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Ecological optima and tolerances of coastal benthic diatoms in the freshwater-mixohaline zone of the Río de la Plata estuary

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ABSTRACT: The purpose of this study was to explore the autecology of diatom species inhabiting the epipsammon and epiphyton in the freshwater-mixohaline zone of the Río de la Plata estuary. The diatoms are a conspicuous component of those communities. We discuss the optima and tolerance ranges of diatoms for the following environmental variables: conductivity, turbidity, pH, nutrients (phosphate, nitrate, nitrite, and ammonium), and dissolved oxygen levels as well as both the chemical and biological oxygen demand. The study was carried out on the Argentinean coastline between 34° 27′ S, 58° 30′ W and 35° 23′ S, 57° 08′ W. In total, 32 sampling sites influenced by different land uses were monitored along 168 km of shoreline. Epipsammic samples of the intertidal zone were taken at low tide during spring 2005, autumn and winter 2006, spring and summer 2007, and autumn 2008. Epiphytic samples were taken during summer, autumn, and spring 2000 and spring 2002. In total, 224 benthic species were identified in the 120 samples analyzed; 81 species had a frequency greater than 5% in the total sample dataset with more than 1% of relative abundance in at least 1 sample and were chosen for estimation of their optima and tolerances for selected water-quality characteristics. The physicochemical data analyzed indicated 2 gradients — increases in conductivity and turbidity along with decreases in the concentration of nutrients and organic matter — that generated different types of habitats for the species investigated.

KEY WORDS: Diatoms · Optima · Tolerance range · Autecology · Epipsammon · Epiphyton · Coastal-plain estuary · Río de la Plata

INTRODUCTION

Estuaries, commonly regarded as intermediate transitional zones linking freshwater and marine systems, encompass a wide variety of environments. Estuaries are biologically rich regions where the great variety of habitats contributes to a high productivity in these ecosystems. Human populations have used estuaries as food sources and places of settlement, navigation, and waste repositories. As a result, coastal waters have received large inputs of nutrients, organic matter, and other contaminants. Moreover, habitat destruction, over fishing, wetland loss, and the introduction of non-indigenous species are among the further consequences of the presence of many human activities (Ohrel & Register 2006).

Diatoms are an important and often dominant component of the benthic microalgal assemblage in estuarine and shallow coastal environments (Admiraal 1984). Diatom taxa occurring in transitional zones between marine and freshwater habitats can be divided into 2 affinity groups, each containing taxa with either a marine or a freshwater affinity (Snoeijs 1999).

When using organisms as indicators of environmental quality, the essential aspect to be considered is that of the ambient conditions affecting the survival, occurrence, abundance, growth, and fecundity of the constituent organisms (Snoeijs 1999). Diatoms are particularly useful as indicators within estuarine systems for the same reason that they are useful in other aquatic habitats and in paleo-ecological studies (Clarke et al. 2006). Each species has characteristic

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optima and tolerances for various aspects of water quality such as pH, salinity, temperature, nutrients, and light availability (i.e. turbidity; Cooper 1995). In a freshwater ecosystem, the dependence of benthic diatoms on nutrients has been so unequivocally clarified that microalgae have been classified according to trophic and saprobity classes and are thus used as sensitive indicators of water quality (Sládeček 1973, 1985, Lange-Bertalot 1979, Hoffman 1994, Van Dam et al. 1994, Gómez & Licursi 2001, Licursi & Gómez 2002). Although considerable progress has been made in utilizing diatoms to assess water quality in freshwater systems, the situation is quite different in estuarine and shallow marine coastal systems, particularly in the southern hemisphere (Sullivan 1999).

Nevertheless, diatoms have been widely used in the reconstruction of the paleoenvironment (Cooper 1999, Denys & de Wolfs 1999, Clarke et al. 2006), and an understanding of modern ecological data can contribute to an improved knowledge of the local habitat. According to Clarke et al. (2006), diatoms are powerful paleoecological indicators, since their taxonomically distinct frustules allow identification to species level, and they are usually present in diverse, numerically abundant assemblages (Charles et al. 1994) that preserve well in a variety of sedimentary environments (Anderson & Vos 1992). In spite of diatoms having been used largely as indicators of environmental change in marine systems (Stoermer & Smol 1999) and as indicators of eutrophication in coastal waters (Cooper 1995, Clarke et al. 2006), the current lack of precise autecological knowledge for many coastal taxa makes interpretation of bioestratigraphic records difficult (Clarke et al. 2006). A combination of research, monitoring, and paleoecological studies can become a synergistic tool for discerning the trends, causes, and consequences of watershed-land use (Cooper 1999). Along the Argentinean coast, information about modern diatom distribution is scarce and fragmentary (Hassan et al. 2009); consequently, the majority of diatom-based paleoenvironmental reconstructions have been derived from autecological data extrapolated from the European literature.

The purpose of this study was to explore the autecology of diatom species that inhabit the epipsammon and epiphyton from the freshwater-estuarine zone of the Río de la Plata estuary. Diatoms are a conspicuous component of those communities (Gómez et al. 2003, 2009). Here we discuss the ecological optima and tolerance ranges of diatoms for the following environmental variables: conductivity, turbidity, pH, nutrients (phosphate, nitrate, nitrite, and ammonium), dissolved oxygen (DO) levels, and both the chemical and biological oxygen demand (COD and BOD_5, respectively). The overall goal was to provide baseline information for future water-quality assessments as well as for ecological interpretation.

MATERIALS AND METHODS

Study area. The Río de la Plata is located on the east coast of South America and is a shallow, large-scale, turbid coastal-plain estuary that covers an approximate area of 35 000 km^2. The inner region has a pluvial

Table 1. Sampling sites, geographical location, and the main land uses in the study area. U: urban, R: recreational, W: waste effluent, F: fishing, I: industrial effluent, H: harbor, P: water pumping

Code	Site name	Coordinates	Main land uses
S1	Desembocadura de Luján	34° 27′ 10″ S, 58° 30′ 21″ W	U, R
S2	San Isidro	34° 29′ 08″ S, 58° 28′ 49″ W	U, R
S3	Aeroparque-Palermo	34° 32′ 57″ S, 58° 25′ 35″ W	U, R, P
S4	Costanera Sur	34° 36′ 54″ S, 58° 20′ 24″ W	R
S5	Canal Sarandí	34° 39′ 31″ S, 58° 18′ 59″ W	U, W, I
S6	Canal Santo Domingo	34° 40′ 01″ S, 58° 18′ 04″ W	U, W, I
S7	Bernal	34° 41′ 30″ S, 58° 15′ 14″ W	U, R, P
S8	Quilmes	34° 42′ 31″ S, 58° 13′ 30″ W	U, R
S9	Berazategui	34° 44′ 38″ S, 58° 10′ 42″ W	W
S10	Boca Cerrada	34° 46′ 49″ S, 58° 00′ 59″ W	R, F
S11	Punta Lara	34° 49′ 29″ S, 57° 57′ 35″ W	R, P
S12	Puerto La Plata	34° 50′ 01″ S, 57° 52′ 50″ W	H
S13	Los Borrachos	34° 51′ 17″ S, 57° 50′ 21″ W	R, F
S14	Bagliardi	34° 52′ 26″ S, 57° 48′ 33″ W	W
S15	Balandra	34° 55′ 44″ S, 57° 42′ 56″ W	R
S16	Punta Blanca	34° 56′ 31″ S, 57° 40′ 20″ W	R
S17	El Pino	34° 57′ 14″ S, 57° 38′ 58″ W	R
S18	Campos de Alberdi	34° 58′ 31″ S, 57° 37′ 04″ W	R
S19	Atalaya	35° 00′ 49″ S, 57° 32′ 07″ W	R
S20	Marcelo	35° 01′ 16″ S, 57° 31′ 13″ W	R
S21	Magdalena	35° 01′ 50″ S, 57° 29′ 38″ W	R
S22	Juncal 1	35° 01′ 39″ S, 57° 30′ 22″ W	R
S23	Juncal 2-1	35° 02′ 22″ S, 57° 30′ 01″ W	R
S24	Juncal 2-2	35° 02′ 00″ S, 57° 29′ 57″ W	R
S25	Playa nueva	35° 02′ 08″ S, 57° 29′ 44″ W	R
S26	Gauchito Gil	35° 02′ 22″ S, 57° 29′ 28″ W	R
S27	Ricardo	35° 03′ 44″ S, 57° 27′ 36″ W	R
S28	Juan Blanco	35° 05′ 20″ S, 57° 25′ 37″ W	R
S29	Pearson	35° 07′ 27″ S, 57° 22′ 53″ W	R
S30	Sarandí Sur	35° 12′ 57″ S, 57° 17′ 07″ W	R
S31	Punta Indio	35° 16′ 45″ S, 57° 13′ 19″ W	R
S32	Punta Piedras	35° 23′ 28″ S, 57° 08′ 50″ W	R

