

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. Epipsammonic 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

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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 biostratigraphic 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 BOD₅, 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 km². 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

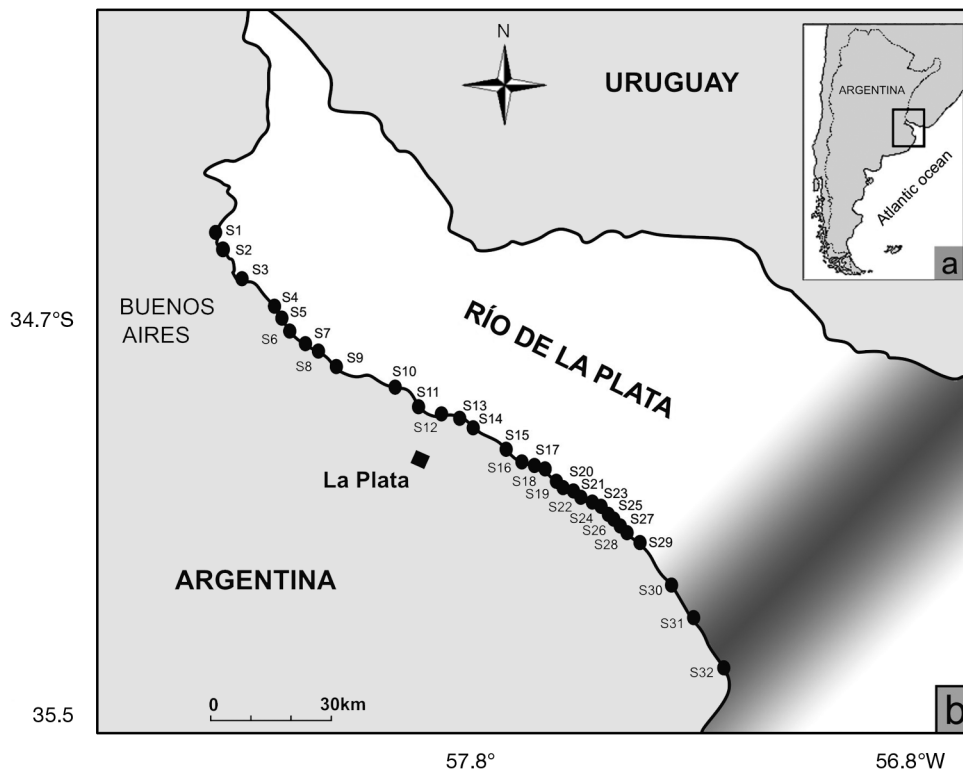


Fig. 1. Study area. (a) Río de la Plata estuary and (b) sampling sites. Shaded area corresponds to the maximum turbidity front

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 cm²) 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 H₂O₂, 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-NH₄⁺, N-NO₂⁻, N-NO₃⁻, P-PO₄⁻³, BOD₅, 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 (Muyllaert 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

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

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 BOD₅, 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-NO₃⁻ 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-NO₂⁻ 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-NH₄⁺ 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-PO₄⁻³ 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 \pm 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 $\mu\text{mol l}^{-1}$. BOD₅: biological oxygen demand; COD: chemical oxygen demand; DO: dissolved oxygen; No. obs.: number of observations

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

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 $\mu\text{S cm}^{-1}$), 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 gouldarii*, and *Geissleria decussis* were linked with less turbid and mineralized environments (optima at <67 NTU, <403 $\mu\text{S cm}^{-1}$). Among these species, *N. lacunarum*, *C. accomoda*, *N. iridis*, *F. gouldarii*, 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

