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DEFINING MACROINVERTEBRATE ASSEMBLAGE TYPES OF HEADWATER STREAMS: IMPLICATIONS FOR BIOASSESSMENT AND CONSERVATION

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Abstract. We used data from 235 boreal headwater streams in Finland to examine whether macroinvertebrate assemblages constitute clearly definable types, and how well biologically defined assemblage types can be predicted using environmental variables. Two-way indicator species analysis produced 10 assemblage types, which differed significantly from each other (multiresponse permutation procedure, MRPP). However, based on MRPP and nonmetric multidimensional scaling, there was wide variation among sites within each assemblage type, and high degrees of overlap among assemblage types. Such continuous variation was also evidenced by the low number of effective indicator taxa (indicator value method) for each assemblage type. Furthermore, discriminant function analysis based on environmental variables showed a moderate yet variable prediction success (59.6% of sites correctly predicted; range 0–96% per group). Canonical correspondence analysis indicated that variation in assemblage structure was primarily related to latitude and water chemistry, especially pH and water color. The absence of discrete macroinvertebrate assemblage types in boreal headwater streams may stem from a number of reasons: (1) macroinvertebrate taxa inhabiting boreal streams tend to exhibit individualistic, taxon-specific responses to environmental gradients, (2) they have wide environmental tolerances and geographic distributions, and (3) boreal streams are characterized by frequent, unpredictable disturbances. Our results suggest that local filters in headwater streams are relatively weak, resulting in poorly distinguishable assemblage types. By contrast, the major latitudinal gradients in macroinvertebrate assemblage structure suggest that regional-scale filters, e.g., temperature, exert strong control over taxon distributions in headwater streams. We suggest that a tiered approach combining regional stratification and subsequent prediction of assemblage structure could provide a suitable framework for the bioassessment and conservation of boreal headwater streams.

Key words: *aquatic conservation; aquatic insects; assemblage types; benthic invertebrates; bioassessment; boreal regions; headwater streams; latitudinal gradients; lotic communities.*

INTRODUCTION

A major controversy in the history of community ecology has centred on whether biotic communities exist as discrete entities (“community-unit concept”) or as a continuum of gradually changing composition (“individualistic concept”) (for reviews, see Austin 1985, Allen and Hoekstra 1992, McIntosh 1995). More recently, it has been shown that this dichotomy is too limited (Shipley and Keddy 1987) and that the two viewpoints are not mutually exclusive (Brown 1995). However, glimpses of both concepts still frequently come up in the ecological literature. One example that reflects the old controversy is the frequent use of clustering techniques to distinguish assemblage types in

bioassessment programs. Although most ecologists concur that setting strict boundaries among gradually changing communities is artificial (Begon et al. 1996, Maurer 1999), many bioassessment approaches are based on community classifications, with an implicit assumption that communities can be divided into distinct, ecologically meaningful groups (see Anderson and Clements 2000).

A major approach to understanding community organization has revolved around the concept of assembly rules. The early advocates of assembly rules attempted to predict community composition based on competitive interactions and niche requirements of potential colonists (Diamond 1975, Diamond and Gilpin 1982). The second generation of assembly rules gave less weight to interspecific competition, emphasizing the role of colonization history and local environmental filters (Drake 1991, Keddy 1992). Environment is regarded as a filter, selecting only a subset of regionally

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available taxa that possess traits allowing persistence under prevailing habitat conditions (Tonn 1990, Weiher and Keddy 1995, Poff 1997). If a series of filters set strong constraints to species traits and, ultimately, species identities, community composition along natural environmental gradients should be highly predictable (e.g., Matthews 1998).

