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Distribution of periphytic diatoms in the rivers of the Lake Ladoga basin (Northwestern Russia)

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Relationships between distribution of periphytic diatoms and environmental variables in 19 rivers of the Lake Ladoga basin (Northwestern Russia) were examined using gradient analysis. On the basis of geology and river water chemistry, the Lake Ladoga basin could be separated into two main parts, the northern and the southern sub-basin. The rivers in the northern sub-basin are slightly acidic and low in conductivity (mean value 53 μS cm^{-1}); the rivers in the southern sub-basin have neutral to slightly alkaline waters with higher conductivities (mean value 168 μS cm^{-1}). A detrended correspondence analysis (DCA) defined two groups of rivers generally corresponding to the two main parts of the Lake Ladoga basin. *Fragilaria capucina* var. *rumpens*, *Frustulia saxonica* and *Tabellaria flocculosa* were the typical species for the northern sub-basin, whereas *Cocconeis placentula* var. *euglypta*, *Ulnaria ulna* and *Gomphonema parvulum* were characteristic species for the southern sub-basin. A canonical correspondence analysis (CCA) identified conductivity, pH, bicarbonate, total phosphorus and water colour as the most important environmental variables related to changes in assemblage structure. Both DCA and CCA ordination showed that conductivity related to geology was the most important variable, while concentration of total phosphorus was the second most important variable. Weighted averaging was used to infer total phosphorus from relative biomass of diatoms. The predictive ability of the inference model was sufficiently strong with $r^2 = 0.71$ and RMSEP = 1.9 μg L^{-1}. These results strongly support the use of a diatom-based inference phosphorus model for indicating eutrophication in the rivers of the Lake Ladoga basin.

Keywords: Diatom, periphyton, distribution, gradient, eutrophication, Lake Ladoga, Russia

Introduction

Periphytic diatoms are excellent indicators of ecological condition of rivers and streams, because of their ability to respond rapidly to changes in nutrient concentrations. The sensitivity of diatoms to eutrophication has led to development of monitoring methods

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and indices to assess water quality of rivers. Several diatom-based indices are being used to estimate trophic status of European rivers (e.g. KELLY and WHITTON 1995, ROTT et al. 2003). However, the applicability of these indices may be limited to specific geographic regions, because autecological metrics of diatoms can vary across different geographic areas (POTAPOVA and CHARLES 2007). Species response to nutrient enrichment may also depend on other environmental factors, which are related to geology of the underlying bedrocks, land use and other landscape characteristics. Therefore, in order to improve diatom-based water-quality assessment, autecological metrics of indicator species should be developed by quantifying species distribution along environmental gradients within a particular region.

In this study, distributional patterns of periphytic diatoms in relation to environmental variables in 18 inflow rivers of the Lake Ladoga and the outflowing Neva River were investigated using multivariate ordination methods. In addition, this study assessed the potential use of periphytic diatoms as indicators of eutrophication in the rivers of the Lake Ladoga basin by developing a diatom-based inference model for total phosphorus.

