Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients

Janne Soininen, Riku Paavola and Timo Muotka

Soininen, J., Paavola, R. and Muotka, T. 2004. Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients. – Ecography 27: 330–342.

An important goal for community ecology is the characterization and prediction of changes in community patterns along environmental gradients. We aimed to identify the major environmental correlates of diatom distribution patterns in boreal running waters. We classified 197 stream sites based on their diatom flora. Direct ordination methods were then used to identify the key environmental determinants of this diatom-based stream typology. Finally, we tested whether a regional classification scheme based on terrestrial landscapes (ecoregions) provides a reasonable framework for a regional grouping of streams based on their diatom flora. Two-way indicator species analysis produced 13 site groups, which were primarily separated by chemical variables, mainly conductivity, total P and water colour. In partial CCA, the environmental and spatial factors accounted for 38% and 24%, respectively, of explained variation in community composition. A high proportion (almost 40%) of variation explained by the combined effect (spatially-structured environmental) indicated that diatom communities of boreal streams incorporate a strong spatial component. At the level of subecoregions, classification strength was almost equally strong for all sites as for near-pristine reference sites only. Procrustes analysis indicated that spatial factors and patterns in diatom community structure were strongly concordant. Our data support the argument that diatom communities are strongly spatially structured, with distinctly different communities in different parts of the country. Because of the strong spatial patterns of community composition, bioassessment programs utilising lotic diatoms would clearly benefit from regional stratification. A combination of regional stratification and the prediction of assemblage structure from local environmental features might provide the most robust framework for diatom-based assessment of the biological integrity of boreal streams.

J. Soininen (janne.soininen@helsinki.fi), Dept of Biological and Environmental Sciences, P.O. Box 65, FIN-00014 Univ. of Helsinki, Finland. – R. Paavola, Dept of Zoology, Univ. of Toronto, Toronto, ON, Canada M5S 3G5. – T. Muotka, Finnish Environment Inst. Research Dept, P.O. Box 140, FIN-00251 Helsinki, Finland and Dept of Biology, Univ. of Oulu, P.O. Box 3000, FIN-90014 Univ. of Oulu, Finland.

An important goal for community ecology is to identify major patterns of community structure and to characterize and predict changes in those patterns in relation to environmental gradients. These goals can only be achieved through spatially-extensive sampling that allows ecologists to assess the relative importance of various environmental factors, often effective at different, yet partly overlapping, spatial and temporal scales.

Stream bioassessment programs typically use local environmental variables to predict the composition of biotic communities (the RIVPACS approach and its many variants; e.g. Marchant et al. 1997, Wright et al.

1998, Reynoldson et al. 2001). However, when viewed across large areas, stream communities frequently exhibit strong spatially-structured variation (Li et al. 2001, Heino et al. 2003, Parsons et al. 2003). Therefore it is important that the relative roles of local, in-stream variables vs large-scale spatial factors be reliably identified. If such spatial structuring proves to be a rule rather than an exception, it may be that stream assessment programs need to be based on a priori regional delineations. Ecoregions provide a reasonable starting point for such spatial stratification, but because of their generally non-aquatic conception (e.g. climate, geology, vegetation cover, land use, etc.), they need to be rigorously tested before being accepted as an appropriate level of spatial resolution for long-term biomonitoring of freshwater communities.

Ecoregion-level differences in freshwater communities have been mainly studied with macroinvertebrates (e.g. Johnson 2000, Hawkins and Vinson 2000, Sandin and Johnson 2000, Heino et al. 2002) and fish (Van Sickle and Hughes 2000, McCormick et al. 2000, Oswood et al. 2000). Studies of benthic algae are rare, and they have shown rather subtle regional patterns in algal community structure (Whittier et al. 1988, Pan et al. 1999, 2000; but see Potapova and Charles 2002). In addition, some studies have shown stronger spatial patterns among near-pristine sites than randomly-selected sites (Pan et al. 2000). In boreal areas, riverine diatoms have been used to assess stream water quality (e.g. Eloranta and Andersson 1998, Eloranta and Soininen 2002), but even the basic knowledge of diatom distribution patterns in boreal streams is still scarce.

Running waters in Finland typically are rather low in conductivity and high in humic content. Nevertheless, pristine or near-pristine streams in Finland exhibit distinct geographical patterns in their physicochemical characteristics, especially north-to-south, that parallels regional trends in geology, soil type, topography, land use, and potential natural vegetation (Heino et al. 2002). Many rivers in the southernmost, densely populated parts of the country are affected by nutrient loading from diffuse sources (Puomio et al. 1999).

The purpose of this study was to identify the major environmental correlates of diatom distribution patterns in these boreal running waters. We classified our sampling sites based on their diatom flora. Then, direct ordination methods were used to identify the key environmental determinants for this diatom-based stream classification. We also examined the proportions of variation in diatom community structure explained by environmental and spatial variation alone, and by their interaction. Finally, we tested whether a regional classification scheme based on terrestrial landscapes provides a reasonable framework for a corresponding regional variation of streams according to their benthic diatom assemblages. In particular, we tested whether ecoregional differences in diatom community structure, if any, were more evident in near-pristine streams than in variously impacted streams.

Material and methods

Ecoregional delineations

Ecoregions were defined using the delineations of Alalammi and Karlson (1988) based on climate, relief, vegetation, and land use. Our diatom material represented all five ecoregions of Finland, i.e. hemiboreal, south boreal, middle boreal, north boreal, and arctic-alpine ecoregions (Fig. 1). Since some of the ecoregions span large areas known to differ in many features important for freshwater biota (Heino et al. 2002), we further stratified our data according to subecoregion, based on major drainage systems and regional landscape characteristics within each ecoregion, mainly following Alalammi and Karlson (1988). Hemiboreal and arctic-alpine ecoregions were not stratified further, because they both cover a minor part of the country (southern and southwestern coastal areas, and northernmost Lapland, respectively; see Fig. 1) and therefore exhibit little within-region environmental variability. Also, due to insufficient number of sites, we could not divide diatom data from the north boreal ecoregion any further, although, considering the relatively large are spanned by these sites (Fig. 1), such stratification might have been desirable. Thus, at the level of subecoregions, we had eight regions: hemiboreal, south boreal (south) and south boreal (north), mid boreal (south), mid boreal (west), mid boreal (east), north boreal, and arctic-alpine regions (Fig. 1).

Hemiboreal ecoregion (HB) is restricted to the southern and southwestern coastal areas of Finland. Forests are primarily mixed, but deciduous forests are also rather typical in this region. South boreal ecoregion (SB) encompasses most of southern and southeastern Finland. The ecoregion is characterized by mixed and coniferous forests. The southern subecoregion (SB-S) is located in the southern Finland and is characterized by agricultural land and mixed forests. The northern subecoregion (SB-N) is located in the Finnish lake district and the catchments are dominated by coniferous forests. Middle boreal ecoregion (MB) encompasses the central parts of Finland. Vegetation is mainly a mixture of coniferous forests and peatlands. The southern subecoregion (MB-S) encompasses mainly lowlands dominated by agriculture. The eastern subecoregion (MB-E) is composed of peatland areas and forests dominated by spruce and pine. The northern subecoregion (MB-N) is mainly lowlands covered by mixed and coniferous forests and extensive peatlands. North boreal ecoregion (NB) encompasses most of Lapland, as well as eastern parts of northern Finland. Vegetation is mainly a

mixture of coniferous forests and peatlands. Mountain birch stands and treeless fields are typical features of the vegetation in the Arctic-Alpine ecoregion (AA) at the northernmost part of Lapland. This ecoregion is part of the Scandinavian mountain range, with altitudes ranging between 500 and 1300 m a.s.l. For a more detailed description of the characteristics of the ecoregions and subecoregions, see Heino et al. (2002).

