoneis amphiceros	R. amp	B		1.9	2.9	9.6		8.4		0.6
Rhizosolenia imbricata	R. imbr	P							1.7	2.5
R. pungens	R. pug	P								2.5
Thalassionema frauenfeldii	T. frau	P								0.9
T. nitzschioides	T. nitz	P								0.8
Thalassiosira anguste-lineata	T. ang	P		3.1	13.4		9.4		10.1	
T. curviseriata	T. curv	P		9.5	41.3	18.6	13.8		18.9	1.8
T. hendeyi	T. hend	P		33.6				81.8		
Diatom resting spores										
Resting spores $< 10\,\mu m$	Rs < 10					9.7	1.3	2.8	1.3	
Resting spores 10–20 μm	Rs < 20					3.1	3.5			1.4
Resting spores $> 20\,\mu m$	Rs > 20					50.7				43.6
Cryptophytes										
Cryptophytes $< 5\,\mu m$	Cr < 5			0.3				1.3	0.4	
Cryptophytes 5–10 μm	Cr < 10			3.7	0.5	2.1	2.3	2.0	2.2	1.2
Cryptophytes $> 10\,\mu m$	Cr < 20							0.9	0.4	0.1
Prasinophytes										
Pyramimonas spp. $< 10\,\mu m$	Py < 10							0.8	0.3	0.1
Dinoflagellates										
Dinoflagellates $< 20\,\mu m$	Di < 20							0.8		
Dinoflagellates $> 20\,\mu m$	Di > 20							5.6	12.5	
Unidentified phytoflagellates										
Phytoflagellates $< 5\,\mu m$	Fl < 5		1.5	4.5	3.1	2.7	1.3	1.8	2.2	0.5
Phytoflagellates 5–10 μm	Fl < 10		12.2	27.9	21.4	15.7	9.7	19.0	8.2	6.0
Phytoflagellates 10–20 μm	Fl < 20			12.0	4.1	15.9	2.1			3.3

Note: Abbreviated species names are used in Fig. 5. P, planktonic; B, benthic.

The spring and autumn phytoplankton communities were characterized by the relatively low cell abundance and carbon biomass of all algal groups (Table 2). Species present all year round characterized the phytoplankton community in spring and autumn (Fig. 5b), with *Thalassiosira* Cleve (*T. curviseriata* and *T. anguste-lineata*) being the only diatom genus present with relatively high carbon biomass (Table 3). In autumn 1998, a small maximum in dinoflagellate carbon biomass occurred, representing 19% of the total phytoplankton biomass (Table 2).

Diatom taxonomic notes

A total of 117 diatom species and 17 taxa were identified during the two-year study in Anegada Bay (Table 4). The centric diatoms *Minidiscus trioculatus, M. decoratus* and *T. tealata* represent new records for the Argentinean Sea. Morphological features are presented for these latter species as well as for the rarely reported *Tryblioptychus cocconeiformis* from the southern hemisphere.

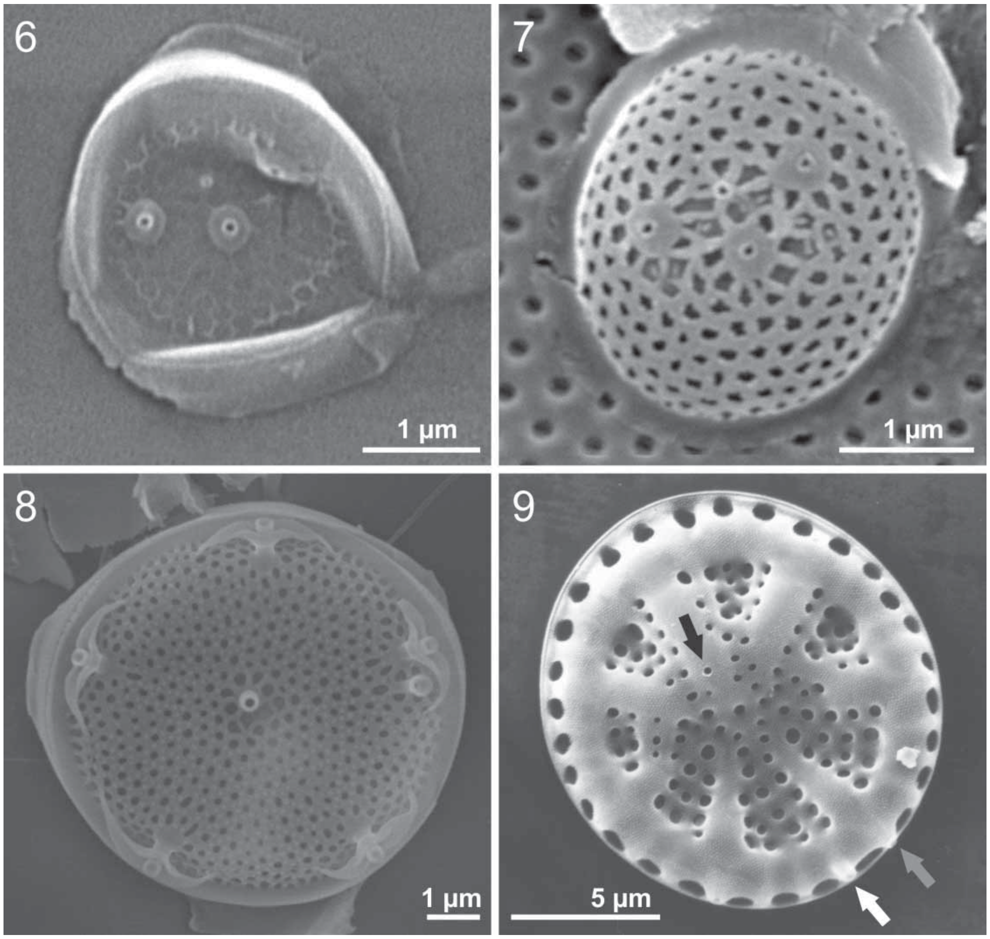
Minidiscus decoratus Chrétiennot-Dinet & Quiroga
(Fig. 6)