Characteristics of the water bodies

The Lake Ladoga basin (Republic of Karelia and Leningrad Oblast, Northwestern Russia) has a length of more than 1,000 km (north-south) and a catchment area of 260,000 km^2. It can be divided into two main parts, the northern and the southern sub-basin, which differ in geomorphology and geology. The northern part is located on the Baltic Shield comprised of acid crystalline and metamorphic rocks (granite in majority and gneiss). The southern part is dominated by terrigenous and carbonaceous sedimentary rocks (sandstone, limestone and dolomite) of the Russian Platform. The rivers flowing into Lake Ladoga on the northern and eastern coasts (Burnaya, Khiitolan, Iijoki, Mijnola, Yanis, Uksun, Tulema, Vidlitsa, Tuloksa, Olonka, Svir) belong to the northern sub-basin, while rivers of the western, southern and southeastern coasts (Avloga, Morje, Lava, Volkhov, Syas, Pasha, Oyat,) belong to the southern sub-basin (Fig. 1). The division of the Lake Ladoga basin into two areas is reflected in differences in the water chemistry of their rivers (SOLOVIEVA 1967). The rivers of the northern sub-basin generally have slightly acidic waters with low conductivities, whereas the rivers of the southern sub-basin have neutral to slightly alkaline waters with high conductivities (up to 350 μS cm^{-1}) (Tab. 1). The studied rivers range widely in water colour, which reflects differences in the percentage of lakes/wetlands in the river catchments. The Pasha, Tulema, Iijoki, Avloga, Olonka, Tuloksa and Morje rivers with wetland-dominated catchments are characterized by darker water colour with values ranging from 150 to 275 Pt-Co units (Tab. 1). In contrast, the rivers Khiitolan, Svir and Burnaya with a high percentages of lakes in the catchments (14–20%) have less coloured water (<50 Pt-Co units). Due to anthropogenic eutrophication in the 1970s and 1980s, the amount of nutrients transported by the rivers increased considerably (RASPLETINA 1982). The highest concentrations of total phosphorus were recorded where the drainage area was subjected to the greatest anthropogenic impact, mainly in the southern rivers Volkhov and Lava, rivers of the western coast Morje and Avloga, some rivers of the eastern coast Olonka and Tuloksa, and in the northern river Iijoki (Tab. 1). Only in the rivers of the northern and north-eastern coast, less subject to anthropogenic influence (Burnaya, Yanis, Uksun, Tulema and Svir), did the concentration of nutrients remain at the level of the 1960s (total phosphorus: 15–24 μg L^{-1}). The hydrochemistry of the Neva River source is largely determined by

Fig. 1. Location of the sampling sites in the rivers of the Lake Ladoga basin. Open (group A) and filled (group B) circles are rivers which were included in groups defined by DCA ordination of diatom composition data.

hydrochemical regime of Lake Ladoga and to a lesser extent by the water mass supplied by the major inflows of Lake Ladoga, the Volkhov and Burnaya rivers (RASPLETINA et al. 2006).

Materials and methods

Periphytic diatom samples were collected from stones and macrophytes in the mouths of 18 tributaries of Lake Ladoga and in the source of the Neva River in May, July and September 2000–2001. In all, 135 diatom samples were collected and analyzed. Water samples were taken simultaneously with diatom samples. They were analyzed for electric conductivity, bicarbonate, pH, soluble reactive phosphorus, total phosphorus and water colour.

After acid cleaning and mounting diatoms on slides, diatom valves were identified and enumerated using a light microscope (1000× magnification), by scanning transects until

Tab. 1. Hydrological and average hydrochemical characteristics for the 19 study rivers.

River	Discharge (m^3 sec^{-1})	TP (μg L^{-1})	SRP (μg L^{-1})	Conductivity (μS cm^{-1})	HCO_3 (mg L^{-1})	pH	Color (Pt-Co units)
Neva	2400.0	28	5	89	34	7.5	29
Svir	661.0	24	6	55	22	7.1	49
Burnaya	613.0	16	5	65	15	7.1	30
Volkhov	535.0	68	30	197	76	7.5	108
Syas	63.8	34	14	193	129	7.8	131
Pasha	73.7	34	9	115	59	7.3	149
Ojat	58.6	30	14	86	47	7.3	129
Yanis	41.7	18	5	34	8	6.8	69
Olonka	35.2	88	50	61	21	6.9	187
Tulema	21.8	20	8	33	11	6.8	149
Khiitolan	14.7	35	10	92	25	7.1	38
Vidlitsa	18.5	46	8	44	19	6.9	102
Uksun	15.0	17	3	26	6	6.6	128
Tuloksa	8.6	70	35	41	16	6.6	218
Mijnola	5.2	32	15	58	19	6.8	130
Lava	4.2	102	67	347	196	8.1	123
Morje	4.5	149	80	61	16	6.6	275
Avloga	1.8	395	360	258	121	7.3	155
Iijoki	1.5	190	161	61	18	7.1	179

300 valves were counted. Diatoms were identified to species level using KRAMMER and LANGE-BERTALOT (1986–1991). For common taxa the dimensions of 20–25 cells (fewer cells measured on rare taxa) were measured with an ocular micrometer and were used to calculate biovolume. Biovolume for each diatom taxon was estimated with the geometrical equations proposed by HILLEBRAND et al. (1999).