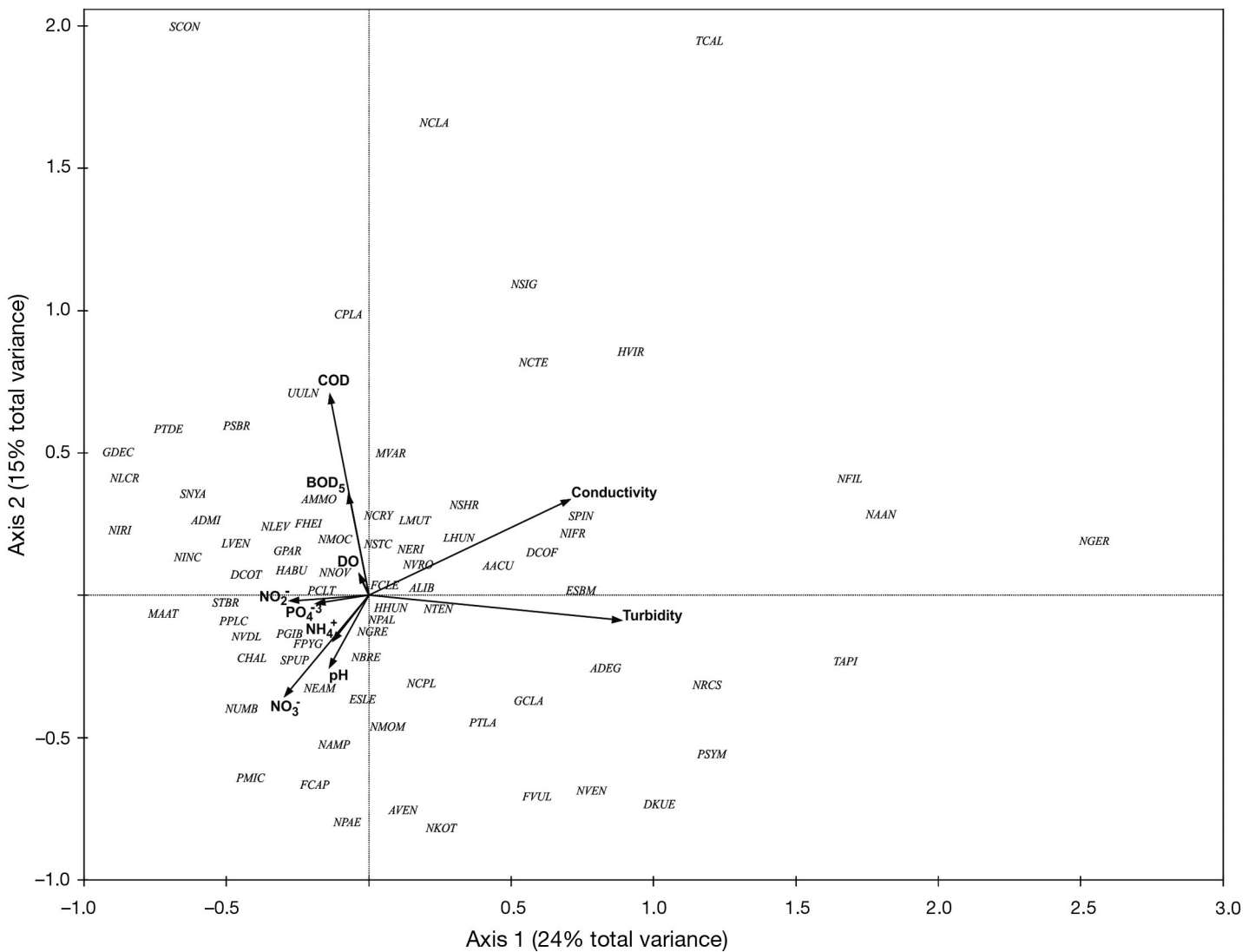


Fig. 3. Biplot of the first 2 axes of the canonical correspondence analysis showing environmental variables and diatom taxa. Acronyms correspond to those in Table 3