References. Aké-Castillo et al. 2001, p. 102, figs 1–3, as *Minidiscus trioculatus*; Quiroga & Chrétiennot-Dinet 2004, p. 342, figs 9–12, 17.

Description. Cells solitary, 2.0–2.5 μm in diameter. Valves circular and slightly silicified, with areolae (60–62

Table 4. List of diatom species recorded in Anegada Bay, El Rincón estuary, Argentina from December 1996 to September 1998.

Actinocyclus australis Grunow
A. curvatulus Janisch
A. octonarius Ehrenberg
Actinocyclus spp.
Actinoptychus senarius (Ehrenberg) Ehrenberg
A. splendens var. *glabrata* (Grunow) Pantocsek
A. vulgaris Schumann
Amphitetras antediluviana Ehrenberg
Amphora cf. *arcus* var. *sulcata* (Schmidt) Cleve
Amphora spp.
Asterionellopsis glacialis (Castracane) Round
Auliscus sculptus (W. Smith) Ralfs
Biddulphia alternans (Bailey) Van Heurck
Campylosira cymbelliformis (Schmidt) Grunow
Catacombas sp.
Cerataulina pelagica (Cleve) Hendey
Chaetoceros atlanticus Cleve
C. costatus Pavillard
C. didymus Ehrenberg
C. lorenzianus Grunow
C. radicans Schütt
C. socialis Lauder
Chaetoceros spp. < 20 µm
Cocconeis costata Gregory
C. fasciolata (Ehrenberg) Brown
C. scutellum Ehrenberg
Cocconeis spp.
Corethron pennatum (Grunow) Ostenfeld
Coscinodiscopsis jonesiana (Greville) Sar & Sunesen
Coscinodiscus asteromphalus Ehrenberg
C. centralis Ehrenberg
C. curvatulus Grunow
C. gigas Ehrenberg
C. granii Gough
C. janischii Schmidt
C. oculoides Karsten
C. radiatus Ehrenberg
Coscinodiscus spp.
Cyclotella littoralis Lange & Syvertsen
Cyclotella spp.
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin
Cymatosira atlantica Frenguelli
C. belgica Grunow
Delphineis minutissima (Hustedt) Simonsen
D. surirella (Ehrenberg) Andrews
Dimerogramma sp.
Diploneis sp.
Ditylum brigthwellii (T. West) Grunow
Entopyla cf. *australis* Ehrenberg
Eunotogramma cf. *laevis* Grunow
Grammatophora marina (Lyngbye) Kützing
Guinardia flaccida (Castracane) H. Peragallo
Gyrosigma fasciola (Ehrenberg) Griffith & Henfrey
Helicotheca tamensis Shrubsole
Hyalodiscus scoticus (Kützing) Grunow
Licmophora gracilis (Ehrenberg) Grunow
Lithodesmium undulatum Ehrenberg
Minidiscus chilensis Rivera
M. comicus Takano
M. decoratus Chrétiennot-Dinet & Quiroga
M. trioculatus (F.J.R. Taylor) Hasle
Navicula papula Schmidt
Navicula spp.
Nitzschia hummii Hustedt
Nitzschia spp.
Odontella atlantica (Frenguelli) Sar
O. aurita (Lyngbye) Agardh
Odontella longicruris (Greville) Hoban
O. mobiliensis (Bailey) Grunow
O. rhombus (Ehrenberg) Kützing
O. roperiana (Greville) Grunow
O. rostrata (Hustedt) Simonsen
O. sinensis (Greville) Grunow
Opephora sp.
Paralia crenulata (Grunow) Gleser
P. cf. *fausta* (Schmidt) Sims & Crawford
P. cf. *marina* (W. Smith) Heiberg
P. sulcata (Ehrenberg) Cleve
Petrodictyon cf. *patrimonii* Sterrenburg
Plagiogrammopsis vanheurckii (Grunow) Hasle, von Stosch & Syvertsen
Pleurosigma angulatum (Queckett) W. Smith
P. formosum W. Smith
Pleurosigma spp.
Psammodictyon panduriformis (Gregory) Mann
Pseudo-nitzschia australis Frenguelli
P. fraudulenta (Cleve) Hasle
P. pungens (Grunow ex Cleve) Hasle
Pseudopodosira westii (W. Smith) Sheshukova-Poretzskayar
Pseudosolenia calcar-avis (Schultze) Sundström
Raphoneis amphiceros (Ehrenberg) Ehrenberg
Rhabdonema adriaticum Kützing
R. arcuatum (Lyngbye) Kützing
Rhizosolenia bergonii H. Peragallo
R. cf. *imbricata* Brightwell
R. pungens Cleve-Euler
R. setigera Brightwell
Rhizosolenia spp.
Roperia tesselata (Roper) Grunow
Shionodiscus endoseriatus (Hasle & Fryxell) Alverson, Kang & Theriot
Stauropsis membranacea (Cleve) Meunier
Stellarima stellaris (Roper) Hasle & Sims
Stephanopyxis turris (Greville & Arnot) Ralfs
Surirella sp.
Thalassionema frauenfeldii (Grunow) Hallegraeff
T. nitzschioides (Grunow) Mereschkowsky
T. pseudonitzschioides (Schuette & Schrader) Hasle
Thalassiosira allenii Takano
T. anguste-lineata (Schmidt) Fryxell & Hasle
T. curviseriata Takano
T. decipiens (Grunow) Jørgensen
T. eccentrica (Ehrenberg) Cleve
T. hendeyi Hasle & Fryxell
T. hibernalis Gayoso
T. lentiginosa (Janisch) Fryxell
T. lundiana Hasle & Fryxell
T. mala Takano
T. minima Gaarder
T. minuscula Krasske
T. nanolineata (Mann) Fryxell & Hasle
T. nodulolineata (Hendey) Hasle & Fryxell
T. oestrupii var. *venrickae* Fryxell & Hasle
T. pacifica Gran & Angst
T. proschkinae var. *spinulata* (Takano) Makarova
T. punctigera (Castracane) Hasle
T. rotula Meunier
T. tealata Takano
T. tenera Proschkina-Lavrenko
Thalassiosira spp.
Trachyneis aspera (Ehrenberg) Cleve
Triceratium favus Ehrenberg
T. scitulum Brightwell
Trigonium sculptum (Shadbolt) Mann
Tryblionella sp.
Tryblioptychus cocconeiformis (Grunow ex Cleve) Hendey