The 61 most abundant diatom taxa contributing on average 96.8% (min 62.1%, max 99.7%) to the total diatom biovolume in periphyton samples were included in the statistical analyses. Ordination analyses of periphytic diatom assemblages were performed using CANOCO (TER BRAAK and SMILAUER 1998). Detrended correspondence analysis (DCA) was used to elucidate main patterns in diatom assemblage and to assess similarity among rivers in terms of assemblage composition. Canonical correspondence analysis (CCA) was subsequently used to investigate species-environment relationships. The variance explained in the DCA and CCA ordinations were 3–4% more using counts based upon percent biovolume than percent cell abundance of taxa; therefore diatom assemblage structure was expressed as percent biovolume. Weighted-averaging (WA) regression-calibration models were developed for electric conductivity, pH and total phosphorus (TP) using the computer program C2 (JUGGINS 2003). The strength of the inference models was assessed by the determination coefficient (r^2) between the observed and inferred values, and the root mean squared errors of prediction (RMSEP). Prior to the analyses, all environmental variables were log-transformed and percent biovolumes of diatom taxa were arcsine square root transformed to approximate a normal distribution.

Two trophic diatom indices TDI and TID were calculated following KELLY and WHITTON (1995) and ROTT et al. (2003) using the OMNIDIA software (LECOINTE et al. 1993). The relationships between the diatom indices and TP were assessed using simple linear regression.

Results

Diatom-environmental relationships

The eigenvalues of the first two DCA axes accounted for 17% of the variance in the data set. The first axis was significantly correlated with electric conductivity, bicarbonate and pH (correlation coefficient r = –0.67, –0.65 and –0.63, respectively). The second axis was most correlated with TP and SRP (correlation coefficient r = 0.51, 0.47, respectively). The DCA diagram shows centroids of seasonal samples of the investigated rivers in the ordination space of the first and second axes (Fig. 2). The DCA diagram separates all rivers along the first axis into two groups based on diatom species composition. Group A in the left side of the DCA diagram consists of rivers from the southern part of the Lake Ladoga basin (including the Neva River), except for one northern river, the Khiitolan (Figs. 1, 2). Group B in the right side of the DCA diagram mainly consists of rivers from the northern part of the Lake Ladoga basin with one exception, the southern river Morje (Figs. 1, 2). Conductivity, bicarbonate and pH in group A were significantly higher than in group B (Tab. 2). It is noticeable that TP and SRP were not significantly different between the two river groups. Species replacement from group A to group B was evident in diatom assemblages (Tab. 2). Diatom assemblages in group A were dominated by *Cocconeis placentula* var. *euglypta*, *Ulnaria ulna* and *Gomphonema parvulum*. The dominance of these three species was replaced by that of *Tabellaria flocculosa* and *Fragilaria capucina* var. *rumpens* in group B. Comparisons between groups A and B for relative biomasses of these species showed sta-