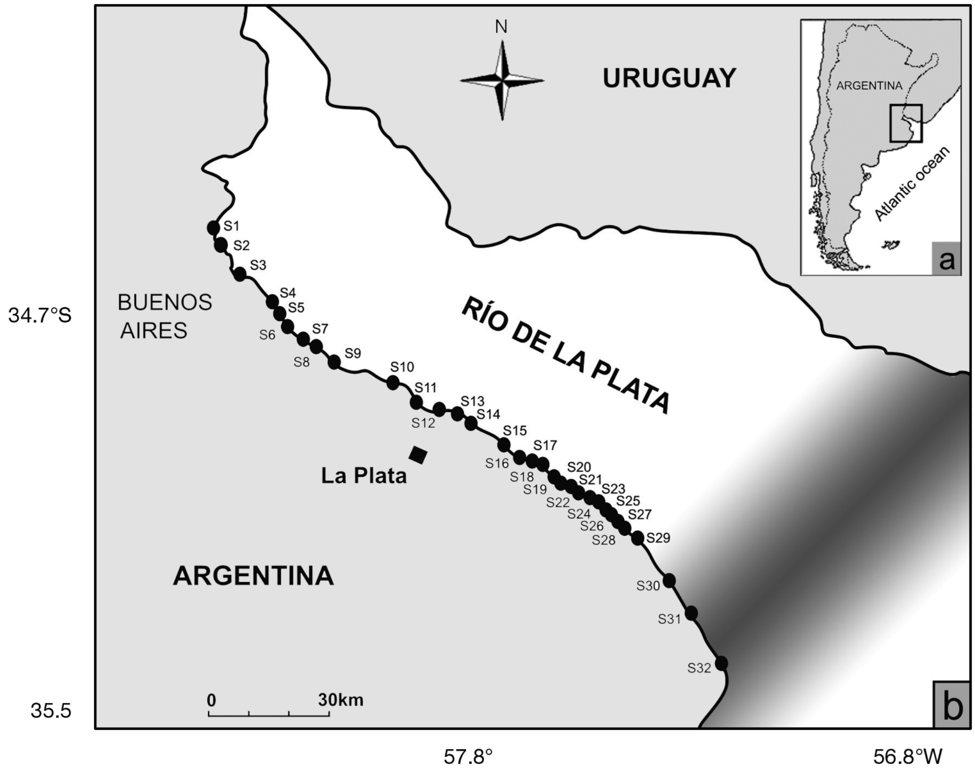

Fig. 1. Study area. (a) Río de la Plata estuary and (b) sampling sites. Shaded area corresponds to the maximum turbidity front

regime with a depth range between 1 and 5 m. The outer region is mainly mixohaline, and the depth ranges between 5 and 25 m. The isohaline region of 0.5 practical salinity units (psu) constitutes the boundary between the freshwater and mixohaline zones (Mianzan et al. 2001). This study was carried out on the Argentinean coastline between coordinates 34° 27′ S, 58° 30′ W and 35° 23′ S, 57° 08′ W (Fig. 1). A total of 32 sampling sites were selected along 168 km of shoreline in locations influenced by different land uses, as summarized in Table 1. The northernmost sites (S1 to S8) were exposed directly to the impact of the city of Buenos Aires and neighboring towns. Site S9 was located close to the sewage effluent of Buenos Aires. Site S10 was situated in the natural reserve Selva Marginal de Punta Lara. Sites S11 to S14 were located in the surrounding area of the city of La Plata. The remaining sampling sites were exposed to small-scale recreational and fishing activities, and sites S29 to S32 were the closest to the maximum turbidity front of the estuary (Fig. 1). The sediment composition in the study area consisted mainly of both fine and very fine sand (Gómez et al. 2009). Along the coastline, the perennial and littoral helophyte with rhizomes *Scirpus californicus* (Mey) Steud is frequent.

Sampling and laboratory analysis. Epipsammic samples of the intertidal zone were taken at low tide during spring 2005, autumn and winter 2006, spring and summer 2007, and autumn 2008. At each site, 5 replicates of the surface layer (0.5 cm) were collected with a core (area: 3.14 cm^2) for diatom taxonomic identifications and counts and transferred to formalin (final concentration, 4% v/v) for preservation. Epiphytic samples were taken during summer, autumn, and spring 2000 and in spring 2002. Ten stems of the bulrush *Scirpus californicus* were cut randomly, and the bottom 15 cm were retained and transferred to a flask with distilled water. The biofilm was removed by brushing, thus combining the material collected at each sampling site, and likewise preserved in formalin (Gómez et al. 2003). Diatoms were cleaned with H_2O_2, washed thoroughly with distilled water, and mounted on microscope slides with Naphrax®. Three hundred valves from each sample were identified under an Olympus BX 51 microscope with either interference, phase-contrast, or Nomarski differential interference contrast (DIC) optics. The following keys were used for species identification: Krammer & Lange-Bertalot (1986, 1988, 1991a,b), Patrick & Reimer (1966, 1975), Krammer (1992, 2000), and Frenguelli (1941). The conductivity (Lutron 4303-CD), DO levels (Oxymeter 600-ESD), turbidity (Turbidity Meter 800-ESD), temperature, and pH (Hanna HI 8633) were measured *in situ*. Water samples were also collected to analyze N-NH_4^+, N-NO_2^-, N-NO_3^-, P-PO_4^{-3}, BOD_5, and COD (Mackereth et al. 1978, APHA 1998). Nutrient concentrations are expressed as mg l^{-1} (for civil servant organizations) and are also given as µmol l^{-1} (scientific notation) in the supplement at www.int-res.com/articles/suppl/m418p105_supp.pdf.

Data analysis. We excluded all planktonic species from the diatom counts and calculated relative abundance of the benthic diatoms exclusively. For statistical analysis and optimum and tolerance estimations, only those species present in at least 5% of the total sample dataset and with more than 1% of relative abundance in at least 1 sample were included.

For the optima and tolerance determination, environmental variables (except pH) were log-transformed to approximate a normal distribution.

Canonical correspondence analysis (CCA) was employed to explore the relationship between species composition and the environmental variables measured. When the gradient length (in standard deviation units) in a preliminary detrended correspondence analysis exceeds 2 units, unimodal species response curves could be expected and, subsequently, ordination techniques based on weighted averaging are recommended (Muylaert et al. 2000). Species abundance data were ln transformed. Environmental data were standardized, and only those variables with a variance inflation factor <10 were retained in the analysis, because a greater value would indicate multicollinearity among variables (ter Braak & Verdonschot 1995). Epiphytic samples were not considered for this analysis due to the lack of some environmental data. Samples with extreme environmental values were also excluded. The overall significance of the ordination and the significance of the first axis were tested with a Monte Carlo permutation test ($p < 0.01$) using restricted permutations.

Weighted average estimates of the species optima (u_k) were calculated, considering abundance of the species in each sample, according to Potapova & Charles (2003) as

$$u_k = \sum_{i=1}^{n} y_{ik} x_i \Big/ \sum_{i=1}^{n} y_{ik} \quad (1)$$

where y_{ik} is the relative abundance of species k in the sample i; x_i is the value of the environmental parameter in sample i; and n is the total number of samples in the dataset. Tolerance or weighted SD (t_k) was calculated according to Potapova & Charles (2003) as:

$$t_k = \sqrt{\frac{\sum_{i=1}^{n} y_{ik}(x_i - u_k)^2}{\sum_{i=1}^{n} y_{ik}}} \quad (2)$$

Pearson correlations were performed to explore the relationship between the relative abundance of diatom species and environmental variables measured. Correlations with a $p < 0.05$ are reported in the text.

RESULTS

Water quality and diatom assemblage

The physicochemical parameters employed for the estimation of optima and tolerances of the diatom species are shown in Table 2. In 52% of the samples analyzed, the conductivity was <500 µS cm^{-1} (<0.3 psu), in 25% it was between 500 and 1000 µS cm^{-1} (0.3 to 0.5 psu), and the remaining values were all >1000 µS cm^{-1} (>0.5 psu). For turbidity, 75% of the samples had values <300 nephelometrical turbidity units (NTU), 16% lay between 300 and 600 NTU, while 9% were >600 NTU. The pH exhibited values of <7 in 5% of the samples, between 7 and 8 in 41%, and higher in the remainder. The concentrations of DO, expressed as a percent of saturation, were <50% in 2% of the samples, between 50 and 100% in 51%, and above normal saturation in the rest.

For oxygen demand, 20% of the data gave values of <3 mg l^{-1} of BOD_5, 56% showed values between 3 and 10 mg l^{-1}, while the remaining values were higher. The COD values were <10 mg l^{-1} in 21% of the observations, between 10 and 20 mg l^{-1} in 48%, and higher in the rest. The concentrations of N-NO_3^- were <1 mg l^{-1} (<71.4 µmol l^{-1}) in 50% of the samples, between 1 and 2 mg l^{-1} (71.4 to 142.8 µmol l^{-1}) in 29%, and above this value in the rest; the concentrations of N-NO_2^- were <0.05 mg l^{-1} (<3.6 µmol l^{-1}) in 60%, between 0.05 and 0.1 mg l^{-1} (3.6 to 7.1 µmol l^{-1}) in 25%, and >0.1 mg l^{-1} (<7.1 µmol l^{-1}) in the remainder. The values of N-NH_4^+ were <0.1 mg l^{-1} (<7.1 µmol l^{-1}) in 40% of the samples, between 0.1 and 1 mg l^{-1} (7.1 to 71.4 µmol l^{-1}) in 51%, and above this value in the rest; and the concentrations of P-PO_4^{-3} were <0.1 mg l^{-1} (<3.2 µmol l^{-1}) in 7% of the samples, between 0.1 and 0.5 mg l^{-1} (3.2 to 16.1 µmol l^{-1}) in 80%, and above this value in the remainder.