Data collection

Diatom sampling was performed between 1996 and 2001 at 141 stations encompassing all the five ecoregions of Finland (see Fig. 1). The sampled sites were 20–30 m long, relatively homogeneous riffle sections and they were chosen to cover long gradients in conductivity, pH, humus, and nutrient concentrations (see Table 1). Most of the sites are described in more detail by Soininen (2002) and Soininen and Niemelä (2002). Diatoms were sampled by brushing stones with a toothbrush, following Kelly et al. (1998). At least five, pebble-to-cobble (5–15 cm) sized stones were brushed and the resulting diatom suspensions were put in a small plastic bottle. The samples were preserved in ethanol. Sampling was conducted during low flow conditions in June–August.

We also included a set of 56 sites sampled by Eloranta (1995; see also Eloranta and Kwandrans 1996). These
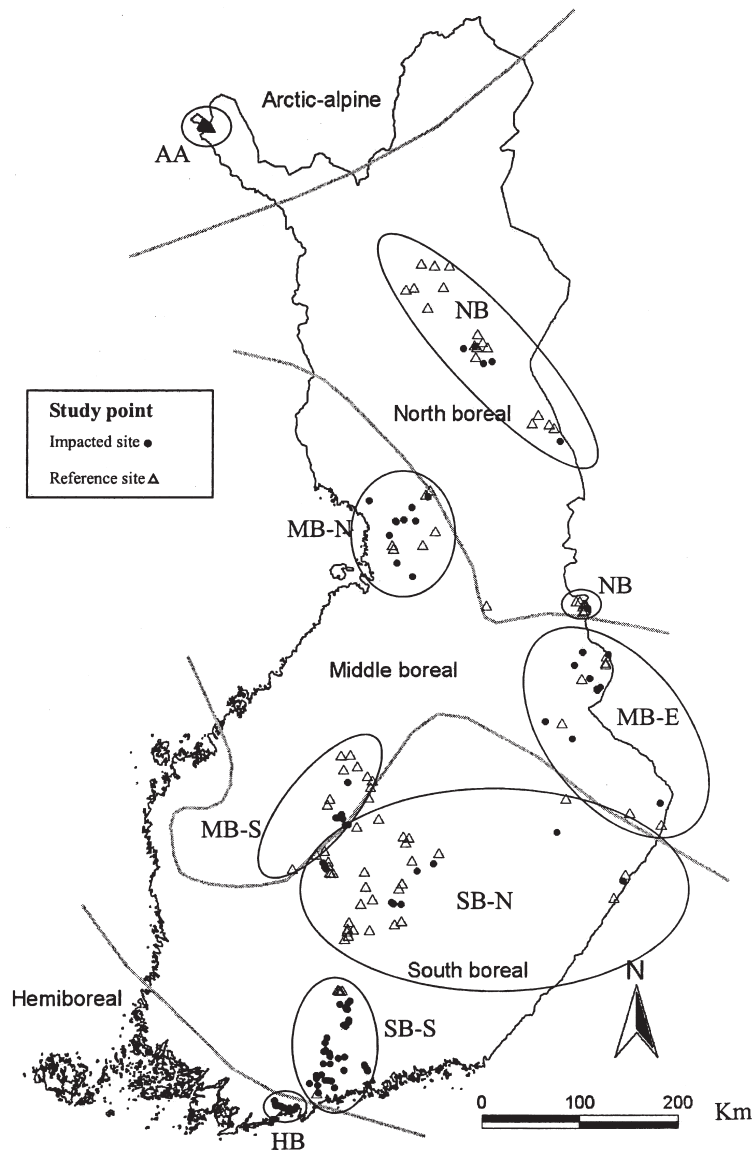

Fig. 1. Map of Finland showing the locations of the sampling sites within the five ecoregions of Finland. Middle boreal and south boreal ecoregions are further divided into subecoregions. Ecoregions and subecoregions were delineated according to Alalammi and Karlson (1988). Abbreviations: AA = Arctic-alpine, NB = north boreal, MB-N = middle boreal northern, MB-E = middle boreal eastern, MB-S = middle boreal southern, SB-N = south boreal northern, SB-S = south boreal southern, HB = hemiboreal.

Table 1. Means and ranges for the environmental variables in each TWINSPAN group (A–M).

	Colour mg l^{-1} Pt	pH	Total P µg l^{-1}	Conductivity mS m^{-1}	Shading %	Width m	Current velocity cm s^{-1}
A	200 (60–400)	5.7 (4.5–6.6)	19 (4–35)	2.3 (0.9–4.8)	46 (11–74)	9 (2–50)	34 (10–71)
B	115 (80–180)	6.3 (5.3–6.9)	27 (7–140)	2.9 (1.6–9.5)	27 (1–66)	7 (2–21)	30 (10–64)
C	90 (15–230)	6.5 (5.6–7.0)	22 (4–100)	4.3 (2.3–9.7)	54 (20–100)	6 (2–30)	81 (10–167)
D	115 (35–350)	6.5 (4.5–7.2)	28 (10–62)	3.9 (2.5–5.9)	48 (20–100)	12 (2–30)	85 (38–174)
E	170 (80–240)	6.6 (4.5–7.2)	36 (14–95)	3.8 (2.5–8.9)	5 (0–30)	62 (5–90)	26 (7–83)
F	75 (20–200)	7.4 (6.6–8.1)	17 (2–71)	8.4 (3.7–16.1)	20 (0–59)	8 (2–20)	38 (16–69)
G	45 (10–80)	7.3 (6.6–8.2)	15 (2–27)	8.5 (4.5–20.4)	32 (10–60)	16 (3–40)	74 (10–190)
H	15 (10–20)	7.0 (6.8–7.4)	7 (2–18)	3.4 (1.6–15.6)	0	1.5 (1.5–1.5)	70 (70–70)
I	130 (50–250)	7.1 (6.8–7.3)	101 (72–170)	14.4 (10.9–17.6)	20 (0–50)	10 (5–15)	36 (30–50)
J	80 (60–110)	7.0 (6.8–7.5)	87 (49–150)	19.7 (10.1–32.6)	25 (0–80)	11 (5–15)	32 (20–50)
K	90 (5–160)	7.3 (6.9–7.7)	77 (18–190)	24.4 (11.2–36.0)	38 (0–70)	4 (0.5–15)	33 (0–80)
L	95 (00–140)	7.1 (6.9–7.4)	46 (26–85)	24.0 (20.8–27.2)	47 (30–70)	5 (3–7)	29 (0–70)
M	75 (55–100)	7.0 (6.8–7.1)	30 (18–48)	11.6 (7.1–15.4)	24 (0–50)	9 (4–20)	46 (30–150)

stations are located in fast-flowing rivers in central Finland (i.e., south boreal ecoregion) and were sampled in 1986. These sites were included, because most represent near-pristine conditions, being only slightly affected by agriculture and fish farming. Furthermore, recent visits to these sites verified they (stream channel +riparian zone) had not been modified to any noticeable degree between 1986 and 1996. Therefore, we consider these samples to be comparable with the rest of the material, especially because they were sampled using the same methods as in all other samples.

Sampling stations were classified into reference sites (near-pristine or, especially in southern Finland, least-impacted streams) and impacted sites. We considered reference sites as those where the level of catchment disturbance (mainly forestry or agriculture) was < 10%, and the integrity of the riparian zone (% human disturbance in the water-riparian ecotone, assessed in situ) was > 80%.

At most of the sites, water samples were taken simultaneously with diatom samples (see Soininen (2002) and Soininen and Niemelä (2002) for details). They were analysed for water colour, conductivity, pH, and total phosphorus using national standards. For some of the sites (ca 20%), water chemistry data were taken from the national water quality database, using results from the nearest sampling occasion. Current velocity, shading by the riparian canopy, and stream width were also measured at each site along transects (n = five per site) perpendicular to the flow and covering the whole study section. Diatom samples were cleaned from organic material in the laboratory using wet combustion with acid (HNO$_3$:H$_2$SO$_4$; 2:1) and mounted in Dirax or Naphrax. Two or three replicate slides were prepared for each sample. A total of 250–500 frustules per sample were identified and counted using phase contrast light microscopy (1000 ×). Species were identified according to Krammer and Lange-Bertalot (1986–1991) and Lange-Bertalot and Metzeltin (1996).