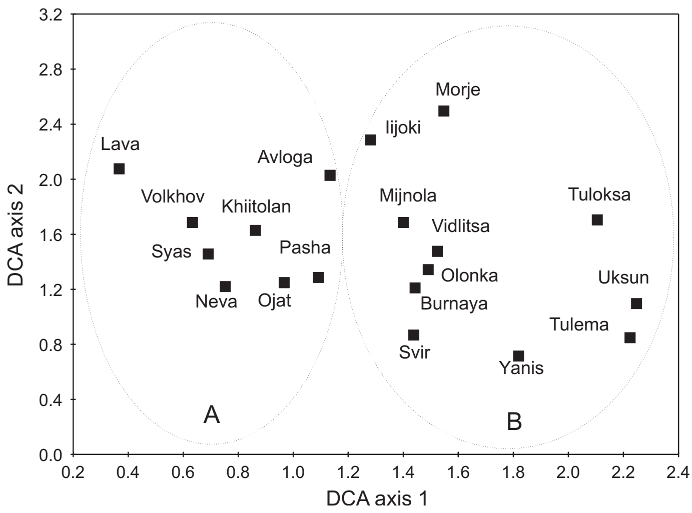

Fig. 2. DCA diagram showing centroids of seasonal periphyton samples for each river. Group A mostly consists of rivers from the southern part of the Lake Ladoga basin, whereas group B mainly contains rivers from the northern part of the Lake Ladoga basin (explanation in text).

Tab. 2. Differences in mean values (and range) of environmental variables and relative biomass of dominant diatom taxa between the two river groups defined by DCA. *p*-values are the results of Mann-Whitney U test.

Variables	River group		*p*
	A (*n* = 57)	B (*n* = 78)	
Environmental variables			
Conductivity (μS cm^{-1})	161 (43–363)	48 (21–90)	< 0.001
pH	7.5 (6.8–8.3)	6.8 (5.9–7.6)	< 0.001
HCO_3 (mg L^{-1})	81 (19–201)	16 (3–36)	< 0.001
TP (μg L^{-1})	79 (14–450)	54 (10–335)	NS
SRP (μg L^{-1})	53 (1–430)	28 (1–300)	NS
Color (Pt-Co units)	110 (25–242)	136 (25–360)	NS
Diatoms (% biovolume)			
Cocconeis placentula var. *euglypta*	19.1 (0–97.4)	4.6 (0–68.6)	< 0.001
Ulnaria ulna	14.5 (0–63.7)	8.5 (0–56.6)	< 0.05
Gomphonema parvulum	11.3 (0–81.9)	5.8 (0–79.5)	< 0.01
Tabellaria flocculosa	2.5 (0–12.3)	21.2 (0–83.6)	< 0.001
Fragilaria capucina var. *rumpens*	3.2 (0–14.8)	12.5 (0–66.5)	< 0.001
Frustulia saxonica	0.5 (0–17.2)	3.2 (0–48.9)	< 0.05
Eunotia bilunaris	0.3 (0–4.7)	4.1 (0–64.1)	< 0.05
Eunotia incisa	0.4 (0–19.2)	3.3 (0–46.9)	< 0.001
Eunotia praerupta	0.1 (0–2.3)	2.3 (0–31.9)	< 0.05
Melosira varians	12.6 (0–65.1)	16.1 (0–89.4)	NS

NS – differences are not significant ($p > 0.05$).

tistical differences (Tab. 2). Other common species, which had a significantly higher relative biomass in group B than group A, included *Frustulia saxonica*, *Eunotia bilunaris*, *E. incisa* and *E. praerupta*.

The eigenvalues of the first two CCA axes were both significant ($p < 0.01$; Monte Carlo permutation test), and they explained 14% of the variance in the species data. The diatom-environment correlations for CCA axis 1 (0.86) and 2 (0.83) were high, indicating a strong relation between diatoms and the measured environmental variables. Conductivity, bicarbonate and pH were the most significant factors contributing to the first axis, whereas TP, SRP and colour were the most important variables along the second axis (Fig. 3). CCA separated rivers primarily according to their conductivity, pH and bicarbonate concentration, related to geology, and secondarily according to their trophic status related to phosphorus concentration. The first axis mainly separated rivers with high conductivity and neutral to slightly alkaline waters in the southern sub-basin from rivers with low conductivity and slightly acidic waters in the northern sub-basin. On the right side of the first axis alkaliphilous taxa (according to VAN DAM et al. 1994) like *Amphora ovalis*, *Cocconeis placentula* var. *euglypta*, *Diatoma vulgaris*, *Frustulia vulgaris*, *Gomphonema olivaceum*, *Navicula tripunctata*, *Planothidium lanceolatum*, *Rhoicosphenia abbreviata*, and *Ulnaria ulna* were located, while on the left side of the first axis acidophilous species (according to