The first 2 axes of the canonical correspondence analysis accounted for 39% of the sum of all canonical eigenvalues and were selected for graphical representation (Figs. 2 & 3). According to this statistical analysis, the nutrients and organic matter exhibited the highest values at sites influenced by anthropogenic activities (S6, S10, S11, S14, S9, and S8). These sampling sites correspond to a diversified use of the

Table 2. Physicochemical characteristics of each sampling site: mean ±SD. Nutrient concentrations are expressed as mg l^{-1}; see Table S1 in the supplement at www.int-res.com/articles/suppl/m418p105_supp.pdf for the same data expressed as µmol l^{-1}. BOD_5: biological oxygen demand; COD: chemical oxygen demand; DO: dissolved oxygen; No. obs.: number of observations

Site	$N\text{-}NO_3^-$ (mg l^{-1})	$N\text{-}NO_2^-$ (mg l^{-1})	$N\text{-}NH_4^+$ (mg l^{-1})	$P\text{-}PO_4^{-3}$ (mg l^{-1})	Conductivity (µS cm^{-1})	Salinity (psu)	pH	Turbidity (NTU)	BOD_5 (mg l^{-1})	COD (mg l^{-1})	% DO saturation
S1	0.77 ± 0.27	0.043 ± 0.012	0.249 ± 0.217	0.27 ± 0.32	593 ± 813	0.33 ± 0.48	7.9 ± 0.9	193 ± 211	2.2 ± 1.2	8.7 ± 5.8	87 ± 28
S2	1.11 ± 0.22	0.086 ± 0.026	0.263 ± 0.140	0.24 ± 0.10	314 ± 64	0.16 ± 0.04	7.6 ± 0.4	114 ± 146	3.8 ± 2.2	11.4 ± 5.3	81 ± 8
S3	1.04 ± 0.41	0.069 ± 0.023	0.243 ± 0.129	0.13 ± 0.02	751 ± 1091	0.42 ± 0.65	7.5 ± 0.4	171 ± 193	3.2 ± 2.0	9.2 ± 4.6	72 ± 13
S4	1.42	0.058	0.242 ± 0.000	0.12	346	0.18	8.0	420	2.0	4.0	85
S5	0.20	0.030	2.336 ± 0.000	0.27	516	0.32	7.1	213	14.0	27.0	59
S6	1.16 ± 1.70	0.016 ± 0.003	1.387 ± 1.339	2.09 ± 1.04	1235 ± 523	0.67 ± 0.27	7.6 ± 0.3	203 ± 186	13.0 ± 1.0	21.3 ± 4.2	23 ± 23
S7	0.03	0.023	2.035	1.24	884	0.53	7.3	248	14.0	23.0	55
S8	1.71	0.169	0.688	0.38	669	0.40	7.9	208	5.0	8.0	80
S9	1.08 ± 0.32	0.172 ± 0.039	0.812 ± 0.732	0.38 ± 0.09	490 ± 64	0.25 ± 0.06	8.4 ± 0.3	127 ± 180	6.3 ± 3.3	12.4 ± 4.3	117 ± 32
S10	0.93 ± 0.44	0.043 ± 0.019	0.091 ± 0.098	0.24 ± 0.06	367 ± 58	0.18 ± 0.04	8.6 ± 0.5	76 ± 74	6.6 ± 5.0	18.5 ± 9.3	115 ± 19
S11	0.99 ± 0.54	0.052 ± 0.030	0.226 ± 0.239	0.38 ± 0.19	351 ± 116	0.18 ± 0.09	8.6 ± 0.5	93 ± 110	8.0 ± 3.7	20.0 ± 10.4	134 ± 38
S12	1.10	0.113	0.304	0.21	429	0.21	8.0	229	2.4	7.7	84
S13	1.07	0.151	0.438	0.32	449	0.22	8.4	204	4.5	10.6	117
S14	0.47 ± 0.38	0.075 ± 0.118	0.497 ± 0.503	0.59 ± 0.41	572 ± 219	0.30 ± 0.15	7.8 ± 0.2	69 ± 58	14.7 ± 8.1	30.5 ± 25.7	96 ± 16
S15	1.19 ± 1.71	0.024 ± 0.031	0.069 ± 0.128	0.18 ± 0.08	431 ± 160	0.20 ± 0.08	8.2 ± 0.7	125 ± 119	6.6 ± 1.3	14.6 ± 5.9	107 ± 11
S16	2.23	0.050	0.240								
S17	0.05	0.008	0.131	0.13	564	0.29	8.4	300	3.2	16.1	127
S18	7.28	0.005	0.005	0.11							
S19	0.43 ± 0.26	0.012 ± 0.009	0.348 ± 0.513	0.13 ± 0.06	775 ± 481	0.43 ± 0.34	8.2 ± 0.2	194 ± 282	8.1 ± 3.8	19.4 ± 7.9	104 ± 13
S20	2.19 ± 1.52	0.013 ± 0.015	0.192 ± 0.089	0.20 ± 0.13	955	0.42	7.1				
S21	0.76 ± 0.62	0.005 ± 0.003	0.049 ± 0.031	0.18 ± 0.08	1333 ± 1311	0.74 ± 0.72	8.1 ± 0.7	860 ± 198	5.1 ± 5.8	12.2 ± 3.1	92 ± 7
S22	2.62 ± 1.82	0.036 ± 0.060	0.126 ± 0.046	0.15 ± 0.09	998	0.44	6.9				
S23	2.55 ± 1.69	0.069 ± 0.092	0.272 ± 0.127	0.28 ± 0.32	1510	0.68	6.7				
S24	3.19	0.002	0.048	0.18	1048	0.47	7.2				
S25	4.13 ± 0.15	0.095 ± 0.133	0.196 ± 0.105	0.20	1048	0.47	7.1				
S26	1.50 ± 1.39	0.036 ± 0.026	0.118 ± 0.054	0.19 ± 0.12	1380	0.62	6.6				
S27	1.30 ± 1.14	0.017 ± 0.019	0.890 ± 0.719	0.40 ± 0.29	1568	0.71	6.7				
S28	2.72 ± 0.61	0.010 ± 0.011	0.294 ± 0.140	0.19 ± 0.05	1429	0.64	6.7				
S29	2.62 ± 3.06	0.005 ± 0.002	0.029 ± 0.020	0.16 ± 0.06	1151 ± 824	0.59 ± 0.38	8.3 ± 0.4	683 ± 149	2.9 ± 2.7	16.4 ± 4.8	110 ± 1
S30	0.17	0.001	0.058	0.08	5393	2.81	8.0	1000	4.3	16.4	105
S31	0.30 ± 0.18	0.009 ± 0.006	0.058 ± 0.053	0.17 ± 0.07	4463 ± 5217	2.77 ± 3.54	8.2 ± 0.6	344 ± 307	5.8 ± 3.5	27.9 ± 14.9	94 ± 6
S32	0.37 ± 0.10	0.005 ± 0.001	0.003 ± 0.003	0.13 ± 0.08	14833 ± 7967	10.08 ± 6.74	7.9 ± 0.5	1000 ± 1	3.8 ± 2.6	11.1 ± 1.2	98 ± 5
No. obs.	120	120	120	115	98	98	98	89	89	89	89

land, mainly urban and waste and industrial effluents (Table 1). The species that were associated with these conditions were, in decreasing order of strength, *Nitzschia umbonata*, *Pinnularia microstauron*, *N. paleacea, Fragilaria capucina, Sellaphora pupula*, *Placoneis placentula*, *Mayamea atomus*, *Diadesmis contenta*, *Gomphonema parvulum*, *N. inconspicua*, *Achnanthidium minutissimum*, *Neidium iridis*, *Sellaphora nyassensis*, *Nitzschia lacunarum*, *Geissleria decussis*, *Planothidium delicatulum*, *Pseudostaurosira brevistriata*, *Ulnaria ulna*, and *Staurosira construens* (Fig. 3).

The conductivity and turbidity increased significantly in those sites nearer to the maximum turbidity front: S21, S30, S31, and S32 (Fig. 2). *Navicula germainii*, *N. angusta*, *Nitzschia filiformis*, *Tryblionella calida*, *T. apiculata*, *Hantzschia virgata*, *Nitzschia sigma*, *Staurosirella pinnata, Diadesmis confervacea,* and *Amphora acutiuscula* were linked with these conditions of high turbidity and conductivity (Fig. 3).

Optima and tolerances of diatom species

Of 224 benthic species identified, 81 had a frequency greater than 5% of the total sample dataset and more than 1% of relative abundance in at least 1 sample;