Table 3. Diatom species optima and tolerance limits (low, L, and high, H) for nutrients (N-NO₃⁻, N-NH₄⁺, N-NO₂⁻, N-NH₄⁺, P-PO₄⁻³), conductivity, pH, dissolved oxygen (as % DO saturation), turbidity, biological and chemical oxygen demand (BOD₅ 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	Acro- nym (%)	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										
<i>Achnanthes exiguum</i>	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	87	74	102	358	169	759	2.4	1.5	4.0	5.4	3.1	9.6			
<i>Achnanthes minutissimum</i>	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	2782	328	1048	83	57	121	82	31	217	2.9	1.1	8.2	12.5	5.2	30.3			
<i>Amphora acutiscula</i>	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	94	77	115	400	139	1148	3.1	2.0	4.9	11.7	6.3	21.5			
<i>Amphora libyca</i>	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	81	79	130	189	55	651	5.3	2.6	10.9	15.8	10.4	24.0			
<i>Amphora montana</i>	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	81	77	84	92	78	108	224	4.1	1.5	11.3	18.9	11.8	30.2		
<i>Amphora veneta</i>	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	81	79	84	89	81	97	264	110	633	2.9	1.8	4.6	4.8	2.8	8.4
<i>Cocconeis placentula</i>	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
<i>Craticula accomoda</i>	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	84	5.8	12.1	16.7	9.8	28.3	
<i>Craticula halophila</i>	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
<i>Denticula kuetzingii</i>	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
<i>Diadema confervacea</i>	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
<i>Diadema contenta</i>	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
<i>Eucyanea silesiacum</i>	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	490	254	1066	8.3	7.8	8.8	111	81	153	60	20	185	6.8	3.7	12.5	12.9	8.2	20.1
<i>Eolimna subminuscula</i>	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	207	788	8.1	7.7	8.6	101	75	116	121	41	360	4.8	2.1	11.0	16.8	9.5	29.5
<i>Fallacia clepsidroides</i>	FCLE	67	0.48	0.15	1.49	0.018	0.006	0.058	0.048	0.005	0.454	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
<i>Fallacia pygmaea</i>	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
<i>Fragilaria capucina</i>	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
<i>Fragilaria goulardii</i>	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
<i>Fragilaria heidenii</i>	FHHE	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
<i>Frustulia vulgaris</i>	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
<i>Gensleria decussis</i>	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	117	91	149	49	18	136	6.8	3.1	14.9	14.1	8.3	23.9
<i>Gomphonema clavatum</i>	GCLA	22	0.48	0.12	2.01	0.037	0.013	0.107	0.208	0.053	0.824	0.26	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
<i>Gomphonema parvulum</i>	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	8.2	7.8	8.7	107	87	131	109	36	333	6.1	3.4	11.2	14.3	9.1	22.5
<i>Hantzschia abundans</i>	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
<i>Hantzschia virgata</i>	HVIR	5	0.44	0.15	1.28	0.024	0.005	0.122	0.066	0.041	1.08	0.18	0.11	0.30	866	516	1455	7.6	7.2	8.0	91	80	103	113	20	638	3.5	1.9	6.4	9.7	3.9	24.1
<i>Hippodonta hungarica</i>	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
<i>Lemnicola hungarica</i>	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
<i>Luticola goeppertiana</i>	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
<i>Luticola mutica</i>	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
<i>Luticola ventricosa</i>	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
<i>Mayamea atomus</i>	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
<i>Melosira varians</i>	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
<i>Navicula angusta</i>	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
<i>Navicula cryptocephala</i>	NCRY	14	1.40	0.69	2.84	0.030	0.006	0.144	0.071	0.034	1.146	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
<i>Navicula cryptotenella</i>	NCTE	5	0.53	0.38	0.74	0.020	0.006	0.063	0.064	0.040	1.010	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
<i>Navicula erifuga</i>	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	1277	8.1	7.4	8.8	100	75	134	78	20	302	3.7	1.6	8.6	9.7	4.3	21.9
<i>Navicula germainii</i>	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
<i>Navicula gregaria</i>	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
<i>Navicula kotschy</i>	NKOT	5	0.82	0.31	2.16	0.040	0.017	0.095	0.199	0.116	3.341	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
<i>Navicula monoculata</i>	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	

Table 3 (continued)