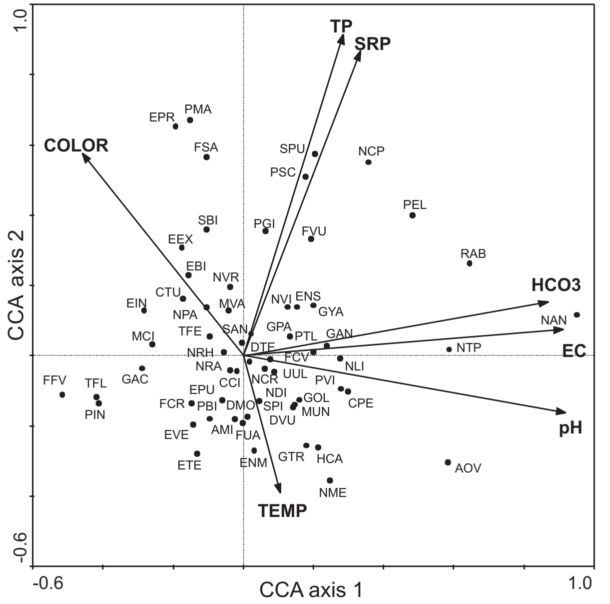

Fig. 3. CCA diagram showing environmental variables and diatom species. Codes for environmental variables: EC – electric conductivity, HCO3 – bicarbonate, pH – water pH, TP – total phosphorus, SRP – soluble reactive phosphorus, COLOR – water color, and TEMP – water temperature. Species codes can be found in table 3.

VAN DAM et al. 1994) such as *Tabellaria flocculosa*, *Eunotia bilunaris*, *E. incisa*, *E. pectinalis* var. *undulata*, *E. praerupta*, *E. tenella*, *E. veneris*, *Fragilariforma virescens*, and *Frustulia saxonica* were positioned (Fig. 3). The second axis primarily separated phosphorus-enriched and humic rivers, such as the Morje, Avloga, Iijoki and Tuloksa, from oligo-mesotrophic, clear-water rivers, including the rivers Burnaya, Svir and Yanis. Species indicative of high phosphorus concentration such as *Navicula capitatoradiata*, *Placoneis elginensis*, *Sellaphora pupula*, *Frustulia vulgaris* and *Pinnularia gibba* were positioned on the positive side of the second axis, whereas species indicative of low nutrient status such as *Eunotia tenella*, *E. pectinalis* var. *undulata*, *Achnanthidium minutissimum* and *Fragilaria capucina* var. *rumpens* were on the negative side of the second axis (Fig. 3). Such ordination of these species corresponded to their trophic preferences known from the literature (e.g. VAN DAM et al. 1994). Some species such as *Frustulia saxonica* and *Eunotia praerupta*, often found at low nutrient concentrations (VAN DAM et al. 1994), grouped with eutrophic taxa (Fig. 3). These species reached the highest relative abundances (48.9% and 31.9%, respectively) in eutrophic humic rivers such as the Morje and the Iijoki.

Weighted-averaging models

A series of weighted-averaging (WA) models were developed to test for their suitability to infer water quality variables. Environmental variables should be considered only if the ratio of the first eigenvalue (λ_1) to the second eigenvalue (λ_2) is large in a CCA constrained for an environmental variable (HALL and SMOL 1992). Analyses constrained by conductivity ($\lambda_1/\lambda_2 = 0.61$), pH ($\lambda_1/\lambda_2 = 0.57$), and TP ($\lambda_1/\lambda_2 = 0.54$) yielded ratios that suggested the potential for developing a model. Thus, diatom inference models were constructed for each of these three variables using weighted-averaging (WA).