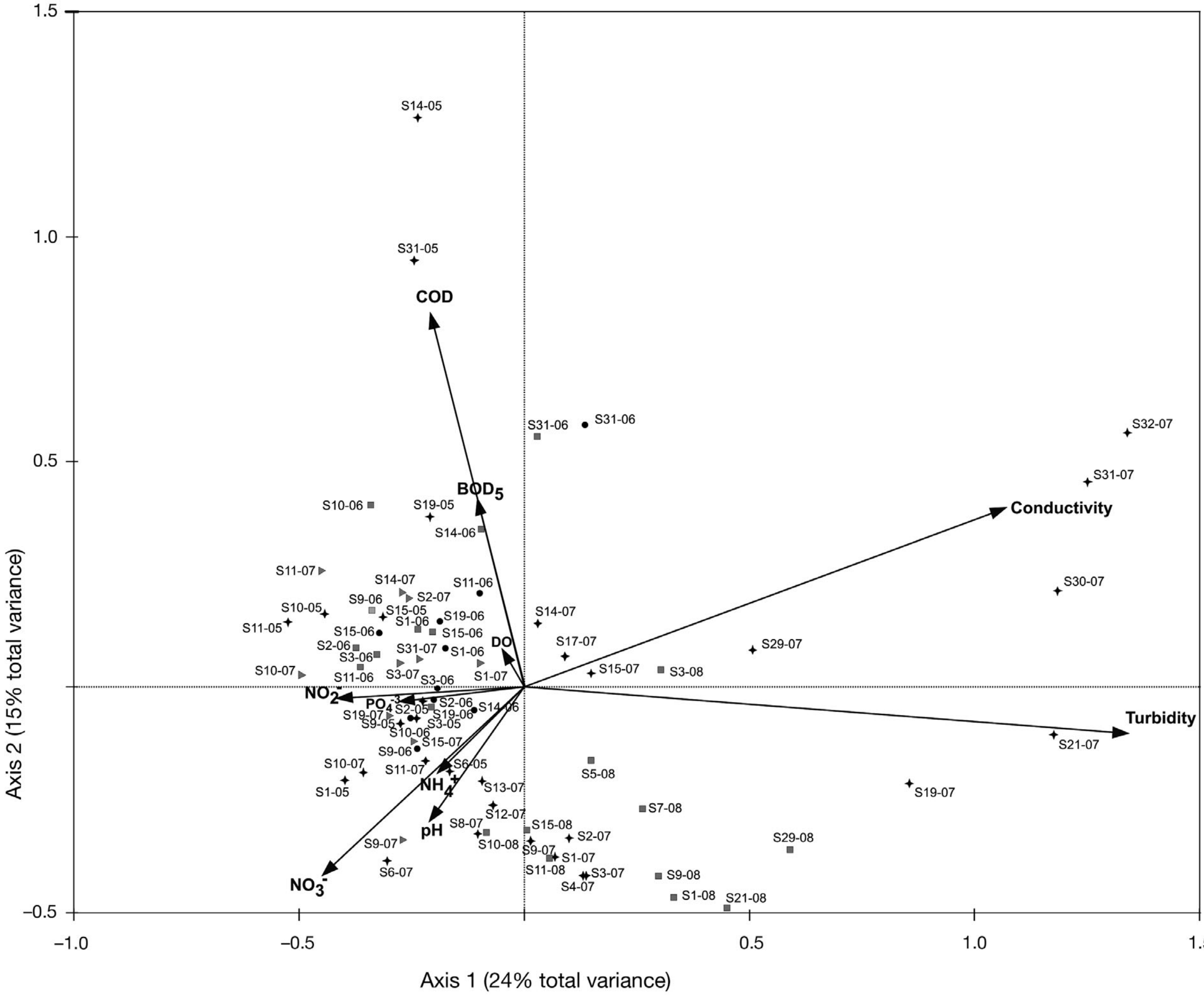

Fig. 2. Biplot of the first 2 axes of the canonical correspondence analysis showing environmental variables and sampling sites. Squares: autumn; circles: winter; triangles: summer; stars: spring

thus they were selected to estimate the optima and tolerances for specific water-quality characteristics (Table 3).

Turbidity and conductivity. Species such as *Navicula germainii*, *N. angusta*, *Amphora acutiuscula*, *Tryblionella calida*, and *T. apiculata* were associated with high turbidity (optimum at >388 NTU) and conductivity (optimum at >1643 µS cm^{-1}), as these species were better represented in the area close to the zone of maximum turbidity of the estuary and their relative abundance exhibited significant correlations with those 2 variables. Among these diatoms, *N. germainii* was recognized as a taxon with a tight range of tolerance to turbidity. By contrast, in the freshwater sector, species such as *Sellaphora nyassensis*, *Nitzschia lacunarum*, *Stauroneis brasiliensis*, *Craticula accomoda*, *Neidium iridis*, *Fragilaria goulardii*, and *Geissleria decussis* were linked with less turbid and mineralized environments (optima at <67 NTU, <403 µS cm^{-1}). Among these species, *N. lacunarum*, *C. accomoda*, *N. iridis*, *F. goulardii*, and *G. decussis* presented a tight range of tolerance to turbidity, while *N. iridis*, *C. accomoda*, and *N. lacunarum* did so to conductivity (Table 3).

Inorganic phosphate. The abundances of species such as *Nitzschia umbonata*, *Placoneis placentula*, *Sellaphora pupula*, and *Mayamea atomus* showed a close correlation with increases in the concentration of P-PO_4^{-3} (optimum at >0.38 mg l^{-1}). Most of the species selected for this study, however, had prevalence optima at concentrations <0.35 mg l^{-1}, and only the

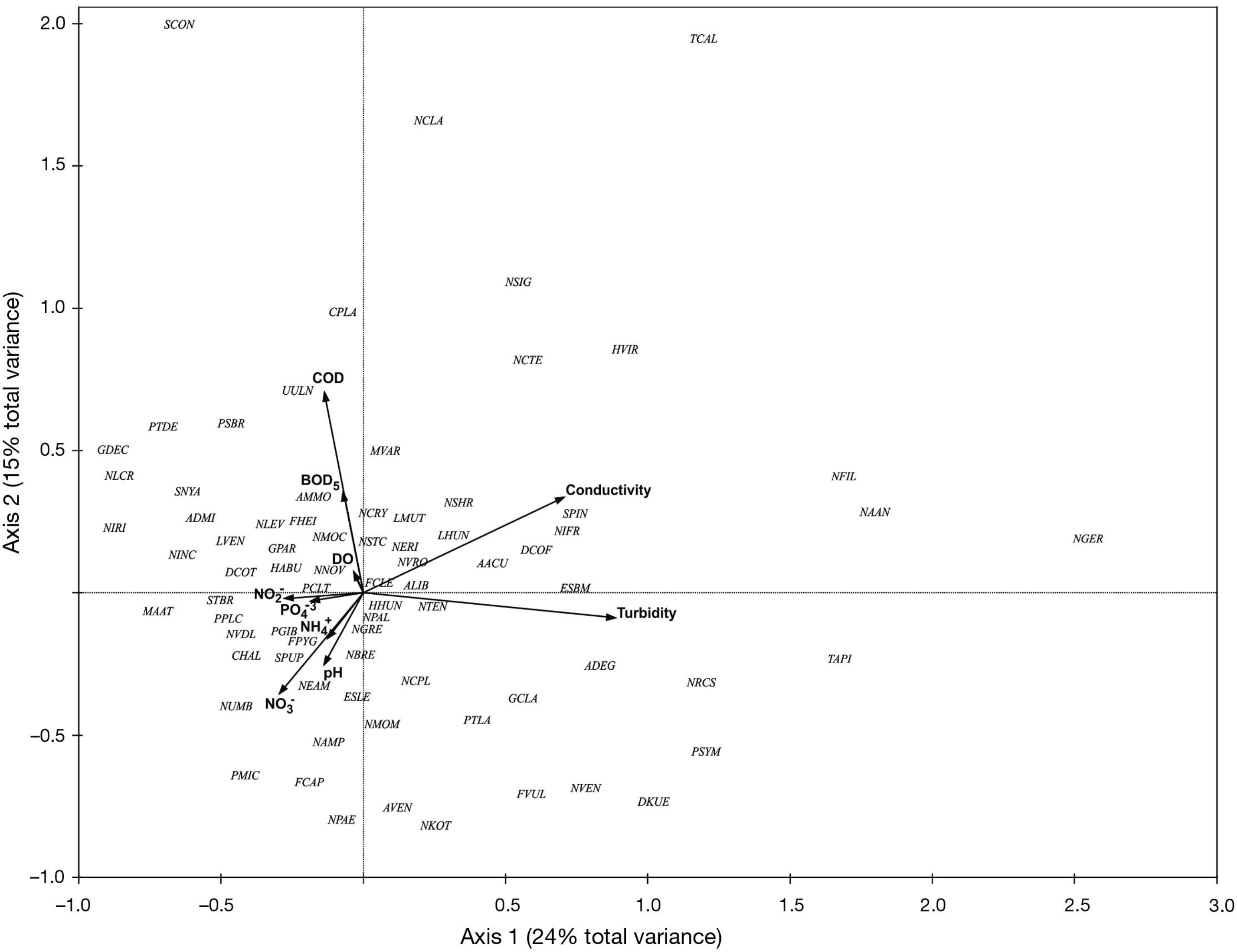

Fig. 3. Biplot of the first 2 axes of the canonical correspondence analysis showing environmental variables and diatom taxa. Acronyms correspond to those in Table 3

Table 3. Diatom species optima and tolerance limits (low, L, and high, H) for nutrients ($N\text{-}NO_3^-$, $N\text{-}NO_2^-$, $N\text{-}NH_4^+$, $P\text{-}PO_4^{-3}$), conductivity, pH, dissolved oxygen (as % DO saturation), turbidity, biological and chemical oxygen demand (BOD_5 and COD, respectively). Diatom taxa selected were found in at least 5% of the total sample dataset and with more than 1% of relative abundance in at least 1 sample. Acronyms of species and their frequency (Fr) in samples analyzed are shown. See Table S2 in the supplement at www.int-res.com/articles/suppl/m418p105_supp.pdf for taxonomical information for each species