Species	Acro- nym (%)	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											
<i>Navicula sanctaecrucis</i>	NSTC	13	0.67	0.23	1.94	0.031	0.011	0.090	0.833	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
<i>Navicula schroeteri</i>	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	
<i>Navicula tenelloides</i>	NTEH	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	
<i>Navicula veneta</i>	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	
<i>Navicula viridula</i> var. <i>tostellata</i>	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	
<i>Naviculadicta laterostrata</i>	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	
<i>Neidium ampliatum</i>	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	
<i>Neidium iridis</i>	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	
<i>Nitzschia amphibia</i>	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	
<i>Nitzschia brevissima</i>	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	
<i>Nitzschia capitellata</i>	NCPL	12	0.55	0.32	0.93	0.007	0.004	0.111	0.003	0.001	0.101	0.15	0.25	0.35	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	
<i>Nitzschia clausii</i>	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	
<i>Nitzschia filiformis</i>	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	
<i>Nitzschia frustulum</i>	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	
<i>Nitzschia inconspicua</i>	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	102	80	131	124	35	441	5.5	3.4	9.0	9.8	5.4	17.6	
<i>Nitzschia lacunarum</i>	NLCR	8	0.88	0.52	1.50	0.008	0.004	0.015	0.027	0.004	2.05	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	
<i>Nitzschia levidensis</i>	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	
<i>Nitzschia palea</i>	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	
<i>Nitzschia paleacea</i>	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	
<i>Nitzschia sigma</i>	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	
<i>Nitzschia umbonata</i>	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	
<i>Pinnularia gibba</i>	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	
<i>Pinnularia microstauron</i>	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	
<i>Placoneis clementis</i>	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	
<i>Placoneis placentula</i>	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	
<i>Placoneis symmetrica</i>	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	
<i>Planothidium delicatulum</i>	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	
<i>Planothidium lanceolatum</i>	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	
<i>Pseudostaurora brevistriata</i>	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	
<i>Sellaphora nyassensis</i>	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	
<i>Sellaphora pupula</i>	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	
<i>Stauroneis brasiliensis</i>	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	
<i>Stauroneis construens</i>	SCON	6	0.29	0.12	0.74	0.012	0.003	0.061	0.033	0.002	0.428	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	
<i>Stauroneis pinnata</i>	SPIN	16	0.37	0.13	1.07	0.016	0.004	0.068	0.040	0.003	0.524	0.19	0.08	0.44	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	
<i>Tryblionella apiculata</i>	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	
<i>Tryblionella calida</i>	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			