Considering both RMSEP and coefficients of determination (r^2) between measured and inferred values of the environmental variables, WA with tolerance down-weighting and classical de-shrinking procedure performed best in the construction of conductivity, pH and TP models. The inference models for conductivity, pH and TP had RMSEP/r^2 values of 0.199/0.80, 0.021/0.74 0.291/0.71, respectively. The WA estimated optima of conductivity, pH and TP for the 61 most common diatom taxa are listed in table 3 together with the number of occurrences.

Diatom indices

The TDI values for the Lake Ladoga tributaries data set ranged from 16.3 to 89.4 on a scale of 1 (oligotrophic) to 100 (eutrophic). The index values were not significantly related to TP ($r = 0.16$, $p > 0.05$). The TID values ranged from 3.2 to 15.5 on a scale of 1 (eutrophic) to 20 (oligotrophic). Values for the TID were significantly related to TP ($r = -0.47$, $p < 0.001$), but the coefficient of determination value ($r^2 = 0.22$) indicated that only a relatively small amount of the variance in the relationship was explained.

Tab. 3. Code, the number of occurrences (n) (of 135 samples) and optima values for electric conductivity (EC, μS cm^{-1}), pH, and total phosphorus (TP, μg L^{-1}) of 61 most common diatom taxa in the Lake Ladoga rivers.

Code	Taxon	n	EC	pH	TP
ADM	*Achnanthidium minutissimum* (Kütz.) Czarn.	80	72	7.1	35
AOV	*Amphora ovalis* (Kütz.) Kütz.	10	242	7.9	46
CPE	*Cocconeis placentula* var. *euglypta* (Ehrenb.) Grun.	72	124	7.5	52
CCI	*Cymbella cistula* (Ehrenb.) Kirchn.	4	64	7.1	71
CTU	*Cymbella tumida* (Breb. ex Kütz.) V. H.	11	58	6.9	60
DMO	*Diatoma moniliformis* Kütz.	8	83	7.0	30
DTE	*Diatoma tenuis* Ag.	14	123	7.1	37
DVU	*Diatoma vulgaris* Bory	21	107	7.4	35
ENM	*Encyonema minutum* (Hilse) D.G. Mann	69	74	7.2	14
ENS	*Encyonema silesiacum* (Bleisch) D.G. Mann	25	100	7.3	72
EBI	*Eunotia bilunaris* (Ehrenb.) Mills	35	51	6.9	74
EEX	*Eunotia exigua* (Breb. ex Kütz.) Rabenh.	14	48	6.8	104
EIN	*Eunotia incisa* W. Smith ex Greg.	32	47	6.7	52
EPU	*Eunotia pectinalis* var. *undulata* (Ralfs) Rabenh.	14	53	6.9	24
EPR	*Eunotia praerupta* Ehrenb.	12	63	6.8	159
ETE	*Eunotia tenella* (Grun.) Cleve	30	50	6.9	20
EVE	*Eunotia veneris* (Kütz.) De Toni	7	69	6.8	28
FCR	*Fragilaria capucina* var. *rumpens* (Kütz.) Lange-B.	100	57	6.9	30
FCV	*Fragilaria capucina* var. *vaucheriae* (Kütz.) Lange-B.	25	81	7.1	48
FUA	*Fragilaria ulna* (Nitz.) Lange-B. var. *acus* (Kütz.) Lange-B.	6	72	7.2	23