Data analysis

Diatom taxa occurring in at least three samples, with a relative proportion of 1% or more in at least one sample were included in the statistical analyses. Thus, a total of 212 diatom taxa and on average 90.6% (min 64.9%, max 99.5%) of the counted cells were included in data analyses.

We used two-way indicator species analysis (TWIN-SPAN) to define diatom assemblage types. Then, we tested the significance of between-group differences at each TWINSPAN division with multi-response permutation procedure (MRPP). MRPP is a non-parametric method testing for differences in assemblage structure among a priori defined groups (Zimmerman et al. 1985). The Sorensen coefficient on log(x+1) abundance data was used as the distance measure in MRPP. The significance of the null hypothesis that there was no difference among the TWINSPAN groups was tested with a Monte Carlo randomization procedure with 10 000 permutations.

We used the indicator value method (IndVal) (Dufrene and Legendre 1997) to identify species discriminating among the TWINSPAN groups. The indicator value of a taxon varies from 0 to 100, and it attains its maximum value when all individuals of a taxon occur at all sites of a single group. The method thus selects indicator species based on both high specificity for and high fidelity to a specific group. IndVal is considered superior to more traditional methods of identifying indicators (e.g. TWINSPAN) on both statistical and practical grounds (Legendre and Legendre 1998, McGeoch and Chown 1998). For example, it is robust to differences in within-group sample sizes and abundances across species. The significance of the indicator value for each species was tested with a Monte Carlo randomization procedure with 1000 permutations.

All analyses were conducted with log-transformed ln(x+1) abundance data, except IndVal which uses untransformed abundances. For TWINSPAN, we used

five pseudospecies cut levels and five as the minimum group size. TWINSPAN, MRPP, and IndVal were run using PC-Ord (McCune and Mefford 1999).

We used canonical correspondence analysis (CCA) to examine the distribution of the diatom assemblage types defined by TWINSPAN along the major environmental gradients. We used forward selection of environmental variables. At each step, only variables significantly ($p < 0.05$; Monte Carlo randomization test with 100 permutations) related to assemblage structure were included in the model. CCA was run using CANOCO ver. 4.0 (ter Braak and Smilauer 1998).

We ran partial CCA (see Borcard et al. 1992, Økland and Eilertsen 1994) to partition variation in species data into three components: 1) pure environmental (fraction of species variation explained by the physical and chemical factors independently of any spatial structure), 2) pure spatial (fraction of variation explained by the spatial factors independently of any environmental factors), and 3) spatially structured environmental (fraction jointly explained by the two groups of variables). We first performed a Principal Component Analysis (PCA) on correlation matrix of the environmental variables to reduce the dimensionality of the original data into a few easily interpretable principal components (i.e. environmental gradients). By accepting only the three first components for subsequent analysis, we ensured that the dimensionality of the environmental data matched closely that of the spatial data (represented by longitude and latitude of the study sites). Roughly similar numbers of environmental variables in different groups of explanatory variables are considered beneficial for variation partitioning in CCA (Borcard et al. 1992). Because the use of unexplained variation in pCCA has been questioned (Økland 1999), we concentrated on the relative amounts of variation explained by the two sets of explanatory variables.

The classification strength (CS) of ecoregions and subecoregions was tested using the randomization protocol of Van Sickle and Hughes (2000). The mean of all between-class similarities (B) and the within-class mean similarity (W) were first calculated using Sorensen similarity coefficient. CS is defined as the difference between these similarities ($CS = W - B$). Values of this measure range from 0 to 1, with those near zero indicating that sites are randomly assigned to classes. The observed values of CS were compared to permuted values, obtained through 1000 random reassignments of sites to groups. Such permutation tests, however, are known to be too powerful (i.e. even very small differences between observed and expected values of CS are statistically significant, if sample size is moderately large). We therefore followed the recommendation of Van Sickle and Hughes (2000) to place more emphasis on comparisons of the relative magnitude of CS statistic than on the p-values from the randomization tests.
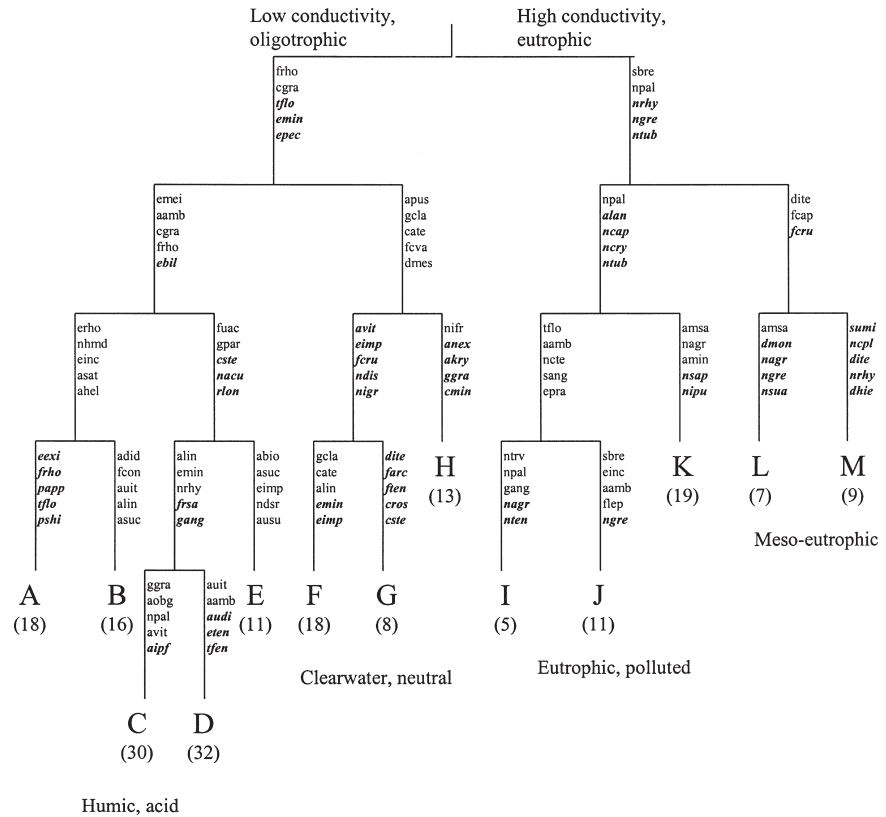
We first tested the classification strength of ecoregions. Because many of our sites were located close to ecoregion boundaries, and such transitional regions may have intermediate biota (Hughes and Larsen 1988), we recalculated these statistics with "purified" ecoregions, removing all sites within < 25 km from the closest ecoregion boundary. Next, we tested the strength of classification at the subecoregion level, separately for data containing only reference sites (n = 99 streams) or the combined data. We then compared the performance of subecoregions to that of a biological classification produced by TWINSPAN. In this comparison, the number of groups was eight in both classifications.

Finally, we tested whether the proximity of sites in a biological classification could be explained by mere spatial distance between the sampling sites. This is, does site similarity arise from spatial autocorrelation rather than from ecological similarity? We therefore tested the strength of congruence between the spatial coordinates (longitude and latitude) of the study sites and a biotic ordination (non-metric multidimensional scaling, NMDS). Stress value was used to determine the number of dimensions in NMDS. Stress is a measure of deviation from monotonicity in the relationship between distance in the original space and the reduced ordination space. The analysis was stopped when the stress value did not change appreciably with additional dimensions. To avoid the problem of local minima, we ran the NMDS analyses in an autopilot mode, letting the program choose the best solution (i.e. solution with the lowest stress value) from 100 separate runs of real data (McCune and Mefford 1999). Sorensen coefficient was used as the distance measure in all analyses. NMDS were run using PC-Ord (McCune and Mefford 1999). Procrustes analysis was used to investigate the degree of concordance among the two ordinations. The method used for Procrustean fitting is based on the least-squares criterion, which minimizes the sum of the squared residuals (m^2) between two configurations. The m^2 statistic is then used as a measure of association between the two ordinations (Digby and Kempton 1987), with low values of m^2 indicating strong concordance. ProTest extends Procrustes analysis by providing a permutation procedure to assess the statistical significance of the Procrustean fit (Jackson 1995). We used ProTest (with 9999 permutations) for a pairwise comparison between the spatial and the biotic (NMDS) ordination configurations.