Figs 6–9. Centric diatoms from the Argentinean Sea, SEM, external views. **Fig. 6.** *Minidiscus decoratus*, valve. **Fig. 7.** *Minidiscus trioculatus*, valve. **Fig. 8.** *Thalassiosira tealata*, valve. **Fig. 9.** *Tryblioptychus cocconeiformis*, valve showing external apertures of the rimoportula (white arrow), and the central (black arrow) and marginal fultoportulae (gray arrow).

in 10 µm) arranged in radial rows and a narrow hyaline margin. The rimoportula is solitary, located eccentrically and opening to the exterior through a small circular pore. Two to three fultoportulae are located on the valve face, distant from the valve margin and separated by an irregular areolation.

Remark. This species was described from the English Channel (France) and has also been reported from the Mexican Pacific Ocean as *M. trioculatus* by Aké-Castillo et al. (2001).

Minidiscus trioculatus (F.J.R. Taylor) Hasle (Fig. 7)

References. Hasle 1973, p. 29, figs 101–108; Takano 1990, p. 174, figs A–E; Bérard-Therriault et al. 1999, p. 20, pl. 2c; Aké-Castillo et al. 2001, p. 102, figs 1–3.

Description. Cells solitary, 2.5–5.5 µm in diameter. Valves circular and heavily silicified, with a prominent hyaline margin. A solitary central rimoportula opens to the exterior through a small circular tube. Three fultoportulae are present on the valve face, somewhat distant from the margin, and are separated from each other by an irregular row of areolae (40–42 in 10 µm).

Remark. *Minidiscus trioculatus* is mainly distinguished from *M. decoratus* by its prominent hyaline margin and its regular areolation extending from the valve center to the margin; it is considered a cosmopolitan species (Hasle 1973).

Thalassiosira tealata Takano (Fig. 8)

References. Takano 1980, p. 55, figs 1–17; Bérard-Therriault et al. 1987, p. 92, figs 54–55, 58; Takano 1990, p. 230, figs A–F; Hernández-Becerril & Tapia Peña 1995, p. 552, figs 62–67; Bérard-Therriault et al. 1999, p. 28, pl. 11c.

Description. Disc-shaped cells in girdle view. Valves flat, 7.0–7.5 µm in diameter. Areolae (30–35 in 10 µm) in radial rows, slightly fasciculated. A single fultoportula is present at the valve center. Morphologically different fultoportulae, with wing-like projections, are located near the valve margin separated by ca. 3–5 µm from the mantle itself. A single rimoportula is positioned very close to one marginal fultoportula, and is characterized by a conspicuous external tube.

Remark. This species has been predominantly reported from subtropical to temperate regions (Hernández-Becerril & Tapia Peña 1995).

Tryblioptychus cocconeiformis (Grunow ex Cleve) Hendey (Fig. 9)

References. Hendey 1958, p. 46, pl. 2, fig. 10; Prasad et al. 2002, p. 294, figs 1–44.

Description. Frustules are elliptical to circular in valve view (8.4 × 15.0 μm) and cuneate in girdle view (7.2 × 14.4 μm). Valve faces are transversely and radially undulate, with alternate depressed fascicles and elevated triangular interfascicles. Each fascicle has 3–5 irregular rows of areolae (ca. 15 in 10 μm), radiating from the center to the valve margin. Depressed fascicles have large rows of areolae extending from the mantle to the valve center, whereas they are shorter in elevated fascicles. The interfascicles are hyaline and of variable length. A series of chambers (7–10 in 10 μm) open near to the edge of the mantle and are internally occluded by a thin perforated plate (15 pores in 1 μm). A solitary rimoportula located close to the mantle edge opens to the exterior by a long tube. A solitary fultoportula is located close to the valve center, whereas a marginal ring of fultoportulae is located between the valve face and the mantle. Marginal fultoportulae open to the exterior by short rimmed apertures and to the interior by four satellite pores.