Tab. 3. – continued

Code	Taxon	n	EC	pH	TP
FFV	*Fragilariforma virescens* (Ralfs) Williams et Round	6	34	6.6	28
FSA	*Frustulia saxonica* Rabenh.	20	64	6.9	105
FVU	*Frustulia vulgaris* (Thwaites) De Toni	17	119	7.3	122
GAC	*Gomphonema acuminatum* Ehrenb.	21	50	6.8	36
GAN	*Gomphonema angustatum* (Kütz.) Rabenh.	15	117	7.2	71
GOL	*Gomphonema olivaceum* (Hornemann) Breb.	22	101	7.2	49
GPA	*Gomphonema parvulum* (Kütz.) Kütz.	110	70	7.0	67
GTR	*Gomphonema truncatum* Ehrenb.	29	94	7.4	33
GYA	*Gyrosigma acuminatum* (Kütz.) Rabenh.	13	84	7.2	79
HCA	*Hippodonta capitata* (Ehr.) Lange-B., Metzeltin et Witkowski	13	127	7.4	43
MUN	*Melosira undulata* (Ehrenb.) Kütz.	5	158	7.7	34
MVA	*Melosira varians* Ag.	62	77	7.1	68
MCI	*Meridion circulare* (Grev.) Ag.	35	48	6.8	51
NCP	*Navicula capitatoradiata* Germain	13	203	7.3	189
NCR	*Navicula cryptocephala* Kütz.	103	72	7.1	50
NME	*Navicula menisculus* Schum.	7	93	7.4	16
NRA	*Navicula radiosa* Kütz.	33	76	7.1	41
NRH	*Navicula rhynchocephala* Kütz.	55	67	7.1	42
NTP	*Navicula tripunctata* (O.F. Müll.) Bory	11	196	7.6	71
NVI	*Navicula viridula* (Kütz.) Ehrenb.	14	92	7.2	47
NVR	*Navicula viridula* var. *rostellata* (Kütz.) Cleve	11	82	7.0	81
NAN	*Nitzschia angustata* (W. Smith) Grun.	3	362	8.1	102
NDI	*Nitzschia dissipata* (Kütz.) Grun.	20	87	7.2	34
NLI	*Nitzschia linearis* (Ag.) W. Smith	10	116	7.3	52
NPA	*Nitzschia palea* (Kütz.) W. Smith	40	75	7.0	71
PGI	*Pinnularia gibba* (Ehrenb.) Ehrenb.	15	91	7.0	91
PIN	*Pinnularia interrupta* W. Smith	11	35	6.7	20
PMA	*Pinnularia major* (Kütz.) Rabenh.	5	59	7.1	112
PSC	*Pinnularia subcapitata* Greg.	14	103	7.0	162
PVI	*Pinnularia viridis* (Nitz.) Ehrenb.	4	124	7.2	41
PEL	*Placoneis elginensis* (Greg.) E.J. Cox	11	103	7.4	115
PTL	*Planothidium lanceolatum* (Breb. ex Kütz.) Lange-B.	47	106	7.2	64
PBI	*Psammothidium bioretii* (Germain) Bukhtiyarova et Round	7	57	7.1	28
RAB	*Rhoicosphenia abbreviata* (Ag.) Lange-B.	12	261	7.8	237
SPU	*Sellaphora pupula* (Kütz.) Meresck.	12	150	7.1	168
SPI	*Staurosirella pinnata* (Ehrenb.) Williams et Round	27	137	7.4	32
SAN	*Surirella angusta* Kütz.	15	106	7.2	55
SBI	*Surirella biseriata* Breb. et Godey	7	66	7.0	88
TFE	*Tabellaria fenestrata* (Lyngb.) Kütz.	41	60	7.0	70
TFL	*Tabellaria flocculosa* (Roth) Kütz.	56	37	6.7	32
UUL	*Ulnaria ulna* (Nitz.) Compère	86	82	7.2	51

Discussion

In our study, two main groups of rivers were identified. They reflected the two geomorphological regions of the Lake Ladoga basin, which are characterized by granitoid crystalline rocks in the northern sub-basin and carbonaceous sedimentary rocks in the southern sub-basin and corresponding differences in hydrochemistry. In the northern sub-basin, crystalline rocks with low buffering capacity led to slightly acidic rivers, whereas in the southern sub-basin, carbonaceous sedimentary rocks led to neutral to slightly alkaline waters. This was reflected by differences in diatom assemblages with acidophilus taxa occurring in the north and alkaliphilous taxa in the south. Misclassified rivers such as the Morje and Khiitolan indicate that local features of river catchments can influence hydrochemistry and distribution pattern of the diatom assemblages. For example, the southern river Morje had a high percentage of wetlands in its catchment and a significantly lower pH than the mean pH of the southern sub-basin rivers. It was also characterized by acidophilous diatom assemblages similar to those in the northern sub-basin.