Results

TWINSPAN produced 13 site groups (Fig. 2), and all groups were validated by MRPP (all $p < 0.0001$). The physical-chemical characteristics of the 13 TWINSPAN groups are presented in Table 1 and their geographical

Fig. 2. TWINSPAN classification of the study streams. Figures refer to the number of sites in each TWINSPAN group (A–M). Taxa in bold italics were identified as indicators only by the Indicator Value method (IndVal), while all others were identified by both TWINSPAN and IndVal. See Appendix 1 and Table 2 for species abbreviations.

Low conductivity, oligotrophic

High conductivity, eutrophic

frho cgra *tflo emin epec*

sbre npal *nrhy ngre ntub*

emei aamb cgra frho *ebil*

apus gcla cate fcva dmes

npal *alan ncap ncry ntub*

dite fcap *fcru*

erho nhmd einc asat ahel

fuac gpar *cste nacu rlon*

avit eimp fcru ndis nigr

nifr *anex akry ggra cmin*

tflo aamb ncte sang epra

amsa nagr amin *nsap nipu*

amsa *dmon nagr ngre nsua*

sumi ncpl dite nrhy dhie

eexi frho papp tflo pshi

adid fcon auit alin asuc

alin emin nrhy *frsa gang*

abio asuc eimp ndsr ausu

gcla cate alin *emin eimp*

dite farc ften cros cste

H (13)

ntrv npal gang *nagr nten*

sbre einc aamb flep *ngre*

K (19)

L (7)

M (9)

Meso-eutrophic

A (18)

B (16)

ggra aobg npal avit *aipf*

auit aamb *audi eten tfen*

E (11)

F (18)

G (8)

I (5)

J (11)

Clearwater, neutral

Eutrophic, polluted

C (30)

D (32)

Humic, acid

positions within Finland in Fig. 3. The most important indicator taxa for each group, with associated indicator values, are given in Table 2.

The first TWINSPAN division primarily separated oligotrophic, electrolyte-poor streams in central and northern Finland (groups A–H) from eutrophic southern Finnish streams (groups I–M). This division was mainly indicated by oligotrophic, acidophilic species (e.g. *Frustulia rhomboides* and *Tabellaria flocculosa*) and by epipelic taxa indicative of higher trophy and saprobity (e.g. *Nitzschia palea* and *Surirella brebissonii*) (see Van Dam et al. 1994). A further major division (level 2) in the left-hand branch of the TWINSPAN tree separated circumneutral, clear-water, oligotrophic streams (groups F–H, indicated by e.g. *Achnanthes pusilla*) from acid, humic rivers (groups A–E, indicated by e.g. *Eunotia meisteri*). The second division on the right-hand branch of the hierarchy separated mesotrophic rivers (groups L–M, indicated by e.g. *Diatoma tenuis*) from eutrophic, polluted rivers (groups I–K, indicated by e.g. *Nitzschia palea*).

Group A contained polyhumic, acid streams originating mainly from eastern Finland. These streams were characterized by species of the genus *Eunotia*. This was a well-defined group with a high number of significant indicator taxa. Group B consisted of oligotrophic streams with higher pH and lower humic content than the group A streams. The most important species characterizing this group indicate oligotrophic, circumneutral waters (e.g. *Fragilaria construens* and *Gomphonema exilissimum*) (see Krammer and Lange-Bertalot 1986–1991, Van Dam et al. 1994). These are woodland streams located in eastern Finland. Sites of the two largest groups, C (n = 30 streams) and D (n = 32 streams), were slightly acid, humic rivers with low conductivity, and they primarily originate from the south boreal ecoregion in central Finland. Most of the group D streams were short riffles connecting adjacent lakes, whereas group C mainly consisted of small forest streams. Not surprisingly, many of the best indicators for group D were planktonic taxa (e.g. *Aulacoseira italica* and *Rhizosolenia longiseta*). Group E consisted of rivers with mesotrophic, circumneutral, and humic conditions in the northern parts of the middle boreal ecoregion. *Achnanthes bioretii*, *Aulacoseira subarctica*, and *Navicula densestriata* were strong indicators of these rivers.

Groups F (north boreal ecoregion) and H (arctic-alpine ecoregion) contained circumneutral, clear-water, oligotrophic streams. Especially streams in Finnish

Lapland (group H) had very distinctive diatom communities, due probably to the rather extreme subarctic conditions prevailing in these streams. The number of significant indicators in group H (20) was highest among all TWINSPAN groups. Group G was composed of a few clear-water, slightly alkalic or circumneutral streams. This was a poorly-defined group with only three rather weak indicator species.

The smallest group I included tributaries of the eutrophic River Vantaanjoki in southernmost Finland. These streams resembled rather closely those in group J, which also mainly were from the River Vantaanjoki drainage system. Group J streams, however, contained many planktonic species (e.g. *Aulacoseira ambigua* and *Cyclotella meneghiniana*), indicating the influence of small lakes and ponds in these watercourses. The most important indicators of this division, especially *Navicula trivialis* and *Nitzschia palea*, are considered to indicate relatively high trophy and saprobity (Krammer and Lange-Bertalot 1986–1991, Van Dam et al. 1994). Group K was formed by several south-Finnish streams, most of which are impacted by treated sewage or diffuse loading from agriculture. These sites were characterised by motile, biraphid species (e.g. *Surirella brebissonii*). Group L was composed of headwater streams on the southern coast of Finland. These streams are influenced
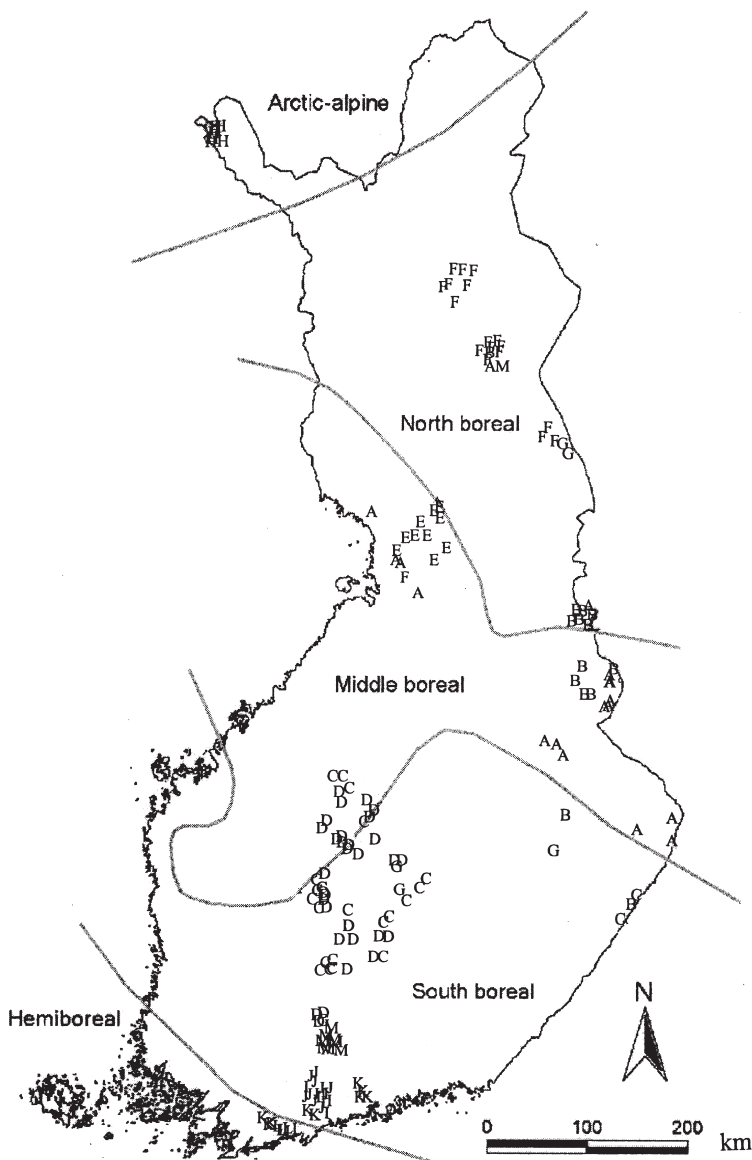

Fig. 3. Geographical position of the sampling sites within each TWINSPAN group. For clarity, locations of some of the sites have been slightly shifted.