Species	Acronym	Fr (%)	$N\text{-}NO_3^-$ (mg l^{-1})			$N\text{-}NO_2^-$ (mg l^{-1})			$N\text{-}NH_4^+$ (mg l^{-1})			$P\text{-}PO_4^{-3}$ (mg l^{-1})			Conductivity (µS cm^{-1})			pH%			DO saturation			Turbidity (NTU)			BOD_5 (mg l^{-1})			COD (mg l^{-1})		
			Opt.	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H
Achnanthidium exiguum	ADEG	12	**1.02**	0.41	2.53	**0.046**	0.019	0.115	**0.218**	0.089	0.535	**0.13**	0.08	0.22	**489**	198	1211	**8.0**	7.8	8.3	**87**	74	102	**358**	169	759	**2.4**	1.5	4.0	**5.4**	3.1	9.6
Achnanthidium minutissimum	ADMI	14	**2.01**	1.25	3.25	**0.015**	0.004	0.053	**0.160**	0.072	0.352	**0.23**	0.17	0.32	**587**	328	1048	**7.5**	7.1	7.9	**83**	57	121	**82**	31	217	**2.9**	1.1	8.2	**12.5**	5.2	30.3
Amphora acutiuscula	AACU	14	**0.38**	0.11	1.28	**0.012**	0.003	0.055	**0.038**	0.006	0.254	**0.16**	0.09	0.27	**2782**	531	14568	**8.1**	7.8	8.3	**94**	77	115	**400**	139	1148	**3.1**	2.0	4.9	**11.7**	6.3	21.5
Amphora libyca	ALIB	65	**0.28**	0.09	0.85	**0.009**	0.002	0.038	**0.038**	0.003	0.443	**0.15**	0.07	0.31	**961**	307	3007	**8.1**	7.7	8.6	**101**	79	130	**189**	55	651	**5.3**	2.6	10.9	**15.8**	10.4	24.0
Amphora montana	AMMO	18	**0.30**	0.17	0.52	**0.009**	0.002	0.030	**0.039**	0.005	0.301	**0.27**	0.10	0.71	**5051**	1106	23063	**8.1**	7.7	8.4	**92**	78	108	**224**	44	1129	**4.1**	1.5	11.3	**18.9**	11.8	30.2
Amphora veneta	AVEN	7	**2.42**	1.92	3.04	**0.010**	0.006	0.018	**0.114**	0.058	0.224	**0.25**	0.21	0.29	**266**	217	326	**8.1**	7.9	8.4	**89**	81	97	**264**	110	633	**2.9**	1.8	4.6	**4.8**	2.8	8.4
Cocconeis placentula	CPLA	5	**0.14**	0.06	0.33	**0.009**	0.003	0.030	**0.185**	0.062	0.557	**0.13**	0.09	0.19	**661**	261	1676	**7.9**	7.2	8.5	**111**	79	156	**57**	23	137	**3.3**	2.4	4.5	**11.7**	9.3	14.7
Craticula accomoda	CRAC	6	**2.03**	1.24	3.34	**0.009**	0.004	0.018	**0.232**	0.130	0.413	**0.25**	0.16	0.38	**361**	310	422	**9.0**	8.7	9.2	**139**	117	165	**43**	43	43	**8.4**	5.8	12.1	**16.7**	9.8	28.3
Craticula halophila	CHAL	37	**0.54**	0.13	2.27	**0.011**	0.003	0.035	**0.069**	0.009	0.542	**0.16**	0.09	0.28	**418**	181	962	**7.9**	7.2	8.6	**88**	66	118	**91**	33	248	**2.6**	1.1	6.4	**14.3**	8.9	22.9
Denticula kuetzingii	DKUE	8	**0.15**	0.04	0.61	**0.017**	0.007	0.044	**0.332**	0.047	2.344	**0.36**	0.13	1.01	**822**	470	1438	**7.7**	7.3	8.1	**73**	57	95	**398**	222	713	**8.0**	3.7	17.2	**15.9**	9.5	26.7
Diadesmis confervacea	DCOF	9	**2.75**	1.26	5.98	**0.006**	0.002	0.016	**0.112**	0.070	0.179	**0.16**	0.09	0.26	**1124**	728	1736	**7.0**	6.7	7.3	**101**	85	120	**223**	50	997	**4.1**	2.7	6.3	**11.4**	7.5	17.2
Diadesmis contenta	DCOT	5	**0.49**	0.29	0.83	**0.044**	0.018	0.108	**0.711**	0.144	3.499	**0.54**	0.26	1.10	**835**	410	1701	**8.0**	7.8	8.3	**102**	97	108	**51**	27	95	**12.5**	7.6	20.7	**16.3**	14.4	18.5
Encyonema silesiacum	ESLE	21	**0.90**	0.25	3.27	**0.038**	0.015	0.093	**0.142**	0.036	0.564	**0.34**	0.20	0.60	**491**	307	788	**8.1**	7.7	8.6	**105**	75	146	**61**	20	185	**6.8**	3.7	12.5	**12.9**	8.2	20.1
Eolimna subminuscula	ESBM	8	**0.50**	0.24	1.06	**0.066**	0.024	0.182	**0.461**	0.156	1.365	**0.27**	0.14	0.50	**520**	254	1066	**8.3**	7.8	8.8	**111**	81	153	**60**	20	176	**4.9**	2.4	9.7	**12.6**	10.2	15.5
Fallacia clepsidroides	FCLE	67	**0.48**	0.15	1.49	**0.018**	0.006	0.058	**0.048**	0.005	0.440	**0.21**	0.12	0.38	**582**	236	1434	**8.2**	7.6	8.7	**93**	75	116	**121**	41	360	**4.8**	2.1	11.0	**16.8**	9.5	29.5
Fallacia pygmaea	FPYG	49	**0.76**	0.21	2.68	**0.042**	0.012	0.149	**0.146**	0.023	0.910	**0.33**	0.15	0.73	**461**	276	770	**8.2**	7.4	9.1	**95**	50	181	**71**	28	180	**6.4**	2.7	15.4	**18.6**	11.8	29.2
Fragilaria capucina	FCAP	16	**0.62**	0.27	1.45	**0.032**	0.009	0.114	**0.056**	0.003	1.003	**0.31**	0.17	0.57	**439**	303	635	**8.3**	7.8	8.9	**111**	87	143	**61**	29	127	**6.9**	3.4	14.1	**15.7**	9.5	25.8
Fragilaria goulardii	FGOU	6	**0.44**	0.19	1.02	**0.020**	0.006	0.063	**0.010**	0.000	0.298	**0.25**	0.15	0.43	**403**	305	533	**8.3**	8.1	8.6	**122**	105	142	**38**	27	54	**6.1**	4.5	8.4	**17.7**	13.5	23.3
Fragilaria heidenii	FHEI	8	**0.43**	0.20	0.91	**0.027**	0.008	0.096	**0.090**	0.004	2.096	**0.41**	0.19	0.91	**615**	383	988	**8.1**	7.7	8.4	**104**	95	113	**49**	27	89	**9.9**	5.6	17.7	**16.7**	12.1	23.2
Frustulia vulgaris	FVUL	6	**0.50**	0.25	1.01	**0.039**	0.013	0.121	**0.474**	0.096	2.338	**0.33**	0.14	0.82	**769**	473	1250	**8.0**	7.8	8.3	**98**	89	107	**88**	29	261	**8.9**	3.9	20.2	**13.8**	9.1	20.9
Geissleria decussis	GDEC	8	**0.73**	0.50	1.08	**0.082**	0.036	0.188	**0.217**	0.039	1.215	**0.28**	0.13	0.59	**397**	249	635	**8.1**	7.4	8.7	**85**	38	193	**31**	17	55	**4.2**	1.7	10.4	**13.9**	6.6	29.2