Remark. *Tryblioptychus cocconeiformis* has been rarely reported in the southern hemisphere, except for its presence in Ascension Islands (Prasad et al. 2002), Argentinean (Ferrario et al. 2002, Sar et al. 2010) and Brazilian waters (Tremarin et al. 2008).

Discussion

The annual cycle of phytoplankton in Anegada Bay was characterized by a strong seasonality, with two periods of high carbon biomass occurring in summer and late autumn–early winter (Fig. 4b and Table 2). Phytoplankton blooms mainly comprised diatoms, although the carbon biomass of all algae groups increased during the summer and winter seasons (Table 2). This pattern of phytoplankton seasonal dynamics is similar to the one described for the inner region of Blanca Bay, in the northernmost area of the El Rincón estuarine system (Fig. 1). In Blanca Bay, a winter–early spring bloom of diatoms has been repeatedly recorded during the past 30 years (Gayoso 1999, Guinder et al. 2010). In addition, a summer maximum in phytoplankton chlorophyll *a* biomass can be observed in the results of most studies done in Blanca Bay (Gayoso 1999, Campuzano et al. 2008, Guinder et al. 2009). Recently, Guinder et al. (2010) showed that the intensity of the summer diatom blooms in Blanca Bay has increased during recent years. Therefore, the close similarity between Anegada Bay and Blanca Bay in total phytoplankton biomass suggests that a general seasonal pattern applies to the phytoplankton dynamics over shoals in the El Rincón estuarine system.

Diatom blooms are recurrent events in estuaries (Cloern & Dufford 2005, Bresnan et al. 2009). The onset and ending of diatom blooms are generally coupled with changes in the nutrient supply, as a result of high concentrations of nutrients occurring during periods of high river discharge (Malone et al. 1988, Cloern & Dufford 2005, Paerl et al. 2010). In Anegada Bay, the summer and winter diatom blooms coincided with periods of maximum discharge of the Negro River (Fig. 2a), suggesting an input of nutrients into the system as a major controlling factor of the diatom blooms. Although the nutrient concentration in Anegada Bay showed marked interannual variability during this study (Fig. 3b), the diatom blooms coincided with increasing concentrations of silicic acid (Figs 3b and 4). Diatom carbon biomass was positively and highly significantly correlated with the concentration of silicic acid ($r = 0.66, p = 0.002$), indicating that diatom blooms developed under conditions of high availability of this nutrient. Moreover, during winter 1998, when silicic acid concentrations remained relatively low, the diatom bloom was two times lower than during winter 1997. Correlations between diatom carbon biomass and the concentration of phosphate, nitrite and nitrate were not significant ($p > 0.01$), suggesting a relatively lower importance for these nutrients in the development of the diatom bloom. Therefore, it can be hypothesized that the occurrence of diatom blooms in Anegada Bay is mainly related to the availability of silicic acid. Studies performed in Blanca Bay have also shown a close relationship between nutrient concentrations (particularly silicic acid) and the occurrence of the winter diatom bloom (Gayoso 1998, Popovich et al. 2008).

Although river inflow regime can affect the observed variations in phytoplankton biomass, it cannot explain the seasonal changes in the diatom taxonomic composition in Anegada Bay. Most diatom species showed a distinct seasonal cycle, and different diatom communities dominated the summer and winter blooms (Fig. 5 and Table 3). In summer, tychoplanktonic diatoms, such as *Paralia* cf. *marina, P. sulcata, R. amphiceros* and *D. surirella* were present with high carbon biomass (Table 3). The presence of these species in the water column indicates the influence of the benthic community in the composition of the planktonic community. In shallow estuaries, benthic microalgae can be easily detached from the sediments by wind-induced turbulence or tidal currents (Shaffer & Sullivan 1988, De Jonge & Van Beusekom 1995), and their resuspension into the water column is a common mechanism for the establishment of diatom blooms (Cloern et al. 1985, Verity et al. 1998, Carstensen et al. 2007). Therefore, the occurrence of the summer diatom bloom in Anegada Bay seems to be strongly influenced by the exchange of microalgae between sediments and the water column, probably due to the high intensity and frequency of winds occurring during this season across El Rincón estuary (Fig. 2b, Lucas et al. 2005).

Another dominant diatom in terms of carbon biomass in the summer blooms in Anegada Bay was *T. hendeyi* (Table 3), which has been frequently reported during blooms in estuarine environments (Muylaert & Sabbe 1999, Cloern & Dufford 2005). This species co-occurred with *P. sulcata* all year round in Blanca Bay (Gayoso 1999). Species of *Thalassiosira* are commonly reported in estuarine phytoplankton, but different species exhibit distinct seasonal behavior or spatial distribution due to differences in temperature, salinity and light regime. *Thalassiosira hendeyi* has been described as a warm meso-eurythermal and polyhaline species (Baars 1979, Muylaert & Sabbe 1996). The minimum temperature for *T. hendeyi* growth is relatively high (6°C), and it performs well at higher temperatures (Baars 1979). Therefore, the bloom of *T. hendeyi* in Anegada Bay is probably stimulated by the increased water temperatures during the summer, whereas this species probably does not survive in winter when water temperatures diminish.