Ordination showed that electric conductivity was the most important factor for diatom assemblages of rivers in the Lake Ladoga basin, similar to findings in other studies on periphytic diatom assemblages (SOININEN 2007, SOININEN et al. 2004). POTAPOVA and CHARLES (2003) showed that conductivity and major ions (including bicarbonate) explained a significant amount of the variation in assemblage composition of benthic diatoms in US rivers. Conductivity reflects watershed processes such as bedrock weathering and consequent dissolution of chemical constituents as well as nutrient enrichment due to agricultural land use (BIGGS 1995).

Phosphorus was the second most important factor. If there are large regional differences between watersheds in dominant rock type, environmental variables reflecting geology such as conductivity, alkalinity and pH may be more important determinants of periphytic diatom assemblages than variables reflecting trophic status such as nutrient concentrations (LELAND 1995, RIMET et al. 2004). Furthermore, at regional spatial scales changes in conductivity may also be related to trophic status, reflecting changes in land use across different regions (DENICOLA et al. 2004). Both geology and land use were important in our study. The southern sub-basin is characterized by more intensive agricultural land use than the northern sub-basin (RASPLETINA 1982). This was evident from a marked shift in dominant diatom taxa between the sub-basins. Diatom assemblages of the southern sub-basin were dominated by taxa typical of meso-eutrophic and eutrophic conditions such as *Cocconeis placentula* var. *euglypta*, *Ulnaria ulna* and *Gomphonema parvulum* (according to VAN DAM et al. 1994). In contrast, diatom assemblages of the northern sub-basin were dominated by *Tabellaria flocculosa* and *Fragilaria capucina* var. *rumpens*, indicating oligo--mesotrophic waters (VAN DAM et al. 1994).

The WA model for TP provided good estimates of measured TP, accurate within ±1.9 μg L^{-1}, with a predictive ability (apparent $r^2 = 0.71$) similar to other studies (c. 0.6–0.8, LELAND and PORTER 2000, WINTER and DUTHIE 2000, DENICOLA et al. 2004). Optima for TP ranged from 14 μg L^{-1} for *Encyonema minutum* to 237 μg L^{-1} for *Rhoicosphenia abbreviata*. Taxa indicative of eutrophic conditions including *Gomphonema parvulum*, *Navicula capitatoradiata*, *Sellaphora pupula*, *Placoneis elginensis*, and *Nitzschia palea* and those typical of low TP concentration such as *Eunotia tenella*, *E. pectinalis* var. *undulata*, *Fragilaria capucina* var. *rumpens*, and *Tabellaria flocculosa* corresponded to classifications by VAN DAM et al. (1994). The calculated optima for several species were different from data suggested in the literature. For example, *Frustulia saxonica* and *Eunotia praerupta* listed as oligotrophic species in VAN DAM et al. (1994) appeared in rivers with high total phosphorus concentrations. These rivers were also rich in humic substances. It is possible that phosphorus was bound by humic acids and therefore not freely available for algae (JONES et al. 1988, MEILI 1992).

Values for two diatom indices TDI and TID calculated in this study were poor indicators of trophic state. Weak relationships between diatom index values and phosphorus concentrations in the studied rivers as well as the observed differences in species responses to nutrient enrichment show the need to develop a regional method for the assessment of river trophic status. The autecological data provided by this study can be used for the development of such a biomonitoring tool for the rivers in the Lake Ladoga basin.

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