Gomphonema clavatum	GCLA	22	**0.48**	0.12	2.01	**0.037**	0.013	0.107	**0.208**	0.053	0.824	**0.26**	0.13	0.52	**453**	273	754	**8.3**	7.9	8.8	**117**	91	149	**49**	18	136	**6.8**	3.1	14.9	**14.1**	8.3	23.9
Gomphonema parvulum	GPAR	39	**1.59**	0.40	6.36	**0.040**	0.012	0.137	**0.110**	0.022	0.558	**0.22**	0.10	0.45	**419**	275	639	**8.3**	7.9	8.8	**112**	83	153	**48**	23	99	**8.3**	4.3	15.8	**16.0**	8.8	29.1
Hantzschia abundans	HABU	21	**0.26**	0.07	0.89	**0.019**	0.004	0.096	**0.053**	0.004	0.731	**0.25**	0.12	0.51	**567**	356	904	**8.2**	7.8	8.7	**107**	87	131	**109**	36	333	**6.1**	3.4	11.2	**14.3**	9.1	22.5
Hantzschia virgata	HVIR	5	**0.44**	0.15	1.28	**0.024**	0.005	0.122	**0.066**	0.041	0.108	**0.14**	0.09	0.22	**910**	220	3754	**7.6**	7.2	8.0	**91**	80	103	**113**	20	638	**3.5**	1.9	6.4	**9.7**	3.9	24.1
Hippodonta capitata	HCAP	8	**2.76**	1.78	4.30	**0.009**	0.002	0.036	**0.084**	0.040	0.179	**0.18**	0.11	0.30	**866**	516	1455	**7.4**	6.6	8.2	**139**	115	169	**43**	43	44	**13.1**	10.8	15.9	**29.6**	27.7	31.6
Hippodonta hungarica	HHUN	77	**0.40**	0.11	1.50	**0.022**	0.005	0.092	**0.104**	0.014	0.752	**0.20**	0.09	0.44	**688**	282	1679	**8.1**	7.6	8.6	**93**	66	130	**178**	64	492	**4.3**	2.0	9.1	**12.8**	7.3	22.4
Lemnicola hungarica	LHUN	9	**1.19**	0.39	3.64	**0.005**	0.001	0.035	**0.102**	0.025	0.426	**0.19**	0.08	0.44	**822**	437	1545	**7.4**	6.7	8.2	**108**	96	123	**68**	16	285	**10.8**	6.3	18.8	**18.1**	12.0	27.4
Luticola goeppertiana	LGOE	10	**1.18**	0.85	1.63	**0.233**	0.086	0.629	**0.320**	0.115	0.888	**0.53**	0.32	0.89	**494**	377	647	**7.6**	7.4	7.8	**77**	67	87	**116**	79	170	**19.8**	8.4	46.8	**59.1**	25.1	139.2
Luticola mutica	LMUT	18	**0.40**	0.17	0.96	**0.018**	0.003	0.107	**0.099**	0.010	0.975	**0.26**	0.09	0.73	**888**	273	2888	**7.9**	7.5	8.3	**90**	68	120	**116**	28	485	**5.1**	2.2	12.1	**15.1**	8.8	26.0
Luticola ventricosa	LVEN	16	**0.67**	0.46	0.97	**0.070**	0.034	0.143	**0.633**	0.137	2.929	**0.61**	0.40	0.91	**622**	455	850	**8.0**	7.7	8.3	**99**	86	115	**50**	32	79	**13.5**	7.7	23.7	**19.0**	10.2	35.3
Mayamea atomus	MAAT	9	**0.44**	0.14	1.41	**0.058**	0.025	0.138	**0.478**	0.204	1.118	**0.38**	0.14	1.04	**501**	321	782	**8.0**	7.4	8.7	**72**	33	161	**43**	20	92	**5.6**	2.6	11.7	**13.5**	7.9	23.0
Melosira varians	MVAR	5	**0.21**	0.05	0.98	**0.038**	0.012	0.122	**0.269**	0.124	0.583	**0.34**	0.19	0.61	**429**	357	515	**8.3**	7.8	8.8	**115**	89	148	**54**	23	125	**8.2**	6.6	10.2	**13.0**	10.0	16.9
Navicula angusta	NAAN	8	**0.53**	0.11	2.48	**0.011**	0.002	0.063	**0.040**	0.003	0.502	**0.14**	0.07	0.29	**2638**	816	8530	**7.9**	7.6	8.2	**98**	90	106	**470**	151	1460	**5.9**	3.6	9.7	**12.5**	9.4	16.7
Navicula cryptocephala	NCRY	14	**1.40**	0.69	2.84	**0.030**	0.006	0.144	**0.071**	0.034	0.146	**0.25**	0.17	0.37	**536**	352	815	**7.7**	7.0	8.4	**89**	76	104	**236**	97	576	**5.2**	2.6	10.5	**12.5**	6.2	25.5
Navicula cryptotenella	NCTE	5	**0.53**	0.38	0.74	**0.020**	0.006	0.063	**0.064**	0.040	0.101	**0.14**	0.09	0.19	**776**	215	2804	**8.1**	7.5	8.7	**111**	92	134	**129**	25	676	**4.7**	2.3	9.6	**11.8**	4.6	30.2
Navicula erifuga	NERI	62	**0.57**	0.21	1.55	**0.021**	0.006	0.079	**0.093**	0.016	0.551	**0.16**	0.09	0.28	**561**	182	1727	**8.1**	7.4	8.8	**100**	75	134	**78**	20	302	**3.7**	1.6	8.6	**9.7**	4.3	21.9
Navicula germainii	NGER	6	**0.27**	0.13	0.59	**0.003**	0.002	0.007	**0.009**	0.001	0.072	**0.09**	0.07	0.12	**4965**	2335	10555	**7.8**	7.5	8.0	**97**	92	103	**939**	787	1121	**5.4**	3.6	8.1	**13.3**	10.5	16.9
Navicula gregaria	NGRE	32	**0.68**	0.25	1.89	**0.049**	0.016	0.145	**0.222**	0.054	0.915	**0.22**	0.11	0.45	**412**	233	726	**7.8**	7.2	8.4	**89**	67	119	**67**	25	176	**4.0**	2.0	7.9	**10.5**	6.5	17.1
Navicula kotschyi	NKOT	5	**0.82**	0.31	2.16	**0.040**	0.017	0.095	**0.199**	0.116	0.341	**0.14**	0.10	0.22	**411**	270	625	**8.0**	7.7	8.4	**89**	76	105	**304**	116	796	**2.6**	1.3	5.3	**5.7**	3.1	10.5
Navicula monoculata	NMOC	11	**0.76**	0.38	1.54	**0.043**	0.018	0.102	**0.368**	0.087	1.558	**0.46**	0.20	1.06	**345**	191	621	**7.7**	7.2	8.2	**90**	73	111	**76**	41	140	**3.7**	2.1	6.4	**14.0**	10.3	18.9
Navicula monoculata var. *omissa*	NMOM	17	**0.57**	0.19	1.72	**0.049**	0.013	0.192	**0.101**	0.035	0.287	**0.21**	0.13	0.35	**335**	201	559	**8.0**	7.4	8.7	**90**	67	120	**106**	27	409	**3.2**	1.4	7.0	**7.8**	4.1	14.9
Navicula novaesiberica	NNOV	68	**0.55**	0.19	1.56	**0.022**	0.006	0.084	**0.061**	0.008	0.495	**0.22**	0.13	0.39	**425**	219	826	**8.1**	7.6	8.7	**102**	82	126	**87**	29	259	**5.3**	2.8	10.1	**14.5**	8.0	26.3
Navicula recens	NRCS	20	**0.54**	0.21	1.35	**0.022**	0.005	0.101	**0.032**	0.004	0.279	**0.19**	0.11	0.33	**694**	210	2289	**8.4**	7.9	8.9	**113**	88	143	**123**	34	445	**6.2**	3.3	11.6	**14.4**	8.6	24.2