In late autumn–early winter, a large diatom bloom occurred in Anegada Bay (Table 2). Although the phytoplankton carbon biomass was about two times higher in 1997 than in 1998, the dynamic of the late autumn–early winter bloom was similar during these two years. In autumn, the bloom was dominated by *T. curviseriata*, which was replaced in winter by other marine diatom species (Table 3). The replacement pattern of *T. curviseriata* by other dominant diatoms is rather similar to the one described by Popovich et al. (2008) for the winter diatom blooms in Blanca Bay. Moreover, most of the species dominating the winter blooms in Anegada Bay are also major components of the winter diatom blooms in Blanca Bay (Gayoso 1999, Popovich et al. 2008). The onset of the winter diatom bloom in Blanca Bay has been attributed to high nutrient concentrations, reduction of the grazing pressure and increased water transparency, whereas the termination of the bloom in early spring has been ascribed to nutrient depletion and intense grazing pressure by zooplankton (Gayoso 1999, Popovich et al. 2008, Guinder et al. 2009). Whether the same mechanisms regulate the winter seasonal dynamic in Anegada Bay should be verified with adequate environmental data for the area.

A major characteristic of the winter blooms in Anegada Bay is the high abundance and carbon biomass of centric diatom resting spores. The presence of resting spores suggests that the occurrence of the winter bloom is closely coupled to the life-cycle strategies of the diatom species. Resting spores can have a profound impact on the seasonal dynamics of neritic phytoplankton communities because they function as benthic surviving stages of the species when environmental conditions in the water column are unfavorable for vegetative cell growth (Garrison 1981, Smetacek 1985). As the environmental conditions improve, spores are resuspended in the water column and act as seeds for the seasonal diatom blooms (McQuoid & Hobson 1996, Chen et al. 2009). Therefore, it is probable that those environmental conditions that have been associated with the initiation of the winter diatom bloom in Blanca Bay, as described above, actually regulate the germination of resting spores. Guinder et al. (2009) reported that the initiation of the winter bloom is associated with a period of increasing solar radiation, which stimulates diatom resting-spore germination and subsequent cell growth (Shikata et al. 2009). In addition, the ending of the bloom has been associated with the depletion of nutrients in the water column (Popovich et al. 2008), a major factor inducing the formation of diatom resting stages (Chen et al. 2009). Gayoso (1999) also reported the occurrence of diatom resting spores during winter in Blanca Bay, another feature indicating striking similarities between the phytoplankton composition and dynamics in Blanca and Anegada bays. In light of these results, we suggest that the species' life-cycle strategies can play a major role determining the temporal patterns of diatom seasonal succession in the El Rincón estuarine system.

Conclusions

Anegada Bay is characterized by the dominance of diatoms over most of the annual cycle. Phytoplankton communities are very rich in species, with 117 diatom species recorded during the two-year study. Some diatoms are reported for the first time in the Argentinean Sea: *Minidiscus trioculatus, M. decoratus* and *T. tealata.* The phytoplankton annual cycle was characterized by a strong seasonality, with summer and late autumn–early winter diatom blooms. Most diatom species showed a distinct seasonal cycle. The summer phytoplankton bloom was in part induced by the resuspension of benthic microalgae from the sediments and by an autochthonous population of *T. hendeyi*. The winter phytoplankton bloom seems to be influenced by the inoculation of the water column by diatom resting spores. Taxon-specific life-cycle strategies, such as the occurrence of alternating vegetative and resting stages, seem to be important in determining the seasonal succession of diatom species. Although our dataset covers a relatively short-term interval, in view of the striking similarities between phytoplankton composition and temporal succession in Anegada and Blanca bays, it is suggested that a common set of physical, chemical and biological conditions, operating on wide spatial scales, controls phytoplankton seasonal dynamics over the shoals of the El Rincón estuarine system.

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References

Acha E.M., Mianzan H.W., Guerrero R.A., Favero M. & Bava J. 2004. Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine Systems* 44: 83–105.

Aké-castillo J.A., Hernández-Becerril D.U., Meave Del Castillo M.E. & Bravo-Sierra E. 2001. Species of *Minidiscus* (Bacillariophyceae) in the Mexican Pacific Ocean. *Cryptogamie, Algologie* 22: 101–107.

Aliotta S., Spagnuolo J.O., Ginsberg S.S. & Gelós E.M. 1999. Sedimentos de fondo-subfondo y aspectos geomorfológicos de la plataforma continental entre el estudario de Bahía Blanca y Bahía Anegada, Provincia de Buenos Aires. *Revista de la Asociación Argentina de Sedimentología* 6: 19–35.

Arrigo K.R. 2005. Marine microorganisms and global nutrient cycles. *Nature* 437: 349–355.

Baars J.W.M. 1979. Autecological investigations on marine diatoms. I. Experimental results in biogeographical studies. *Aquatic Ecology* 13: 123–137.

Barbosa A.B., Domingues R.B. & Galvão H.M. 2010. Environmental forcing of phytoplankton in a Mediterranean estuary (Guadiana estuary, south-western Iberia): a decadal study of anthropogenic and climatic influences. *Estuaries and Coasts* 33: 324–341.

Bérard-therriault L., Cardinal A. & Poulin M. 1987. Les diatomées (Bacillariophyceae) benthiques de substrats durs des eaux marines et saumâtres du Québec. 8. Centrales. *Naturaliste canadien* 114: 81–103.

Bérard-therriault L., Poulin M. & Bossé L. 1999. Guide d'identification du phytoplancton marin de l'estuaire et du golfe du Saint-Laurent, incluant également certains protozoaires. *Publication spéciale canadienne des sciences halieutiques et aquatiques* 128: 1–387.