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

Inorganic nitrogen. Species such as *Diadismis confervacea*, *Hippodonta capitata*, *Gomphonema parvulum*, *Amphora veneta*, *Nitzschia sigma*, *Achnantheidium 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 $>0.07 \text{ mg l}^{-1}$), 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*, *Diadismis contenta*, *Denticula kuetzingii*, *Eolimna subminuscula*, *Sellaphora pupula*, *Navicula schoeteri*, and *Mayamea atomus* (optimum at $>0.28 \text{ mg l}^{-1}$), 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 $<0.07 \text{ mg l}^{-1}$; 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 $>8.3 \text{ mg l}^{-1}$), whereas the presence of *Stauroneis brasiliensis*, *Planothidium lanceolatum*, *Amphora acutiuscula*, *Craticula halophila*, *Navicula viridula* var. *rostellata*, and *Hippodonta hungarica* correlated with much lower concentrations (optimum at $<4.3 \text{ mg l}^{-1}$; Table 3). With respect to the COD, the prevalence of *L. goeppertiana*, *Pseudostauroneis brevistriata*, and *Nitzschia lacunarum* was significantly related to the highest values (optimum at $>26.5 \text{ mg l}^{-1}$), and only *N. lacunarum* showed a stringent range of tolerance. At the lower CODs, the presence of *Amphora veneta*, *Achnantheidium exiguum*, *Navicula kotschyi*, *Stauroneis brasiliensis*, *Pinnularia microstauron*, and *Navicula monoculata* var. *omissa* (optimum at $<7.8 \text{ mg l}^{-1}$) 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 *Stauroneis 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 mesoeutrophic 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 (Sladeczek 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 lanceolatum*, *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 *Diademsis 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.
<i>Amphora acutiuscula</i>		Alkalibiontic	Mesotrophic	β -mesosaprobic	High	NI
<i>Nitzschia lacunarum</i>	Freshwater	Alkalibiontic	Mesotrophic	β - α -mesosaprobic	High	NI
<i>Stauroneis brasiliensis</i>	Freshwater	Alkaliphilous	Oligo-mesotrophic	Oligo-mesosaprobic	Moderate	NI
<i>Navicula monoculata</i> var. <i>omissa</i>	Freshwater		Mesotrophic	β -mesosaprobic	Moderate to high	NI
<i>Fragilaria heidenii</i>	Fresh-brackish water	Alkalibiontic	Eutrophic	α -mesosaprobic	Moderate to high	NI
<i>Placoneis symmetrica</i>	Brackish-freshwater	Alkalibiontic	Mesotrophic	β - α -mesosaprobic	Moderate to high	NI
<i>Navicula sanctaerucis</i>	Fresh-brackish water	Alkalibiontic	Mesotrophic	β - α -mesosaprobic	Moderate to high	NI
<i>Planothidium delicatulum</i>	Fresh-brackish water	Alkaliphilous	Mesotrophic	α -mesosaprobic	Moderate to high	NI
<i>Fragilaria gouldardii</i>	Freshwater	Alkalibiontic	Mesotrophic	β - α -mesosaprobic	Moderate to high	NI
<i>Tryblionella calida</i>	Brackish water	Alkalibiontic	Oligo-mesotrophic	β -mesosaprobic	Moderate to high	NI
<i>Hantzschia virgata</i>	Brackish water	Alkalibiontic	Oligotrophic	β -mesosaprobic	Moderate to high	NI
<i>Fallacia clepsidroides</i>	Brackish-freshwater	Alkalibiontic	Mesotrophic	β - α -mesosaprobic	Moderate to high	NI
<i>Navicula erifuga</i>		Alkalibiontic	Oligo-mesotrophic	β -mesosaprobic	Moderate to high	AI
<i>Navicula recens</i>		Alkalibiontic	Oligo-mesotrophic	β - α -mesosaprobic	Moderate to high	AI
<i>Neidium ampliatum</i>		Alkalibiontic		β - α -mesosaprobic	Moderate to high	AI
<i>Fragilaria capucina</i>	Freshwater	Alkalibiontic		α -mesosaprobic	Moderate to high	AI
<i>Nitzschia capitellata</i>	Fresh-brackish water	Alkalibiontic	Oligo-mesotrophic	β -mesosaprobic	Moderate to high	AI
<i>Naviculadicta laterostrata</i>	Freshwater		Mesotrophic	β -mesosaprobic	Moderate to high	AI
<i>Navicula kotschy</i>		Alkalibiontic	Oligo-mesotrophic	β -mesosaprobic	Moderate to high	AI
<i>Navicula cryptotenella</i>		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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Ecological optima and tolerances of coastal benthic diatoms in the freshwater-mixohaline zone of the Río de la Plata estuary

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Supplement: Additional data

Table S1. Nutrient data from Table 2 of the main article expressed as $\mu\text{mol l}^{-1}$