Table 2. Indicator values (IndVal) for the three most important taxa in each TWINSPAN group. Monte Carlo tests based on 9999 permutations were used to assess the significance of each species as an indicator for the respective stream group. The total number of significant indicator species is also given for each group.

	Observed IndVal (%)													p
	A	B	C	D	E	F	G	H	I	J	K	L	M	
Eunotia rhomboidea. Hust. (erho)	65	9	0	0	0	0	0	0	0	0	0	0	0	0.0001
Eunotia exigua (Breb.) Rabenh. (eexi)	63	5	2	0	7	1	0	1	0	0	0	0	0	0.0002
Eunotia incisa Greg. (einc)	54	15	9	0	0	0	0	2	0	6	0	0	0	0.0003
Achnanthes didyma Hust. (adid)	5	58	0	0	0	1	0	1	1	0	0	0	0	0.0001
Fragilaria construens (Ehrenb.) Grun. (fcon)	5	49	2	6	3	4	4	1	2	0	1	0	1	0.0001
Gomphonema exilissimum (Grun.) Lange-Bertalot & Reich. (gex1)	2	51	58	0	7	1	0	1	0	0	0	0	0	0.0001
Gomphonema gragile Ebrenb. (ggra)	0	0	58	0	0	0	0	6	1	0	0	0	0	0.0001
Achnanthes linearis (W. Sm.) Grun. (alin)	4	28	28	10	7	8	0	0	1	0	0	1	0	0.0039
Fragilaria tenera (W. Sin.) Lange-Bertalot (ften)	0	0	30	8	0	0	5	0	2	0	1	0	3	0.0088
Aulacoseira italica (Ehrenb.) Simons. (auit)	0	9	2	51	0	0	0	0	0	0	0	0	0	0.0025
Rhizosolenia longiseta Zach. (rlon)	0	0	4	34	0	0	0	0	0	0	0	0	0	0.0035
Fragilaria intermedia Grun. (fint)	0	0	6	26	0	0	1	0	0	0	0	0	0	0.0001
Achnanthes bioretii Germ. (abio)	0	0	1	0	83	0	1	0	0	0	0	0	0	0.0001
Aulacoseira subarctica (O. Mueller) Haw. (ausu)	0	0	0	0	64	0	0	0	0	0	0	0	0	0.0001
Navicula densestriata Hust. (ndsr)	0	0	0	0	73	0	0	0	0	0	0	0	0	0.0001
Caloneis tenuis Krammer (Greg.) (cate)	0	1	0	0	0	52	0	22	0	0	0	0	0	0.0001
Gomphonema clavatum Ehrenb. (gcla)	0	8	3	1	0	60	1	11	0	0	0	0	0	0.0001
Amphipleura pellucida Kütz. (apel)	0	0	1	0	0	45	0	0	0	0	0	0	0	0.0002
Cyclotella rossii Håkans. (cros)	0	0	0	0	0	0	36	0	0	0	0	0	0	0.0017
Didymosphenia geminata (Lyngbye) W. M. Schmidt (dgem)	0	0	0	0	0	1	21	3	0	7	3	0	0	0.0217
Cymbella sinuata. Greg. (csin)	0	0	0	0	0	0	14	13	0	0	0	0	0	0.0474
Achnanthes kryophila Peters. (akry)	0	0	0	0	0	0	0	92	0	0	0	0	0	0.0001
Cymbella affinis Kütz. (caff)	0	0	0	0	0	3	0	69	0	0	0	0	0	0.0001
Eunotia arcus Ehrenb. (earc)	0	0	0	0	1	2	0	78	0	0	0	0	0	0.0001
Nitzschia palea (Kütz.) Smith (npal)	0	1	3	0	0	0	0	0	49	12	28	3	0	0.0001
Navicula trivialis Lange-Bertalot (ntrv)	0	0	0	0	1	0	0	0	92	1	1	0	0	0.0001
Nitzschia vermicularis (Kütz.) Hantzsch (nver)	0	2	0	0	0	0	0	0	45	13	0	0	0	0.0001
Aulacoseira ambigua (Grun.) Simons. (aamb)	0	2	1	15	8	0	0	0	7	46	0	0	0	0.0001
Fragilaria leptostauron (Ehr.) Hust. (flep)	0	0	0	0	0	1	0	0	0	57	0	0	0	0.0001
Cyclotella meneghiniana Kütz. (cmen)	0	0	1	0	0	0	0	0	8	37	10	2	10	0.0005
Navicula gregaria Donkin (ngre)	0	0	0	0	0	0	0	0	3	33	38	4	0	0.0007
Nitzschia pusilla (Kütz.) Grun. (nipu)	0	0	0	0	0	0	0	0	0	0	31	9	0	0.0008
Surirella brebissonii Krammer & Lange-Bertalot (sbre)	0	0	0	0	0	0	0	2	2	22	38	17	11	0.0018
Achnanthes minutissima (Kütz.) var. saprophila Kobayasi (amsa)	0	0	0	0	0	0	0	0	0	0	27	60	0	0.0001
Diatoma moniliformis Kütz. (dmon)	0	0	0	0	0	0	0	0	0	0	0	71	0	0.0001
Nitzschia subacicularis Hust. (nsua)	0	0	0	0	0	0	0	9	9	7	7	46	0	0.0001
Nitzschia capitellata Hust. (ncpl)	0	0	0	0	0	0	0	1	1	0	0	0	56	0.0001
Surirella minuta Breb. (sumi)	0	0	0	1	1	0	0	0	18	0	1	0	36	0.0002
Diatoma tenuis Agardh (dite)	0	0	1	1	1	0	27	1	0	0	0	4	39	0.0007
Number of significant indicator species	15	14	7	7	8	11	3	20	16	15	10	7	8	

by agriculture and were thus electrolyte-rich. *Diatoma moniliformis* was the most important indicator for this group. Finally, group M contained mainly south boreal streams slightly impacted by agriculture. The key indicator for this groups was *Nitzschia capitellata*, a species considered to indicate high trophy and saprobity (Van Dam et al. 1994).

The TWINSPAN-groups were rather well separated in the CCA space (Fig. 4). The eigenvalues of the first two CCA axes (0.435 and 0.227) were both significant (p < 0.01; Monte Carlo permutation test, 99 permutations), and they explained 10.2% of the total variation (6.469) in the species data. The diatom-environment correlations for CCA axis 1 (0.959) and 2 (0.926) were high, indicating a relatively strong relation between diatoms and the measured environmental variables. Conductivity, total P, pH, and latitude were the most significant contributors to axis 1. This axis mainly separated soft waters in central and northern Finland from the enriched, hard waters of the southern part of the country. Axis 2 primarily separated humic (or turbid) streams from clear-water streams, colour and pH being the most important variables along this axis.