Stream bioassessment programs typically rely on accurate identification and prediction of community types. When related to regional reference conditions, this allows one to account for variation in biological data caused by natural factors (e.g., stream size, natural acidity) rather than anthropogenic disturbances (e.g., Wright et al. 1984, Marchant et al. 1997, Reynoldson et al. 2001). Concurrently, there have been pleas for redirecting aquatic conservation programs to protection at the community rather than the population level (Angermeier and Schlosser 1995, Angermeier and Winston 1999). Such a shift in conservation policy requires that assemblages worthy of conservation be clearly identifiable. This, however, may not always be a simple task. For instance, stream macroinvertebrate assemblages may exhibit highly variable structure caused by unpredictable disturbances and high extent of dispersal (Palmer et al. 1996). Some authors have suggested, however, that local habitat filters in streams (e.g., water depth, substrate composition, water chemistry) are highly effective, resulting in locally controlled, predictable assemblage types (Hawkins et al. 2000). That stream benthic communities occur as predictable, discrete entities is often implicitly assumed, yet few studies have rigorously examined the potential implications of this dichotomy (continuous vs. discrete nature of communities) to stream bioassessment and conservation (but see Chessman 1999).

In this study, we used data on benthic macroinvertebrate assemblages of near-pristine headwater streams in Finland to answer three questions. (1) Do macroinvertebrate assemblages of boreal headwater streams constitute clearly definable assemblage types? (2) What natural factors are associated with spatial patterns in assemblage structure? (3) How well are biologically defined assemblage types predicted by these environmental factors? Finally, we consider the implications of our results for the implementation of bioassessment and conservation programs in headwater stream ecosystems.

MATERIALS AND METHODS

Stream surveys

We sampled 235 streams across Finland (60°–70° N, 20°–32° E) between 1992 and 2000, the majority (>75%) of samples being collected in 1998 or 2000. Material collected prior to 1998 was included only if sampling methods were identical to those used in 1998/2000. We used a spatially stratified sampling protocol to guarantee adequate representation of headwater

stream types: 10–30 streams from each of 11 major watersheds covering the whole country were included. We stratified our sampling according to stream size, i.e., we considered only headwater streams (base flow <0.6 m³/s, catchment area 1–60 km²) to diminish the overriding effects of stream size. Streams within each watershed were selected as randomly as possible, within a 2 km distance from the nearest road. Streams with obvious human impact, spring-fed streams, and lake outlets were excluded. Nevertheless, our study sites span a wide range of environmental variability present in boreal headwater streams. For example, pH varies from 4.5 to 8.4, water color from 5 to 600 mg Pt/L (Pt = platinum units), canopy cover from 0 to 91%, and current velocity from 7 to 110 cm/s.

Invertebrate data

Invertebrate sampling was conducted between early September and the end of October. At each site, we took a two-minute collective kick sample (net mesh size 0.3 mm), aiming to cover most benthic microhabitats in a riffle section of ~100 m². The samples were immediately preserved in alcohol. In the laboratory, invertebrates were sorted and identified to the lowest possible taxonomic level, usually species or genus. Early instars of some limnephilid caddis larvae and dipteran larvae were not identified to this level, so family level identification was retained.

Habitat characteristics

Several riparian and in-stream habitat measurements were conducted at each site. Tree species composition and integrity of riparian zone (percentage of riparian zone without human influence) were assessed in a 50-m section on both banks directly upstream of the sampling site. Shading was measured as percent canopy cover at 20 locations in evenly spaced transects covering the whole study section. Current velocity and depth were measured at 40 locations along the same transects. Moss cover and particle size were assessed at 10 randomly spaced 50 × 50 cm quadrats. Visual estimates of the percentage cover of nine particle size classes and organic material were made for each quadrat using a modified Wentworth scale: (0) organic matter, (1) sand (diameter 0.25–2 mm), (2) fine gravel (2–6 mm), (3) coarse gravel (6–16 mm), (4) small pebble (16–32 mm), (5) large pebble (32–64 mm), (6) small cobble (64–128 mm), (7) large cobble (128–256 mm), (8) boulder (256–400 mm), and (9) large boulder (>400 mm). These estimates were subsequently averaged to give a mean particle size for a site. Mean stream width was also measured at each sampling site. Latitude and longitude (Finnish national grid) were determined in the field using a GPS navigator.

Water samples were collected simultaneously with benthic sampling, and they were analyzed for pH, alkalinity, conductivity, total nitrogen [TN], total phos-

phorus [TP], color, and iron [Fe] by regional environment centers using national standards.