Sites	N-NO ₃ ⁻ ($\mu\text{mol l}^{-1}$)	N-NO ₂ ⁻ ($\mu\text{mol l}^{-1}$)	N-NH ₄ ⁺ ($\mu\text{mol l}^{-1}$)	P-PO ₄ ⁻³ ($\mu\text{mol l}^{-1}$)
S1	55.0 ± 19.3)	3.1 ± 0.9	17.8 ± 15.5	8.7 ± 10.3
S2	79.2 ± 15.7	6.1 ± 1.9	18.8 ± 10.0	7.7 ± 3.2
S3	74.3 ± 29.3	4.9 ± 1.6	17.3 ± 9.2	4.2 ± 0.6
S4	101.4	4.1	17.3	3.9
S5	14.3	2.1	166.8	8.7
S6	82.8 ± 121.4	1.1 ± 0.2	99.0 ± 95.6	67.5 ± 33.6
S7	2.1	1.6	145.3	40.0
S8	122.1	12.1	49.1	12.3
S9	77.1 ± 22.8	12.3 ± 2.8	58.0 ± 52.3	12.3 ± 2.9
S10	66.4 ± 31.4	3.1 ± 1.4	6.5 ± 7.0	7.7 ± 1.9
S11	70.7 ± 38.6	3.7 ± 2.1	16.1 ± 17.1	12.3 ± 6.1
S12	78.5	8.1	21.7	6.8
S13	76.4	10.8	31.3	10.3
S14	33.6 ± 27.1	5.4 ± 8.4	35.5 ± 35.9	19.0 ± 13.2
S15	85.0 ± 122.1	1.7 ± 2.2	4.9 ± 9.1	5.8 ± 2.6
S16	159.2	3.6	17.1	
S17	3.6	0.6	9.4	4.2
S18	519.8	0.4	0.4	3.6
S19	30.7 ± 18.6	0.9 ± 0.6	24.8 ± 36.6	4.2 ± 1.9
S20	156.4 ± 108.5	0.9 ± 1.1	13.7 ± 6.4	6.5 ± 4.2
S21	54.3 ± 44.3	0.4 ± 0.2	3.5 ± 2.2	5.8 ± 2.6
S22	187.1 ± 129.9	2.6 ± 4.3	9.0 ± 3.3	4.8 ± 2.9
S23	182.1 ± 120.7	4.9 ± 6.6	19.4 ± 9.1	9.0 ± 10.3
S24	227.7	0.1	3.4	5.8
S25	294.9 ± 10.7	6.8 ± 9.5	14.0 ± 7.5	6.5
S26	107.1 ± 99.2	2.6 ± 1.9	8.4 ± 3.9	6.1 ± 3.9
S27	92.8 ± 81.4	1.2 ± 1.4	63.5 ± 51.3	12.9 ± 9.4
S28	194.2 ± 43.6	0.7 ± 0.8	21.0 ± 10.0	6.1 ± 1.6
S29	187.1 ± 218.5	0.4 ± 0.1	2.1 ± 1.4	5.2 ± 1.9
S30	12.1	0.1	4.1	2.6
S31	21.4 ± 12.9	0.6 ± 0.4	4.1 ± 3.8	5.5 ± 2.3
S32	26.4 ± 7.1	0.4 ± 0.1	0.2 ± 0.2	4.2 ± 2.6
No. of observations:	120	120	120	115