In partial CCA with variation partitioning, the environmental (chemical and physical) factors accounted for 38% of explained variation in community composition, and the spatial component explained an additional 24% of the variation. Proportion of variation explained by the combined effect (spatially-structured environmental) was almost 40%, indicating that the diatom communities of boreal streams incorporate a strong spatial component.

The classification strength (CS) of ecoregions was 0.090, and it was only slightly improved by including only sites with at least 25 km to the nearest ecoregion boundary (CS = 0.107). At the level of subecoregions, CS was almost equally strong for all sites (CS = 0.107) than for reference sites only (CS = 0.123). Finally, CS for the biologically-defined TWINSPAN typology only slightly exceeded that of the subecoregions (0.127 vs 0.107). All CS values were stronger than expected by chance (randomisation test with 1000 permutations, all p < 0.001).

Spatial factors (latitude and longitude of the study sites) and patterns in diatom community structure (summarized by NMDS ordination axes) were strongly concordant ($m^2 = 0.862$, p = 0.001), implying that the diatom communities of boreal streams exhibit distinct spatially-structured variation.

Discussion

Although the number of significant TWINSPAN groups was rather high, we found meaningful ecological interpretations for most of them. The groups were primarily separated by chemical variables (mainly conductivity and water colour), yet physical factors also contributed to site classification. Most of the sites in each group were located within a restricted geographical area, demonstrating the tight relation between chemical and regional factors in Finnish streams (see also Heino et al. 2002). Our results are well in concert with previous work emphasizing the primacy of stream water nutrient concentrations and ionic composition in structuring benthic algal communities in running waters (Biggs 1990, Leland and Porter 2000, Griffith et al. 2002, Hirst et al. 2002).

Conductivity has frequently been identified as the key variable associated with periphytic, especially diatom, communities (Biggs 1990, 1995, Pan et al. 1999, Munn et al. 2002). Conductivity primarily indicates concentrations of cations (Ca, Mg) and is closely related to water pH. It also integrates several watershed processes, thus indicating the geological nature of the watershed (Munn et al. 2002). It has therefore been suggested as an easy and conservative surrogate for nutrient enrichment, because major ions are not intensively involved in biological processes, and relative fluctuations in conductivity are smaller than those for nutrients (Biggs 1990, 1995). Based on our data, conductivity is the strongest environmental gradient underlying diatom distribution patterns in Finnish running waters, followed by water colour, which was closely related to community patterns along the secondary axis of CCA. Water colour has also been identified as one of the main correlates of macroinvertebrate assemblage structure in boreal streams (Malmqvist and Mäki 1994, Heino et al. 2003). Similarly, in a study of diatom distributions in Labrador lakes, water colour emerged as one of the key
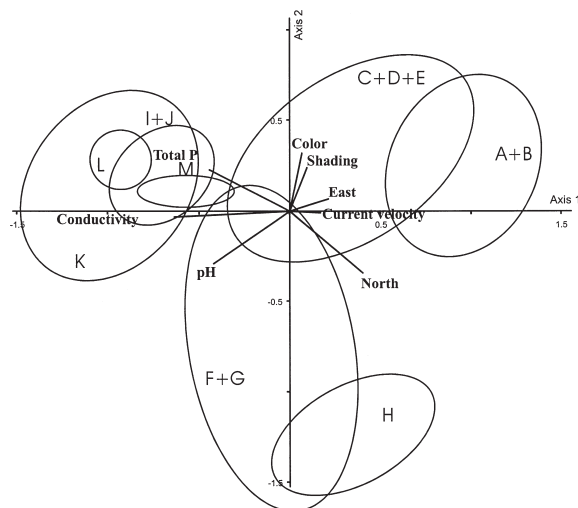
Fig. 4. Ordination diagram showing the distributions of the TWINSPAN site groups (denoted by capital letters) and relative contributions of environmental variables in the CCA space. Ellipses encircle 90% of sites belonging to a given group.

determinants of diatom communities, leading Fallu et al. (2002) to suggest that lake water colour should be generally important in explaining diatom distributions across broad geographic regions in electrolyte-poor, oligotrophic freshwater systems.

Benthic assemblages in streams are controlled by multiple factors prevailing at different temporal and spatial scales (Biggs 1995, Stevenson 1997). Benthic diatom communities are traditionally considered as being regulated more by local environmental conditions than by broad-scale climatic, vegetational, and geological factors (Pan et al. 1999, 2000). Leland et al. (2001), for example, argued that benthic algal assemblages are "extraordinarily similar over very large geographical areas", and that local factors related mainly to stream water chemistry predominate over regional ones in determining diatom species composition. On a more general level, it has been argued that the species composition of unicellular organisms is dominated by cosmopolitan species with a high dispersal ability. Therefore, local factors should be much more important than regional ones, setting a strong environmental filter (sensu Poff 1997) which selects species able to cope with the conditions prevailing at a site. Thus, communities of unicellular organisms should be characterized by a high local relative to regional and global richness (Finlay et al. 1996, Fenchel et al. 1997, Hillebrand and Azovsky 2001). Recently, however, this view has been challenged, and in a meta-analysis Hillebrand et al. (2000) found that although macroecological patterns documented for multicellular organisms may not translate directly to unicellular communities, there is no strict evidence showing that unicellular organisms exhibit higher relative local species richness than metazoans. For freshwater diatoms in particular, the concept of predominantly cosmopolitan distributions has been strongly criticized by Kociolek and Spaulding (2000); see also Mann and Droop 1996) who argued that a considerable proportion of diatoms are in fact endemic or at least show a regionally restricted distribution. They further claimed that in explanations of diatom distributions, more emphasis should be given to broad-scale historical factors than to explanations stressing the role of present-day dispersal capacity.

Clearly, our data support the view that diatom communities exhibit a strong spatial component, with distinctly different communities in different parts of Finland. This was unequivocally shown by a combination of multivariate methods, including a direct comparison of NMDS ordinations of diatom communities and spatial coordinates of the sampling sites. Furhermore, the proportion of variation explained independently by spatial factors was, although lower than the proportion explained by local factors, quite large (25%). Corresponding figures (23–31%) were reported by Potapova and Charles (2002) for both the whole USA and for

Omernik's level 1 ecoregions, whereas in level 2 ecoregions, the scale more closely matching that of our study, their figures were somewhat lower (15–22%).

Although many taxa in our data were truly cosmopolitan, some species exhibited regionally restricted distributions. For example, *Achnanthes biasolettiana*, *A. carissima*, *A. didyma* and *Cymbella affinis* had a distinctly northern distribution, whereas other species, e.g. *Navicula gregaria*, *N. reichardtiana*, *N. tenelloides* and *Surirella minuta*, occurred mainly or exclusively in southern, often slightly eutrophic streams. A similar latitudinal gradient has been previously described for stream macroinvertebrates (Sandin and Johnson 2000, Heino et al. 2002, Sandin 2003) and lake diatoms (Pienitz et al. 1995). This pattern of spatial variability may have been further accentuated by covariation of geographical location and water chemistry across the study area (see Heino et al. 2002). It may thus be that the turnover component of diversity (ß-diversity) of benthic diatoms is much higher than previously believed. Ultimately, however, this is linked to the level of taxonomy used: a "fine-grained" taxonomy which avoids the lumping of taxa with similar morphologies to one category, should lead to recognition of many more species with narrow geographical and ecological distributions (e.g. Potapova and Charles 2002), resulting in higher-than-expected levels of beta-diversity.