Statistical methods

We performed three kinds of multivariate analyses to define macroinvertebrate assemblage types: two-way indicator species analysis (TWINSPAN), nonmetric multidimensional scaling (NMDS), and multiresponse permutation procedure (MRPP). TWINSPAN is based on reciprocal averaging (Gauch 1982, van Tongeren 1995), and it is widely used in freshwater ecology and bioassessment (Ormerod and Edwards 1987, Wright et al. 1997, Moss et al. 1999). Yet this method has been criticized mainly on two grounds: (1) it is based on the assumption that a single strong gradient dominates the data; and (2) the rather arbitrary cutting of the major axis may separate sites with relatively similar species composition (Belbin and McDonald 1993, Legendre and Legendre 1998). Despite its drawbacks, it has been shown that, compared with alternative clustering methods, TWINSPAN performs well in the classification of benthic macroinvertebrate assemblages (Moss et al. 1999). We also used NMDS to assess whether the TWINSPAN groups represented discrete assemblage types in the ordination space. NMDS is an ordination method based on ranked distances, and it is suitable for analyzing ecological data sets for numerous reasons. NMDS performs well with data that are nonnormally distributed, are on arbitrary, discontinuous scales, or contain numerous zero values (McCune and Mefford 1999). Sorensen's coefficient based on $\log(x + 1)$ macroinvertebrate abundance data was used as the distance measure in NMDS. A three-dimensional solution of NMDS was used, because change in stress value was minor with subsequent dimensions. We also tested for significant differences among groups at each TWINSPAN division using MRPP. MRPP is a nonparametric method designed for testing differences in assemblage structure among a priori defined groups (Zimmerman et al. 1985). MRPP was also based on Sorensen's coefficient. The significance of the null hypothesis of no differences among groups was assessed by a Monte Carlo permutation procedure with 1000 permutations. Further, we used the indicator value method (INDVAL) (Dufrene and Legendre 1997) to identify species discriminating between TWINSPAN groups at the first and the fourth division level. The indicator value of a taxon varies from 0 to 100, and it attains maximum value when all individuals of a taxon occur at all sites of a single group. The significance of the indicator value for each taxon was tested by a Monte Carlo randomization test with 1000 permutations.

All analyses were run on transformed [$\log(x + 1)$] abundance data. For TWINSPAN, we used five pseudospecies cut levels, four division levels, and 25 as the minimum group size for each division. This minimum group size was used because, based on preliminary analyses, smaller groups provided less robust classi-

fications and/or were poorly predicted in discriminant function analyses. Rare species were retained in the analysis, because their exclusion may hinder the detection of meaningful ecological gradients in assemblage structure (Cao et al. 2001). Thus, a total of 189 operational macroinvertebrate taxa were included in statistical analyses. TWINSPAN, NMDS, MRPP, and INDVAL were run using PC-Ord (McCune and Mefford 1999).

We used two methods to relate community types to environmental variables. First, we employed discriminant function analysis (DFA) with stepwise selection to reveal which environmental variables were most important in discriminating among the TWINSPAN groups at each division level. DFA (with cross-validation) was also used to predict the group membership of each site according to environmental variables. Second, we used canonical correspondence analysis (CCA) to examine the relationships of assemblage types and indicator species (from INDVAL) with environmental gradients. CCA is a direct gradient analysis that analyzes both species and environmental data by combining ordination and regression techniques (ter Braak 1995, Legendre and Legendre 1998). We used forward selection of environmental variables. At each step, only variables significantly related ($P < 0.05$; Monte Carlo randomization test with 100 permutations) to assemblage structure were included in the model. Additionally, detrended correspondence analysis (DCA) was used to determine gradient lengths for the first three axes, and to assess the degree of species turnover across ecological gradients. Gradient length ≥ 4 SD units indicates complete species turnover (Legendre and Legendre 1998). CCA and DCA were run using CANOCO version 4.0 (ter Braak and Smilauer 1998).