Boltovskoy D. 2008. Cartas de sensibilidad. Bahía Anegada. In: *Atlas de sensibilidad ambiental de la costa y el Mar Argentino* (Ed. by D. Boltovskoy), pp. 1–3. Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires.

Borges M.E. 2006. *Ecología de las ostras en ambientes del sur bonaerense: Cultivo y manejo de sus poblaciones*. Ph.D. Thesis, Universidad Nacional del Sur, Bahía Blanca.

Bresnan E., Hay S., Hughes S.L., Fraser S., Rasmussen J., Webster L., Slesser G., Dunn J. & Heath M.R. 2009. Seasonal and interannual variation in the phytoplankton community in the north east of Scotland. *Journal of Sea Research* 61: 17–25.

Campuzano F.J., Pierini J.O., Leitao P.C., Marcovecchio J.E., Mateus M. & Neves R. 2008. *Ecological conceptual model for the Bahía Blanca estuary.* Ecomanage Report 2.10-2.11, Ecomanage, Lisboa. 24 pp.

Carreto J.I., Montoya N.G., Benavides H.R., Guerrero R. & Carignan M.O. 2003. Characterization of spring phytoplankton communities in the Río de La Plata maritime front using pigment signatures and cell microscopy. *Marine Biology* 143: 1013–1027.

Carstensen J., Henriksen P. & Heiskanen A.-S. 2007. Summer algal blooms in shallow estuaries: definition, mechanisms, and link to eutrophication. *Limnology and Oceanography* 52: 370–384.

Castaños C., Pascual M. & Pérez Camacho A. 2009. Reproductive biology of the nonnative oyster *Crassostrea gigas* (Thunberg, 1793), as a key factor for its successful spread along the rocky shores of northern Patagonia, Argentina. *Journal of Shellfish Research* 28: 837–847.

Chen C., Sun L., Gao Y., Zhou Q., Zheng M., Li B., Yu Y. & Lu D. 2009. Seasonal changes of viable diatom resting stages in bottom sediments of Xiamen Bay, China. *Journal of Sea Research* 61: 125–132.

Cloern J.E. & Dufford R. 2005. Phytoplankton community ecology: principles applied in San Francisco Bay. *Marine Ecology Progress Series* 285: 11–28.

Cloern J.E. & Jassby A.D. 2010. Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. *Estuaries and Coasts* 33: 230–241.

Cloern J.E., Cole B.E., Wong R.L.J. & Alpine A.E. 1985. Temporal dynamics of estuarine phytoplankton: a case study of San Francisco Bay. *Hydrobiologia* 129: 153–176.

Cousseau M.B., Gosztonyi A.E., Elías I. & Ré M.E. 2004. Estado actual del conocimiento de los peces de la plataforma continental Argentina y adyacencias. In: *El Mar Argentino y sus recursos pesqueros* (Ed. by R.P. Sánchez & S.I. Bezzi), pp. 17–38. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata.

De Jonge V.N. & Van Beusekom J.E.E. 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. *Limnology and Oceanography* 40: 766–778.

Esteves J.L., Ciocco N.F., Colombo J.C., Freije R.H., Harris G., Iribarne O., Isla I., Nabel P., Pascual M., Penchaszadeh P.E., Rivas A.L. & Santinelli N. 2000. The Argentine Sea: the southeast South American shelf marine ecosystem. In: *The seas at the millenium* (Ed. by C. Sheppard), pp. 105–127. Elsevier, Amsterdam.

Ferrario M.E., Sar E.A. & Sala S.E. 1995. Metodología básica para el estudio del fitoplancton con especial referencia a las diatomeas. In: *Manual de métodos ficológicos* (Ed. by K. Alveal, M.E. Ferrario, E.C. Oliveira & E.A. Sar), pp. 1–23. Universidad de Concepción, Concepción.

Ferrario M.E., Sala S.E. & Round F.E. 2002. *Tryblioptychus* Hendey (Bacillariophyceae), nuevo registro para la costa del Cono Sur Americano. Abstracts of the VI Congreso Latinoamericano y IV Reunión Iberoamericana de Ficología, 22–28 September, 129 pp. Ponce, Puerto Rico.

Gameiro C. & Brotas V. 2010. Patterns of phytoplankton variability in the Tagus estuary (Portugal). *Estuaries and Coasts* 33: 311–323.

Garibotti I.A., Vernet M., Kozlowski W.A. & Ferrario M.E. 2003. Composition and biomass of phytoplankton assemblages in coastal Antarctic waters: a comparison of chemotaxonomic and microscopic analyses. *Marine Ecology Progress Series* 247: 27–42.

Garrison D.L. 1981. Monterey Bay phytoplankton. II. Resting spore cycles in coastal diatom populations. *Journal of Plankton Research* 3: 137–156.

Gayoso A.M. 1998. Long-term phytoplankton studies in the Bahía Blanca estuary, Argentina. *ICES Journal of Marine Science* 55: 655–660.

Gayoso A.M. 1999. Seasonal succession patterns of phytoplankton in the Bahía Blanca estuary (Argentina). *Botanica Marina* 42: 367–375.

Gómez N., Hualde P. R., Licursi M. & Bauer D. E. 2004. Spring phytoplankton of Río de la Plata: a temperate estuary of South America. *Estuarine, Coastal and Shelf Science* 61: 301–309.

Guerrero R.A. 1998. Oceanografía física del estudario del Río de la Plata y el sistema costero de El Rincón. Noviembre, 1994. *INIDEP Informe Técnico* 21: 29–54.