Table S2. Full taxonomic names of species listed in Table 3 of the main article

Species
<i>Achnantheidium exiguum</i> (Grunow) Czarnecki
<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki
<i>Amphora acutiuscula</i> Kützing
<i>Amphora libyca</i> Ehrenberg
<i>Amphora montana</i> Krasske
<i>Amphora veneta</i> Kützing
<i>Cocconeis placentula</i> Ehrenberg var. <i>placentula</i>
<i>Craticula accomoda</i> (Hustedt) Mann
<i>Craticula halophila</i> (Grunow ex Van Heurck) Mann
<i>Denticula kuetzingii</i> Grunow var. <i>kuetzingii</i>
<i>Diadesmis confervacea</i> Kützing
<i>Diadesmis contenta</i> (Grunow) Mann
<i>Encyonema silesiacum</i> (Bleisch) Mann
<i>Eolimna subminuscula</i> (Manguin) Moser Lange-Bertalot & Metzeltin
<i>Fallacia clepsidroides</i> Witkowski
<i>Fallacia pygmaea</i> Kützing
<i>Fragilaria capucina</i> Desmazieres var. <i>capucina</i>
<i>Fragilaria goulardii</i> (Brebisson) Lange-Bertalot
<i>Fragilaria heidenii</i> Oestrup
<i>Frustulia vulgaris</i> (Thwaites) De Toni
<i>Geissleria decussis</i> (Oestrup) Lange-Bertalot & Metzeltin
<i>Gomphonema clavatum</i> Ehrenberg
<i>Gomphonema parvulum</i> (Kützing) Kützing var. <i>parvulum f. parvulum</i>
<i>Hantzschia abundans</i> Lange-Bertalot
<i>Hantzschia virgata</i> (Roper) Grunow var. <i>virgata</i>
<i>Hippodonta capitata</i> (Ehrenberg) Lange-Bertalot Metzeltin & Witkowski
<i>Hippodonta hungarica</i> (Grunow) Lange-Bertalot Metzeltin & Witkowski
<i>Lemnicola hungarica</i> (Grunow) Round & Basson
<i>Luticola goeppertiana</i> (Bleisch) Mann
<i>Luticola mutica</i> (Kützing) Mann
<i>Luticola ventricosa</i> (Kützing) Mann
<i>Mayamea atomus</i> (Kützing) Lange-Bertalot
<i>Melosira varians</i> Agardh
<i>Navicula angusta</i> Grunow
<i>Navicula cryptocephala</i> Kützing
<i>Navicula cryptotenella</i> Lange-Bertalot
<i>Navicula erifuga</i> Lange-Bertalot
<i>Navicula germainii</i> Wallace
<i>Navicula gregaria</i> Donkin
<i>Navicula kotschyi</i> Grunow
<i>Navicula monoculata</i> Hustedt
<i>Navicula monoculata</i> Hustedt var. <i>omissa</i> (Hustedt) Lange-Bertalot
<i>Navicula novaesiberica</i> Lange-Bertalot
<i>Navicula recens</i> (Lange-Bertalot) Lange-Bertalot
<i>Navicula sanctaerucis</i> Ostrup

Navicula schroeteri Meister var. *schroeteri*
Navicula tenelloides Hustedt
Navicula veneta Kützing
Navicula viridula (Kützing) Ehrenberg var. *rostellata* (Kützing) Cleve
Naviculadicta laterostrata Hustedt
Neidium ampliatum (Ehrenberg) Krammer
Neidium iridis (Ehrenberg) Cleve
Nitzschia amphibia Grunow *amphibia*
Nitzschia brevissima Grunow
Nitzschia capitellata Hustedt
Nitzschia clausii Hantzsch
Nitzschia filiformis (Smith) Van Heurck var. *filiformis*
Nitzschia frustulum (Kützing) Grunow var. *frustulum*
Nitzschia inconspicua Grunow
Nitzschia lacunarum Hustedt
Nitzschia levidensis (Smith) Grunow
Nitzschia palea (Kützing) W.Smith
Nitzschia paleacea (Grunow) Grunow
Nitzschia sigma (Kützing) W.M.Smith
Nitzschia umbonata (Ehrenberg) Lange-Bertalot
Pinnularia gibba Ehrenberg
Pinnularia microstauron (Ehrenberg) Cleve var. *microstauron*
Placoneis clementis (Grunow) Cox
Placoneis placentula (Ehrenberg) Heinzerling
Placoneis symmetrica (Hustedt) Lange-Bertalot
Planothidium delicatulum (Kützing) Round & Bukhtiyarova
Planothidium lanceolatum (Brebisson ex Kützing) Lange-Bertalot
Pseudostaurosira brevistriata (Grunow) Williams & Round
Sellaphora nyassensis (Muller) Mann
Sellaphora pupula (Kützing) Mereschkowsky
Stauroneis brasiliensis (Zimmerman) Compere
Staurosira construens Ehrenberg
Staurosirella pinnata (Ehrenberg) Williams & Round
Tryblionella apiculata Gregory
Tryblionella calida (Grunow) Mann
Ulnaria ulna (Nitzsch.) Compere