Given the strong latitudinal patterns in community composition, it seems evident that bioassessment programs utilising lotic diatoms would benefit from geographical stratification. For this purpose, the reference sites should be restricted to one geographical region to avoid that diatom response to anthropogenic impacts could be overridden by regional, large-scale trends in community structure. This is especially so because the patterns remained similar no matter whether we ran our analysis on reference or impacted streams. Nevertheless, since local in-stream factors were even more important than spatial factors in explaining diatom distributions (see also Potapova and Charles 2002), a combination of regional stratification and predictive modeling based on local (riparian and reach-scale) environmental features might provide the most robust framework for diatom-based bioassessment of boreal streams. Furthermore, the use of functional groups instead of species might alleviate some of the problems introduced by uncertain and variable taxonomy. This approach of aggregating biota into functional groups is consistent with the use of species traits, instead of taxonomic identities, for fishes or macroinvertebrates (Townsend and Hildrew 1994, Poff and Allan 1995), and it has been successfully applied also for benthic algae (Kutka and Richards 1996, Pan et al. 1999, Leland and Porter 2000).

Finally, the spatial patterns exhibited by benthic diatoms in this study corresponded fairly closely with those documented for stream macroinvertebrates by

Heino et al. (2002, 2003). This suggests that the bioassessment of boreal running waters should benefit from integrated monitoring of these two taxonomic groups. Due mainly to reasons based on tradition, macroinvertebrates have a leading role in stream bioassessment in northern Europe, as also in many other parts of the world. Yet, many recent studies have shown that community concordance, i.e. similarity in patterns of community structure among major organism groups, is often rather low in freshwater systems, especially at small (e.g. within-watershed) spatial scales (Allen et al. 1999a,b, Paavola et al. 2003). Therefore, it may be advisable and, ultimately, cost-effective to base stream biomonitoring on multiple taxonomic groups, e.g. macroinvertebrates and benthic diatoms.

References

Alalammi, P. and Karlson, K. P. 1988. Atlas of Finland, Folio 141–143. Biogeography and nature conservation. – National Board of Survey and Geographical Society of Finland.

Allen, A. P. et al. 1999a. Concordance of taxonomic richness patterns across multiple assemblages in lakes of the northeastern United States. – Can. J. Fish. Aquat. Sci. 56: 739–747.

Allen, A. P. et al. 1999b. Concordance of taxonomic composition patterns across multiple lake assemblages: effects of scale, body size, and land use. – Can. J. Fish. Aquat. Sci. 56: 2029–2040.

Biggs, B. J. F. 1990. Periphyton communities and their environments in New Zealand rivers. – N. Z. J. Mar. Freshw. Res. 24: 367–386.

Biggs, B. J. F. 1995. The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. – Freshwater Biol. 33: 419–438.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. – Ecology 73: 1045–1055.

Digby, P. G. N. and Kempton, R. A. 1987. Multivariate analysis of ecological communities. – Chapman and Hall.

Dufrene, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.

Eloranta, P. 1995. Type and quality of river waters in central Finland described using diatom indices. – In: Marino, D. and Montresor, M. (eds), Proc. of the 13th International Diatom Sympsium. Biopress, pp. 271–280.

Eloranta, P. and Andersson, K. 1998. Diatom indices in water quality monitoring of some South-Finnish rivers. – Verh. Int. Verein. Limnol. 26: 1213–1215.

Eloranta, P. and Kwandrans, J. 1996. Distribution and ecology of freshwater red algae (Rhodophyta) in some central Finnish rivers. – Nord. J. Bot. 16: 107–117.

Eloranta, P. and Soininen, J. 2002. Ecological status of some Finnish rivers evaluated using benthic diatom communities. – J. Appl. Phycol. 14: 1–7.

Fallu, M. A., Allaire, N. and Pienitz, R. 2002. Distribution of freshwater diatoms in 64 Labrador (Canada) lakes: species:environment relationships along latitudinal gradients and reconstruction models for water colour and alkalinity. – Can. J. Fish. Aquat. Sci. 59: 329–349.

Fenchel, T., Esteban, G. F. and Finlay, B. J. 1997. Local versus global diversity of microorganisms: cryptic diversity of ciliated protozoa. – Oikos 80: 220–225.

Finlay, B. J., Esteban, G. F. and Fenchel, T. 1996. Global diversity and body size. – Nature 383: 132–133.

Griffith, M. B. et al. 2002. Multivariate analysis of periphyton assemblages in relation to environmental gradients in Colorado Rocky Mountain streams. – J. Phycol. 38: 83–95.

Hawkins, C. P. and Vinson, M. R. 2000. Weak correspondence between landscape classifications and stream invertebrate assemblages: implications for bioassessment. – J. N. Am. Benthol. Soc. 19: 501–517.

Heino, J. et al. 2002. Correspondence between regional delineations and spatial patterns in macroinvertebrate assemblages of boreal headwater streams. – J. N. Am. Benthol. Soc. 21: 397–413.

Heino, J. et al. 2003. Defining macroinvertebrate assemblage types of headwater streams: implications for bioassessment and conservation. – Ecol. Appl. 13: 842–852.

Hillebrand, H. and Azovsky, A. 2001. Body size determines the strength of the latitudinal diversity gradient. – Ecography 24: 251–256.

Hillebrand, H. et al. 2000. Differences in species richness patterns between unicellular and multicellular organisms. – Oecologia 126: 114–124.

Hirst, H., Jüttner, I. and Ormerod, S. J. 2002. Comparing the responses of diatoms and macroinvertebrates to metals in upland streams of Wales and Cornwall. – Freshwater Biol. 47: 1752–1765.

Hughes, R. M. and Larsen, D. P. 1988. Ecoregions – an approach to surface-water protection. – J. Water Pollut. Con. F. 60: 486–493.

Jackson, D. A. 1995. PROTEST: A Procrustes Randomization TEST of community-environment concordance. – Ecoscience 2: 297–303.

Johnson, R. K. 2000. Spatial congruence between ecoregions and littoral macroinvertebrate assemblages. – J. N. Am. Benthol. Soc. 19: 468–475.

Kelly, M. G. et al. 1998. Recommendations for the routine sampling of diatoms for water quality assessments in Europe. – J. Appl. Phycol. 10: 215–224.

Kociolek, J. P. and Spaulding, A. A. 2000. Freshwater diatom biogeography. – Nova Hedw. 71: 223–241.

Krammer, K. and Lange-Bertalot, H. 1986–1991. Bacillariophyceae. Süßwasserflora von Mitteleuropa, 2 (1–4). – Fischer.

Kutka, F. J. and Richards, C. 1996. Relating diatom assemblage structure to stream habitat quality. – J. N. Am. Benthol. Soc. 15: 469–480.

Lange-Bertalot, H. and Metzeltin, D. 1996. Indicators of oligotrophy. 800 taxa repsesentative of three ecologically distinct lake types: carbonate buffered, oligodystrophic, weakly buffered soft water. – Iconographia Diatomologica Vol. 2.

Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier.

Leland, H. V. and Porter, S. D. 2000. Distribution of benthic algae in the upper Illinois River basin in relation to geology and land use. – Freshwater Biol. 44: 279–301.

Leland, H. V., Brown, L. R. and Mueller, D. K. 2001. Distribution of algae in the San Joaquin River, California, in relation to nutrient supply, salinity and other environmental factors. – Freshwater Biol. 46: 1139–1167.

Li, J. et al. 2001. Variability of stream macroinvertebrates at multiple spatial scales. – Freshwater Biol. 46: 87–97.

Malmqvist, B. and Mäki, M. 1994. Benthic macroinvertebrate assemblages in north Swedish streams: environmental relationships. – Ecography 17: 9–16.

Mann, D. G. and Droop, S. J. M. 1996. Biodiversity, biogeography and conservation of diatoms. – Hydrobiologia 336: 19–32.

Marchant, R. et al. 1997. Classification and prediction of macroinvertebrate assemblages from running waters in Victoria, Australia. – J. N. Am. Benthol. Soc. 16: 664–681.

McCormick, F. H., Peck, D. V. and Larsen, D. P. 2000. Comparison of geographic classification schemes for Mid-Atlantic stream fish assemblages. – J. N. Am. Benthol. Soc. 19: 385–404.

McCune, B. and Mefford, M. J. 1999. PC-ORD. Multivariate analysis of ecological data, ver. 4. – MjM Software Design.