Guinder V.A., Popovich C.A. & Perillo G.M.E. 2009. Particulate suspended matter concentrations in the Bahía Blanca Estuary, Argentina: implication for the development of phytoplankton blooms. *Estuarine, Coastal and Shelf Science* 85: 157–165.

Guinder V.A., Popovich C.A., Molinero J.C. & Perillo G.M.E. 2010. Long-term changes in phytoplankton phenology and community structure in the Bahía Blanca Estuary, Argentina. *Marine Biology* 157: 2703–2716.

Hasle G.R. 1973. Some marine plankton genera of the diatom family Thalassiosiraceae. *Beihefte zur Nova Hedwigia* 45: 1–49.

Hasle G.R. & Fryxell G.A. 1970. Diatoms: cleaning and mounting for light and electron microscopy. *Transactions of the American Microscopical Society* 89: 469–474.

Hasle G.R. & Syvertsen E.E. 1997. Marine diatoms. In: *Identifying marine phytoplankton* (Ed. by C.R. Tomas), pp. 5–385. Academic Press, San Diego.

Hendey N.I. 1958. Marine diatoms from some West African ports. *Journal of the Royal Microscopical Society* 77: 28–85.

Hernández-Becerril D.U. & Tapia Peña M.I. 1995. Planktonic diatoms from the Gulf of California and coasts off Baja California: species of the genus *Thalassiosira*. *Botanica Marina* 38: 543–555.

Hill M.O. & Gauch Jr H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.

Hillebrand H., Dürselen C.-D., Kirschtel D., Pollingher U. & Zohary T. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35: 403–424.

Jongman R.H.G., ter Braak C.J.F. & Van Tongeren O.F.R. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge. 299 pp.

Karlson B., Cusak C. & Bresnan E. 2010. *Microscopic and molecular methods for quantitative phytoplankton analysis*. IOC Manuals and Guides no. 55. UNESCO, Paris. 110 pp.

Legendre L. & Rassoulzadegan F. 1995. Plankton and nutrient dynamics in marine waters. *Ophelia* 41: 153–172.

Legendre L. & Rassoulzadegan F. 1996. Food-web mediated export of biogenic carbon in oceans: hydrodynamic control. *Marine Ecology Progress Series* 145: 179–193.

Lepš J. & Šmilauer P. 1999. *Multivariate analysis of ecological data*. University of South Bohemia, Ceske Budejovice. 110 pp.

Licursi M., Sierra M.V. & Gómez N. 2006. Diatom assemblages from a turbid coastal plain estuary: Río de la Plata (South America). *Journal of Marine Systems* 62: 35–45.

Lucas A.J., Guerrero R.A., Mianzán H.W., Acha E.M. & Lasta C.A. 2005. Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34–43°S). *Estuarine, Coastal and Shelf Science* 65: 405–420.

Lucifora L.O., Menni R.C. & Escalante A.H. 2005. Reproduction, abundance and feeding habits of the broadnose sevengill shark *Notorynchus cepedianus* in north Patagonia, Argentina. *Marine Ecology Progress Series* 289: 237–244.

Macchi G.J. & Acha E.M. 1998. Aspectos reproductivos de las principales especies de peces en la zona común de pesca Argentino-Uruguaya y en El Rincón. *INIDEP Informe Técnico* 21: 67–89.

Malone T.C., Crocker L.H., Pike S.E. & Wendler B.W. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Marine Ecology Progress Series* 48: 235–249.

Martos P. & Piccolo M.C. 1988. Hydrography of the Argentine continental shelf between 38° and 42°S. *Continental Shelf Research* 8: 1043–1056.

McQuoid M.R. & Hobson L.A. 1996. Diatom resting stages. *Journal of Phycology* 32: 889–902.

Montagnes D.J.S. & Franklin D.J. 2001. Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: reconsidering some paradigms. *Limnology and Oceanography* 46: 2008–2018.

Montagnes D.J.S., Berges J.A., Harrison P.J. & Taylor F.J.R. 1994. Estimating carbon, nitrogen, protein, and chlorophyll *a* from volume in marine phytoplankton. *Limnology and Oceanography* 39: 1044–1060.

Muylaert K. & Sabbe K. 1996. The diatom genus *Thalassiosira* (Bacillariophyta) in the estuaries of the Schelde (Belgium/The Netherlands) and the Elbe (Germany). *Botanica Marina* 39: 103–115.

Muylaert K. & Sabbe K. 1999. Spring phytoplankton assemblages in and around the maximum turbidity zone of the estuaries of the Elbe (Germany), the Schelde (Belgium/The Netherlands) and the Gironde (France). *Journal of Marine Systems* 22: 133–149.

O'Boyle S. & Silke J. 2010. A review of phytoplankton ecology in estuarine and coastal waters around Ireland. *Journal of Plankton Research* 32: 99–118.

Paerl H.W., Rossignol K.L., Hall S.N., Peierls B.L. & Wetz M.S. 2010. Phytoplankton community indicators of short- and long-term ecological change in the anthropogenically and climatically impacted Neuse River Estuary, North Carolina, USA. *Estuaries and Coasts* 33: 485–497.

Pascual M. & Castaños C. 2000. *Cultivo de ostras cóncavas en Argentina: desde el criadero hasta la cosecha en el mar*. Secretaría de Agricultura, Ganadería, Pesca y Alimentación, Buenos Aires. 45 pp.