Table 3 (continued)

Species	Acronym	Fr (%)	N-NO_3^- (mg l^{-1})			N-NO_2^- (mg l^{-1})			N-NH_4^+ (mg l^{-1})			P-PO_4^{-3} (mg l^{-1})			Conductivity (µS cm^{-1})			pH%			DO saturation			Turbidity (NTU)			BOD_5 (mg l^{-1})			COD (mg l^{-1})		
			Opt.	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H	**Opt.**	L	H
Navicula sanctaecrucis	NSTC	13	**0.67**	0.23	1.94	**0.031**	0.011	0.090	**0.137**	0.023	0.833	**0.25**	0.15	0.42	**433**	202	926	**8.1**	7.7	8.5	**93**	72	120	**140**	53	373	**4.3**	2.2	8.4	**11.7**	5.6	24.2
Navicula schroeteri	NSHR	15	**0.38**	0.15	0.97	**0.049**	0.015	0.164	**0.369**	0.070	1.949	**0.34**	0.15	0.74	**694**	301	1599	**8.2**	7.8	8.7	**112**	86	146	**65**	20	208	**7.3**	3.7	14.5	**13.4**	9.2	19.4
Navicula tenelloides	NTEN	42	**0.48**	0.19	1.22	**0.022**	0.004	0.109	**0.139**	0.015	1.259	**0.19**	0.09	0.40	**825**	252	2705	**8.2**	7.8	8.7	**107**	81	142	**119**	28	497	**5.5**	2.9	10.6	**13.3**	7.8	22.6
Navicula veneta	NVEN	13	**0.61**	0.18	2.03	**0.033**	0.007	0.149	**0.124**	0.023	0.678	**0.28**	0.13	0.57	**668**	320	1393	**8.3**	8.0	8.7	**89**	53	147	**204**	66	632	**6.2**	3.2	12.1	**11.2**	7.5	16.6
Navicula viridula var. *rostellata*	NVRO	23	**0.64**	0.31	1.32	**0.026**	0.007	0.090	**0.061**	0.011	0.336	**0.20**	0.12	0.31	**1212**	204	7201	**8.1**	7.7	8.6	**90**	74	110	**255**	83	787	**2.8**	1.2	6.2	**10.8**	5.3	22.2
Naviculadicta laterostrata	NVDL	10	**0.83**	0.48	1.43	**0.055**	0.036	0.082	**0.380**	0.205	0.708	**0.26**	0.13	0.56	**304**	239	388	**7.5**	7.1	7.9	**80**	67	97	**72**	41	126	**3.9**	2.5	6.2	**9.2**	6.6	12.9
Neidium ampliatum	NEAM	21	**0.45**	0.11	1.88	**0.035**	0.008	0.157	**0.249**	0.053	1.177	**0.32**	0.14	0.74	**589**	333	1042	**8.1**	7.7	8.6	**85**	42	172	**122**	49	304	**5.0**	2.3	11.1	**13.9**	8.8	21.9
Neidium iridis	NIRI	8	**0.76**	0.55	1.05	**0.096**	0.037	0.247	**0.280**	0.030	2.618	**0.28**	0.20	0.41	**391**	331	461	**8.6**	8.2	8.9	**145**	125	168	**30**	18	49	**5.8**	3.8	8.9	**15.1**	10.2	22.2
Nitzschia amphibia	NAMP	24	**1.05**	0.51	2.17	**0.024**	0.007	0.081	**0.151**	0.051	0.448	**0.26**	0.13	0.49	**348**	216	561	**8.1**	7.8	8.5	**86**	48	153	**113**	38	334	**5.3**	2.1	13.2	**12.7**	5.2	30.8
Nitzschia brevissima	NBRE	25	**1.00**	0.24	4.14	**0.025**	0.005	0.123	**0.274**	0.150	0.502	**0.13**	0.04	0.36	**1038**	596	1809	**7.2**	6.5	8.0	**102**	90	116	**62**	28	136	**9.4**	4.6	19.4	**14.3**	10.0	20.5
Nitzschia capitellata	NCPL	12	**0.55**	0.32	0.93	**0.007**	0.004	0.011	**0.003**	0.001	0.010	**0.19**	0.15	0.25	**350**	236	518	**8.4**	8.2	8.5	**111**	105	119	**71**	44	116	**5.3**	4.0	7.0	**11.5**	8.3	15.9
Nitzschia clausii	NCLA	18	**1.17**	0.47	2.90	**0.047**	0.019	0.117	**0.382**	0.090	1.617	**0.54**	0.33	0.89	**884**	580	1347	**7.7**	7.1	8.3	**102**	96	109	**47**	31	70	**14.5**	11.2	18.7	**16.9**	12.5	22.8
Nitzschia filiformis	NFIL	11	**0.32**	0.07	1.36	**0.009**	0.003	0.030	**0.019**	0.002	0.221	**0.16**	0.07	0.34	**2141**	435	10541	**7.9**	7.5	8.3	**101**	82	124	**298**	69	1290	**5.7**	3.5	9.1	**12.0**	9.2	15.6
Nitzschia frustulum	NIFR	16	**0.34**	0.10	1.15	**0.055**	0.018	0.171	**0.359**	0.126	1.025	**0.33**	0.15	0.74	**576**	310	1070	**8.5**	8.2	8.8	**120**	100	143	**50**	22	112	**8.1**	5.6	11.9	**12.3**	9.6	15.9
Nitzschia inconspicua	NINC	10	**0.43**	0.18	1.07	**0.019**	0.006	0.062	**0.052**	0.007	0.378	**0.20**	0.10	0.39	**890**	172	4598	**8.1**	7.4	8.9	**89**	49	161	**97**	25	370	**4.3**	2.2	8.7	**11.2**	6.6	19.0
Nitzschia lacunarum	NLCR	8	**0.88**	0.52	1.50	**0.008**	0.004	0.015	**0.027**	0.004	0.205	**0.24**	0.20	0.30	**279**	217	359	**8.3**	8.0	8.6	**107**	96	119	**49**	41	59	**8.6**	5.2	14.1	**26.5**	19.9	35.3
Nitzschia levidensis	NLEV	21	**0.92**	0.31	2.77	**0.015**	0.004	0.065	**0.072**	0.009	0.573	**0.18**	0.09	0.36	**617**	291	1308	**7.8**	7.2	8.5	**101**	81	126	**73**	33	159	**7.1**	3.2	16.0	**17.1**	9.3	31.5
Nitzschia palea	NPAL	73	**0.82**	0.33	2.08	**0.025**	0.004	0.144	**0.140**	0.023	0.842	**0.25**	0.13	0.48	**739**	218	2505	**7.9**	7.3	8.6	**85**	46	154	**97**	25	382	**3.9**	1.8	8.3	**12.1**	6.9	21.0
Nitzschia paleacea	NPAE	15	**0.85**	0.38	1.93	**0.071**	0.019	0.263	**0.088**	0.017	0.444	**0.28**	0.19	0.42	**386**	294	507	**8.4**	7.9	8.9	**102**	80	131	**124**	35	441	**5.5**	3.4	9.0	**9.8**	5.4	17.6
Nitzschia sigma	NSIG	19	**1.95**	0.87	4.35	**0.014**	0.003	0.062	**0.270**	0.104	0.699	**0.16**	0.09	0.29	**1116**	434	2866	**7.9**	7.6	8.2	**98**	74	129	**103**	29	373	**10.4**	6.5	16.7	**21.6**	11.7	40.1
Nitzschia umbonata	NUMB	14	**0.27**	0.06	1.25	**0.027**	0.011	0.067	**0.740**	0.274	1.999	**1.01**	0.40	2.54	**759**	505	1142	**7.7**	7.2	8.2	**30**	11	86	**70**	19	258	**10.1**	6.3	16.1	**17.6**	11.9	26.2
Pinnularia gibba	PGIB	9	**0.85**	0.51	1.40	**0.046**	0.023	0.092	**0.327**	0.122	0.877	**0.14**	0.09	0.21	**327**	266	402	**7.4**	7.0	7.8	**73**	63	84	**69**	44	106	**4.1**	2.8	5.9	**8.4**	6.6	10.6
Pinnularia microstauron	PMIC	8	**1.04**	0.57	1.90	**0.049**	0.021	0.115	**0.071**	0.019	0.263	**0.28**	0.17	0.45	**322**	213	484	**8.1**	7.4	8.7	**83**	46	149	**48**	18	133	**3.1**	1.4	6.6	**7.9**	4.2	14.9
Placoneis clementis	PCLT	38	**0.45**	0.16	1.29	**0.019**	0.004	0.082	**0.077**	0.009	0.658	**0.21**	0.11	0.41	**460**	237	893	**8.0**	7.5	8.5	**93**	77	113	**117**	48	288	**5.1**	2.6	10.0	**13.2**	8.4	20.8
Placoneis placentula	PPLC	29	**0.27**	0.05	1.49	**0.022**	0.009	0.055	**0.278**	0.020	3.815	**0.62**	0.24	1.58	**653**	359	1186	**7.8**	7.3	8.4	**53**	20	140	**103**	39	273	**9.1**	4.5	18.3	**19.5**	13.0	29.2
Placoneis symmetrica	PSYM	8	**0.39**	0.10	1.57	**0.021**	0.004	0.111	**0.029**	0.003	0.335	**0.23**	0.11	0.46	**730**	282	1894	**8.2**	7.8	8.5	**95**	78	115	**203**	61	674	**6.1**	4.4	8.6	**13.2**	8.8	20.0
Planothidium delicatulum	PTDE	8	**1.31**	0.53	3.27	**0.073**	0.034	0.154	**0.273**	0.132	0.565	**0.27**	0.15	0.49	**733**	409	1313	**7.6**	6.6	8.5	**98**	72	134	**49**	36	66	**6.3**	2.1	18.4	**14.6**	10.7	19.9
Planothidium lanceolatum	PTLA	9	**1.14**	0.41	3.14	**0.012**	0.003	0.048	**0.122**	0.043	0.349	**0.19**	0.13	0.28	**1228**	376	4014	**7.4**	6.7	8.1	**89**	75	106	**328**	175	615	**2.6**	1.7	4.1	**9.7**	5.2	18.1
Pseudostaurosira brevistriata	PSBR	8	**0.39**	0.17	0.92	**0.017**	0.005	0.063	**0.061**	0.010	0.373	**0.26**	0.15	0.46	**670**	409	1099	**8.0**	7.6	8.4	**99**	89	110	**106**	54	205	**7.5**	4.9	11.3	**29.1**	14.4	58.9
Sellaphora nyassensis	SNYA	26	**0.57**	0.31	1.05	**0.027**	0.011	0.065	**0.037**	0.006	0.243	**0.16**	0.11	0.24	**262**	189	363	**7.6**	6.9	8.4	**88**	66	117	**67**	44	102	**2.9**	1.3	6.4	**10.8**	5.5	20.9
Sellaphora pupula	SPUP	49	**0.72**	0.22	2.35	**0.036**	0.011	0.117	**0.322**	0.044	2.330	**0.49**	0.19	1.21	**633**	334	1200	**7.9**	7.4	8.4	**47**	14	152	**127**	52	315	**8.0**	4.2	15.3	**16.3**	9.9	26.8
Stauroneis brasiliensis	STBR	28	**0.77**	0.54	1.11	**0.071**	0.032	0.158	**0.066**	0.023	0.186	**0.13**	0.09	0.21	**258**	144	461	**7.5**	6.9	8.0	**71**	57	89	**39**	15	99	**1.6**	0.7	3.5	**5.8**	3.1	10.8
Staurosira construens	SCON	6	**0.29**	0.12	0.74	**0.012**	0.003	0.061	**0.033**	0.002	0.448	**0.15**	0.07	0.31	**1369**	277	6778	**8.3**	7.9	8.7	**103**	91	117	**123**	36	415	**6.7**	3.0	14.8	**20.6**	12.6	33.5
Staurosirella pinnata	SPIN	16	**0.37**	0.13	1.07	**0.016**	0.004	0.068	**0.040**	0.003	0.524	**0.19**	0.08	0.42	**1252**	294	5338	**7.8**	7.4	8.1	**88**	70	112	**194**	53	711	**4.3**	1.9	9.6	**13.8**	10.0	19.0
Tryblionella apiculata	TAPI	5	**0.28**	0.06	1.31	**0.015**	0.002	0.092	**0.065**	0.004	1.099	**0.28**	0.07	1.03	**1643**	419	6442	**7.8**	7.5	8.1	**79**	62	102	**572**	341	960	**6.0**	3.7	9.9	**11.8**	6.8	20.5
Tryblionella calida	TCAL	7	**0.51**	0.19	1.39	**0.010**	0.001	0.062	**0.054**	0.012	0.246	**0.17**	0.09	0.31	**3484**	916	13260	**8.0**	7.8	8.2	**99**	88	111	**388**	142	1057	**4.4**	2.4	7.9	**24.8**	13.4	46.0
Ulnaria ulna	UULN	14	**1.67**	1.22	2.30	**0.025**	0.010	0.062	**0.108**	0.051	0.228	**0.28**	0.21	0.38	**572**	338	967	**8.1**	7.4	8.9	**101**	68	150	**65**	32	133	**8.9**	5.4	14.5	**18.4**	10.8	31.3

abundance of *A. libyca* presented a significant negative correlation with increases in this anion (Table 3).

Inorganic nitrogen. Species such as *Diadesmis confervacea*, *Hippodonta capitata*, *Gomphonema parvulum*, *Amphora veneta*, *Nitzschia sigma*, *Achnanthidium minutissimum*, and *Craticula accomoda* tolerated concentrations of N-NO_3^- higher than 1.59 mg l^{-1}, though none of them presented statistically significant correlations. The rest of the species studied had prevalence optima at lower concentrations, and *Melosira varians* and *Amphora libyca* were the only ones whose relative abundance was negatively correlated with this ion (Table 3). With respect to nitrite, the prevalence of species such as *Luticola goeppertiana*, *Neidium iridis*, *Nitzschia paleacea*, and *Geissleria decussis* was significantly correlated with the highest values of N-NO_2^- (optimum at >0.07 mg l^{-1}), while half of the species analyzed exhibited optima lower than 0.02 mg l^{-1}. Among them, *A. libyca* and *Fallacia clepsidroides*, 2 species that are widely represented within the area of study, exhibited negative correlations with concentrations of this ion (Table 3). Finally, high concentrations of N-NH_4^+ were associated with higher relative abundances of *Nitzschia umbonata*, *Placoneis placentula*, *Neidium iridis*, *Diadesmis contenta*, *Denticula kuetzingii*, *Eolimna subminuscula*, *Sellaphora pupula*, *Navicula schoeteri*, and *Mayamea atomus* (optimum at >0.28 mg l^{-1}), with *M. atomus* exhibiting the narrowest tolerance range among them. By contrast, *Nitzschia capitellata*, *Navicula germainii*, *Navicula cryptotenella*, *Hantzschia virgata*, *Nitzschia lacunarum*, and *Navicula cryptocephala* proved more sensitive to increases in the concentrations of this ion (optimum at <0.07 mg l^{-1}; Table 3).