McGeoch, M. and Chown, S. L. 1998. Scaling up the value of bioindicators. – Trends Ecol. Evol. 13: 46–47.

Munn, M. D., Black, R. W. and Gruber, S. J. 2002. Response of benthic algae to environmental gradients in an agriculturally dominated landscape. – J. N. Am. Benthol. Soc. 21: 221–237.

Økland, R. H. 1999. On the variation explained by ordination axes and constrained ordination axes. – J. Veg. Sci. 10: 131–136.

Økland, R. H. and Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. – J. Veg. Sci. 5: 117–126.

Oswood, M. W. et al. 2000. Distributions of freshwater fishes in ecoregions and hydroregions of Alaska. – J. N. Am. Benthol. Soc. 19: 405–418.

Paavola, R. et al. 2003. Are biological classifications of headwater streams concordant across multiple taxonomic groups? – Freshwater Biol. 48: 1912–1923.

Pan, Y. et al. 1999. Spatial patterns and ecological determinants of benthic algal assemblages in Mid-Atlantic streams, USA. – J. Phycol. 35: 460–468.

Pan, Y. et al. 2000. Ecoregions and benthic diatom assemblages in Mid-Atlantic Highlands streams, USA. – J. N. Am. Benthol. Soc. 19: 518–540.

Parsons, M., Thoms, M. C. and Norris, R. H. 2003. Development of stream macroinvertebrate models that predict watershed and local stressors in Wisconsin. – J. N. Am. Benthol. Soc. 22: 105–122.

Pienitz, R. et al. 1995. Diatom, chrysophyte and protozoan distributions along a latitudinal transect in Fennoscandia. – Ecography 18: 429–439.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. – J. N. Am. Benthol. Soc. 16: 391–409.

Poff, N. L. and Allan, J. D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. – Ecology 76: 606–627.

Potapova, M. G. and Charles, D. F. 2002. Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. – J. Biogeogr. 29: 167–187.

Puomio, E. R., Soininen, J. and Takalo, S. 1999. The state of watercourses in Uusimaa and Eastern-Uusimaa (southern Finland) in the middle of the 1990's. – Yliopistopaino, in Finnish with English summary.

Reynoldson, T. B., Rosenberg, D. M. and Resh, V. H. 2001. Comparison of models predicting invertebrate assemblages for biomonitoring in the Fraser River catchment, British Columbia. – Can. J. Fish. Aquat. Sci. 58: 1395–1410.

Sandin, L. 2003. Benthic macroinvertebrates in Swedish streams: community structure, taxon richness, and environmental relations. – Ecography 26: 269–282.

Sandin, L. and Johnson, R. K. 2000. Ecoregions and benthic macroinvertebrate assemblages of Swedish streams. – J. N. Am. Benthol. Soc. 19: 462–474.

Soininen, J. 2002. Responses of epilithic diatom communities to environmental gradients in some Finnish rivers. – Int. Rev. Hydrobiol. 87: 11–24.

Soininen, J. and Niemelä, P. 2002. Inferring the phosphorus levels of rivers from benthic diatoms using weighted averaging. – Arch. Hydrobiol. 154: 1–18.

Stevenson, R. J. 1997. Scale-dependent determinants and consequences of benthic algal heterogeneity. – J. N. Am. Benthol. Soc. 16: 248–262.

ter Braak, C. J. F. and Smilauer, P. 1998. Program CANOCO, ver. 4.0. – Centre for Biometry.

Townsend, C. R. and Hildrew, A. G. 1994. Species traits in relation to a habitat templet for river systems. – Freshwater Biol. 31: 265–275.

Van Dam, H., Mertens, A. and Sinkeldam, J. 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. – Neth. J. Aquat. Ecol. 28: 117–133.

Van Sickle, J. and Hughes, R. M. 2000. Classification strengths of ecoregions, catchments, and geographic clusters for aquatic vertebrates in Oregon. – J. N. Am. Benthol. Soc. 19: 370–384.

Whittier, T. R., Hughes, R. M. and Larsen, D. P. 1988. Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. – Can. J. Fish. Aquat. Sci. 45: 1264–1278.

Wright, J. F., Furse, M. T. and Moss, D. 1998. River classification using invertebrates: RIVPACS application. – Aquat. Conserv. Mar. Freshwater Ecosyst. 8: 617–631.

Zimmerman, G. M., Goetz, H. and Mielke, P. W. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. – Ecology 66: 606–611.

Abbreviations used for diatom taxa (see Fig. 2), excluding those presented in Table 2.

aexi = *Achnanthes exilis* Kütz.
ahel = *Achnanthes helvetica* (Hust.) Lange-Bertalot
aipf = *Achnanthes impexiformis* Lange-Bertalot
alan = *Achnanthes lanceolata* (Breb.) Grun.
amin = *Achnanthes minutissima* Kütz.
aobg = *Achnanthes oblongella* Oestrup
apus = *Achnanthes pusilla* (Grunow) De Toni
asat = *Achnanthes subatomoides* (Hust.) Lange-Bertalot et Archib.
asuc = *Achnanthes suchlandtii* Hust.
avit = *Anomoeoneis vitrea* (Grunow) Ross
audi = *Aulacoseira distans* (Ehrenb.) Simonsen
cgra = *Cymbella gracilis* (Ehrenb.) Kütz.
cmin = *Cymbella minuta* Hilse ex Rabenh.
cste = *Cyclotella stelligera* Cleve et Grun.
dhie = *Diatoma hiemale* (Roth) Heiberg
dmes = *Diatoma mesodon* (Ehrenb.) Kütz.
ebil = *Eunotia bilunaris* (Ehrenb.)Mills
eimp = *Eunotia implicata* Nörpel, Lange-Bertalot et Alles
emei = *Eunotia meisteri* Hust.
emin = *Eunotia minor* (Kütz.) Grun.
epec = *Eunotia pectinalis* (Dyllwyn) Rabenh.
epra = *Eunotia praerupta* Ehrenb.
eten = *Eunotia tenella* (Grunow) Hust.
farc = *Fragilaria arcus* (Ehrenb.) Cleve
fcap = *Fragilaria capucina* Desmaz.
fcru = *Fragilaria capucina* (Desmaz.) var. *rumpens* Lange-Bertalot
fcva = *Fragilaria capucina* (Desmaz.) var. *vaucheriae* Lange-Bertalot
frho = *Frustulia rhomboides* (Ehrenb.) De Toni
frsa = *Frustulia rhomboides* (Ehrenb.) De Toni var. *saxonica* (Rabenh.) De Toni
fuac = *Fragilaria ulna* (Nitzsch.) Lange-Bertalot var. *acus* (Kütz.) Lange-Bertalot
gang = *Gomphonema angustatum* (Kütz.) Rabenh.
gpar = *Gomphonema parvulum* Kütz.
nacu = *Nitzschia acula* Hantzsch
nagr = *Navicula agrestis* Hust.
ncap = *Navicula capitata* Ehrenb.
ncry = *Navicula cryptocephala* Kütz.
ncte = *Navicula cryptotenella* Lange-Bertalot
ndis = *Nitzschia dissipata* (Kütz.) Grun.
nhmd = *Navicula heimansioides* Lange-Bertalot
nifr = *Nitzschia frustulum* (Kütz.) Grun.
nigr = *Nitzschia gracilis* Hantzsch
nrhy = *Navicula rhynchocephala* Kütz.
nsap = *Navicula saprophila* Lange-Bertalot & Bonik
nten = *Navicula tenelloides* Hust.
ntub = *Nitzschia tubicola* Grun.
papp = *Pinnularia appendiculata* (Agardh) Cleve
pshi = *Pinnularia subcapitata* Gregory var. *hilseana* (Janisch) Müller
sang = *Surirella angusta* Kütz.
tfen = *Tabellaria fenestrata* (Lyngbye) Kütz.
tflo = *Tabellaria flocculosa* (Roth) Kütz.