Pascual M. & Zampatti. 1998. Cultivo de moluscos bivalvos. In: *El Mar Argentino y sus recursos pesqueros* (Ed. by E.E. Boschi), pp. 167–194. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata.

Piccolo M.C. & Perillo G.M.E. 1990. Physical characteristics of the Bahia Blanca estuary (Argentina). *Estuarine, Coastal and Shelf Science* 31: 303–317.

Popovich C.A. & Marcovecchio J.E. 2008. Spatial and temporal variability of phytoplankton and environmental factors in a temperate estuary of South America (Atlantic coast, Argentina). *Continental Shelf Research* 28: 236–244.

Popovich C.A., Spetter C.V., Marcovecchio J.E. & Freije R.H. 2008. Dissolved nutrient availability during winter diatom bloom in a turbid and shallow estuary (Bahía Blanca, Argentina). *Journal of Coastal Research* 24: 95–102.

Prasad A.K.S.K., Nienow J.A. & Livington R.J. 2002. The marine diatom genus *Tryblioptychus* Hendey (Thalassiosiraceae, Coscinodiscophyceae): fine structure, taxonomy, systematics and distribution. *Diatom Research* 17: 291–308.

Pritchard D.W. 1967. What is an estuary, physical viewpoint. In: *Estuaries* (Ed. by G.H. Lauf), pp. 3–5. American Association for the Advancement of Science, Washington DC.

Quiroga I. & Chrétiennot-Dinet M.-J. 2004. A new species of *Minidiscus* (Diatomophyceae, Thalassiosiraceae) from the eastern English Channel, France. *Botanica Marina* 47: 341–348.

Rothenberger M.B., Burkholder J.M. & Wentworth T.R. 2009. Use of long-term data and multivariate ordination techniques to identify environmental factors governing estuarine phytoplankton species dynamics. *Limnology and Oceanography* 54: 2107–2127.

Round F.E., Crawford R.M. & Mann D.G. 1990. *The diatoms. Biology and morphology of the genera*. Cambridge University Press, Cambridge. 747 pp.

Sar E.A., Sunesen I. & Lavigne A.S. 2010. *Cymatotheca*, *Tryblioptychus*, *Skeletonema* and *Cyclotella* (Thalassiosirales) from Argentinean coastal waters. Description of *Cyclotella cubiculata* sp. nov. *Vie et milieu* 60: 135–156.

Shaffer G.P. & Sullivan M.J. 1988. Water column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. *Journal of Phycology* 24: 132–140.

Shikata T., Nukata A., Yoshikawa S., Matsubara T., Yamasaki Y., Shimasaki Y., Oshima Y. & Honjo T. 2009. Effects of light quality on initiation and development of meroplanktonic diatom blooms in a eutrophic shallow sea. *Marine Biology* 156: 875–889.

Smetacek V.S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Marine Biology* 84: 239–251.

Strickland J.D.H. & Parsons T.R. 1984. *A practical handbook of seawater analysis*. Queen's Printer, Ottawa. 310 pp.

Takano H. 1980. New and rare diatoms from Japanese marine waters. V. *Thalassiosira tealata* sp. nov. *Bulletin of Tokai Regional Fisheries Research Laboratory* 103: 55–63.

Takano H. 1990. Diatoms. In: *Red tide organisms in Japan - An illustrated taxonomic guide* (Ed. by Y. Fukuyo, H. Takano, M. Chihara & K. Matsouka), pp. 162–331. Uchida Rokakuho, Tokyo.

Tremarin P.I., Ludwig T.A.V. & Moreira-Filho H. 2008. Thalassiosirales (Diatomeae) of the Guaraguaçu river, littoral basin, Paraná State, Brazil. *Acta Botanica Brasilica* 22: 1101–1113.

Utermöhl H. 1958. Zur vervollkommung der quantitativen phytoplankton methodik. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* 9: 1–38.

Verity P.G., Blanton J.O., Amft J., Barans C., Knott D., Stender B. & Wenner E. 1998. Influences of physical oceanographic processes on chlorophyll distributions in coastal and estuarine waters of the South Atlantic Bight. *Journal of Marine Research* 56: 681–711.

Villafañe V.E. & Reid F.M.H. 1995. Métodos de microscopia para la cuantificación del fitoplancton. In: *Manual de métodos ficológicos* (Ed. by K. Alveal, M.E. Ferrario, E.C. Oliveira & E.A. Sar), pp. 169–185. Universidad de Concepción, Concepción.

Yorio P., Rábano D., Rabuffetti F., Friedrich P. & Harris G. 1998a. Distribución reproductiva y abundancia de las aves marinas del sur de Buenos Aires. In: *Atlas de la distribución reproductiva de aves marinas en el litoral Patagónico Argentino. Plan de manejo integrado de la zona costera Patagónica* P. (Ed. by Yorio, E. Frere, P. Gandini & G. Harris), pp. 19–28. Fundación Patagonia Natural–Wildlife Conservation Society, Buenos Aires.

Yorio P., Tagliorette A., Harris G. & Giaccardi M. 1998b. Áreas protegidas costeras de la Patagonia: síntesis de información, diagnosis sobre su estado actual de protección y recomendaciones preliminares. In: *Informes técnicos del plan de manejo integrado de la zona costera Patagónica*. (Ed. by P. Yorio, E. Frere, P. Gandini & G. Harris), pp. 1–70. Fundación Patagonia Natural, Puerto Madryn.

Zar J. H. 1996. *Biostatistical analysis*. Prentice Hall International, Englewood Cliffs. 485 pp.