DO and its demands. The relative abundance of *Luticola goeppertiana*, *Lemnicola hungarica*, *Nitzschia sigma*, *Fragilaria heidenii*, *Placoneis placentula*, *Ulnaria ulna*, and *Gomphonema parvulum* showed significant correlations with high concentrations of BOD_5 (optimum at >8.3 mg l^{-1}), whereas the presence of *Stauroneis brasiliensis*, *Planothidium lanceloatum*, *Amphora acutiuscula*, *Craticula halophila*, *Navicula viridula* var. *rostellata*, and *Hippodonta hungarica* correlated with much lower concentrations (optimum at <4.3 mg l^{-1}; Table 3). With respect to the COD, the prevalence of *L. goeppertiana*, *Pseudostaurosira brevistriata*, and *Nitzschia lacunarum* was significantly related to the highest values (optimum at >26.5 mg l^{-1}), and only *N. lacunarum* showed a stringent range of tolerance. At the lower CODs, the presence of *Amphora veneta*, *Achnanthidium exiguum*, *Navicula kotschyi*, *Stauroneis brasiliensis*, *Pinnularia microstauron*, and *Navicula monoculata* var. *omissa* (optimum at <7.8 mg l^{-1}) was significantly correlated (Table 3). The species whose abundances were related to values of oxygen supersaturation were *Neidium iridis*, *Hippodonta capitata*, *Craticula accomoda*, *Navicula recens*, and *Navicula tenelloides*, while *Nitzschia umbonata*, *P. placentula*, and *Sellaphora pupula* were related to low oxygen levels (optimum at <54% saturation; Table 3).

Water pH. *Craticula accomoda* and *Navicula recens* were the species associated significantly with more alkaline water (optimum at >8.4), whereas the presence of *Naviculadicta laterostrata*, *Sellaphora nyassensis*, and *Staurosirella pinnata* showed significant correlations with less alkaline water (with optimum at <7.8; Table 3).

DISCUSSION AND CONCLUSION

The physicochemical data analyzed indicated 2 gradients — increases in conductivity and turbidity along with decreases in the concentration of nutrients and organic matter — that generated different types of habitats for the selected species investigated. On the basis of these gradients, we were able to recognize the optima for the most frequent and abundant species in the study area.

According to the categories proposed by Van Dam et al. (1994) in relation to salinity, 4% of the species analyzed in this study were freshwater, 68% fresh-brackish water, 13% brackish-freshwater, and 15% brackish-water affiliates, with the narrowest tolerance ranges being exhibited by the species found in the area with freshwater characteristics. Our results agree with Carpelan (1978), who indicated that all diatoms living in transitional zones should be considered either marine or freshwater taxa in essence, but with different degrees of euryhalinity. Marine organisms per se were not represented in this study since the species we identified were those habitually associated with the phytobenthos of pampean rivers and streams with different degrees of mineralization (Gómez & Licursi 2001, Licursi 2005).

The species best adapted to a higher degree of variability in physicochemical conditions—mainly conductivity and turbidity—were *Navicula germainii*, *N. angusta*, *Amphora acutiuscula*, *Tryblionella calida*, and *T. apiculata*. Of these species, *A. acutiuscula* has been previously reported in estuaries of the Argentine coast (Hassan et al. 2009) with salinities ranging from 25 to 31 psu, whereas in the present study this species was associated with conditions of lower salinity (with a minimum of 0.37 psu). In the transitional zone between the upper and lower estuary, the processes associated with the interaction of the river freshwater and the saline-shelf water along with the tidal stirring generate a turbidity front in the Río de la Plata whose structure and distribution is temporarily variable (Framiñan et al. 1999).

According to Admiraal (1984), possibly one of the most conspicuous ecophysiological characteristics of estuarine benthic diatoms is their extreme versatility towards the wide ranges of physicochemical conditions in their harsh natural habitat. By contrast, in the freshwater sector with more river-like characteristics, *Nitzschia lacunarum*, *Craticula accomoda*, and *Neidium iridis* have been recognized as the species with a tighter range of tolerance for turbidity and conductivity.

Although the whole study area experiences meso-eutrophic conditions (López & Nagy 2005, Gómez et al. 2009) the species identified were capable of responding to the variations recorded in the ranges of the nutrients. Accordingly, *Amphora libyca* was associated with less eutrophic conditions, while the presence of *Nitzschia umbonata*, *Placoneis placentula*, and *Sellaphora pupula* was correlated with high concentrations of nutrients. According to Van Dam et al. (1994), *A. libyca* is a eutrophic species, although our results as well as those reported by Gómez & Licursi (2001) indicate that this species presents high relative abundances in both mesotrophic to eutrophic environments of pampean rivers and streams and in the Río de la Plata estuary. On the other hand, we found *N. umbonata* to be the species with the highest relative abundance in environments rich in both ammonia and phosphate, and it was previously reported by Van Dam et al. (1994) to be an obligate nitrogen heterotroph.

On the basis of the oxygen demands recorded in this study and their relationship to different levels of saprobity (Sladecek 1973), 80% of the sites we analyzed would correspond to appropriate environments for the development of mesosaprobic species. In accordance with these characteristics, 89% of the species exhibited optima consistent with conditions ranging from α-mesosaprobic to polysaprobic. Among the species strongly associated with environments rich in organic matter, we recorded *Luticola goeppertiana*, *Lemnicola hungarica*, *Nitzschia sigma*, *Fragilaria heidenii*, *Placoneis placentula*, *Ulnaria ulna*, and *Gomphonema parvulum*, whereas the presence of *Stauroneis brasiliensis*, *Planothidium lanceloatum*, *Amphora acutiuscula*, *Craticula halophila*, and *Navicula viridula* var. *rostellata* correlated more closely with oligosaprobic-β-mesosaprobic environments from the standpoint of their optima. According to the pH-optimum-based classification system proposed by Hustedt (in Battarbee et al. 1999), 89% of the species sampled were alkalibiontic (optima and tolerances at pH values >7), while the remaining were alkaliphilous, with only *Diadesmis confervacea* exhibiting an optimum at a value close to neutrality (i.e. pH 7).

The results obtained in this study have provided new or additional information on certain species where previous data were either lacking or fragmented (Table 4).

Diatom studies of an applied nature in estuaries and shallow coastal waters have been few in number, especially when compared to those dealing with freshwater and the ocean (Sullivan 1999). Further studies are

Table 4. Ecological characteristics of diatom species whose previous information was lacking or fragmented. Obs: observations; NI: new information; AI: additional information

Species	Ecological characteristics					
	Salinity	pH	Trophic state	Saprobity	Oxygen	Obs.
Amphora acutiuscula		Alkalibiontic	Mesotrophic	β-mesosaprobic	High	NI
Nitzschia lacunarum	Freshwater	Alkalibiontic	Mesotrophic	β-α-mesosaprobic	High	NI
Stauroneis brasiliensis	Freshwater	Alkaliphilous	Oligo-mesotrophic	Oligo-mesosaprobic	Moderate	NI
Navicula monoculata var. *omissa*	Freshwater		Mesotrophic	β-mesosaprobic	Moderate to high	NI
Fragilaria heidenii	Fresh-brackish water	Alkalibiontic	Eutrophic	α-mesosaprobic	Moderate to high	NI
Placoneis symmetrica	Brackish-freshwater	Alkalibiontic	Mesotrophic	β-α-mesosaprobic	Moderate to high	NI
Navicula sanctaecrucis	Fresh-brackish water	Alkalibiontic	Mesotrophic	β-α-mesosaprobic	Moderate to high	NI
Planothidium delicatulum	Fresh-brackish water	Alkaliphilous	Mesotrophic	α-mesosaprobic	Moderate to high	NI
Fragilaria goulardii	Freshwater	Alkalibiontic	Mesotrophic	β-α-mesosaprobic	Moderate to high	NI
Tryblionella calida	Brackish water	Alkalibiontic	Oligo-mesotrophic	β-mesosaprobic	Moderate to high	NI
Hantzschia virgata	Brackish water	Alkalibiontic	Oligotrophic	β-mesosaprobic	Moderate to high	NI
Fallacia clepsidroides	Brackish-freshwater	Alkalibiontic	Mesotrophic	β-α-mesosaprobic	Moderate to high	NI
Navicula erifuga		Alkalibiontic	Oligo-mesotrophic	β-mesosaprobic	Moderate to high	AI
Navicula recens		Alkalibiontic	Oligo-mesotrophic	β-α-mesosaprobic	Moderate to high	AI
Neidium ampliatum		Alkalibiontic		β-α-mesosaprobic	Moderate to high	AI
Fragilaria capucina	Freshwater	Alkalibiontic		α-mesosaprobic	Moderate to high	AI
Nitzschia capitellata	Fresh-brackish water	Alkalibiontic	Oligo-mesotrophic	β-mesosaprobic	Moderate to high	AI
Naviculadicta laterostrata	Freshwater		Mesotrophic	β-mesosaprobic	Moderate to high	AI
Navicula kotschyi		Alkalibiontic	Oligo-mesotrophic	β-mesosaprobic	Moderate to high	AI
Navicula cryptotenella		Alkalibiontic	Oligo-mesotrophic		Moderate to high	AI

therefore needed in the future that are aimed at determining the tolerance of benthic diatoms to various forms of pollution in order to formulate accurate water-quality indices for estuaries.

The determination of the optimum and tolerance range of a species to major environmental variables that are exposed is a valuable tool to establish its indicator value and its use as a biomonitor in aquatic ecosystems. The results of this study show that diatoms identified in the intertidal zone of the Río de la Plata faithfully respond not only to natural gradients, typical of estuaries, but also to the changes introduced by human activity. On the other hand, the trophic importance of benthic diatoms in this ecosystem highlights the need for further taxonomic and ecophysiological studies and extends the study area towards the outer estuary area, which will provide a broader database to infer environmental conditions.

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