RESULTS

At the fourth division level, TWINSPAN produced 10 site groups (Fig. 1). At each division, MRPP indicated significant among-group differences in assemblage structure (Monte Carlo permutation test, $P < 0.001$). However, values for MRPP's R statistic were generally very low (0.034 to 0.089), indicating that there was wide within-group variation (see McCune and Mefford 1999). Further, when plotted in the NMDS ordination space, TWINSPAN groups did not form distinct site groupings indicative of discrete assemblage types (Fig. 2). The negative and positive groups of the first TWINSPAN division were clearly observable in the NMDS space, but at further division levels, site groups exhibited considerable overlap. At the fourth division level, group A streams (acid streams in eastern Finland) deviated from all others along the first and third NMDS dimensions (Fig. 2).

INDVAL identified significant indicator species for each TWINSPAN division level (Monte Carlo permutation test, $P < 0.001$). For clarity, only the first and the fourth division level will be considered here.

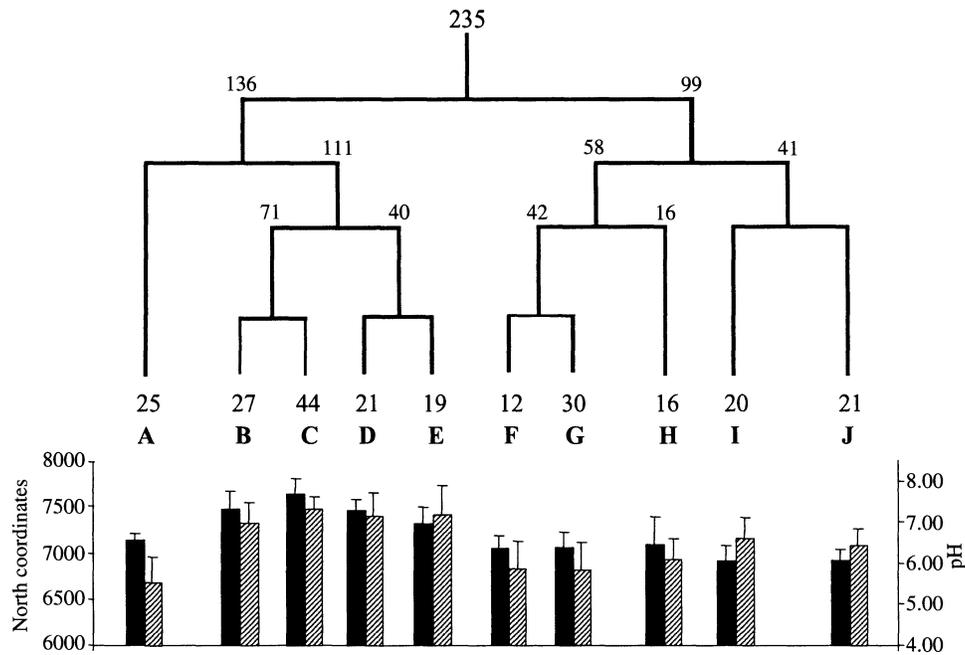


FIG. 1. TWINSpan classification of the study streams. Numbers refer to number of sites in each group. Also shown are mean (+ 1 SD) latitude (Finnish grid system, solid bars) and pH (shaded bars) for each TWINSpan end group.

The negative group ($n = 136$ sites) of the first TWINSpan division level (Fig. 1) was characterized by the mayflies *Ephemerella aurivillii* (Bengtsson) (indicator value 57 [indicator values given in parentheses]) and *Baetis subalpinus* Bengtsson (42), the stoneflies *Protonemura meyeri* (Pictet) (33) and *Diura nanseni*

(Kempny) (63), the riffle beetle *Elmis aenea* (Müller) (36), and the caddisfly *Micrasema gelidum* McLachlan (33). The positive group ($n = 99$ sites) was characterized by the crustacean *Asellus aquaticus* (Linnaeus) (67), the stoneflies *Leuctra hippopus* Kempny (33) and *Nemoura cinerea* (Retzius) (72), and the caddisflies

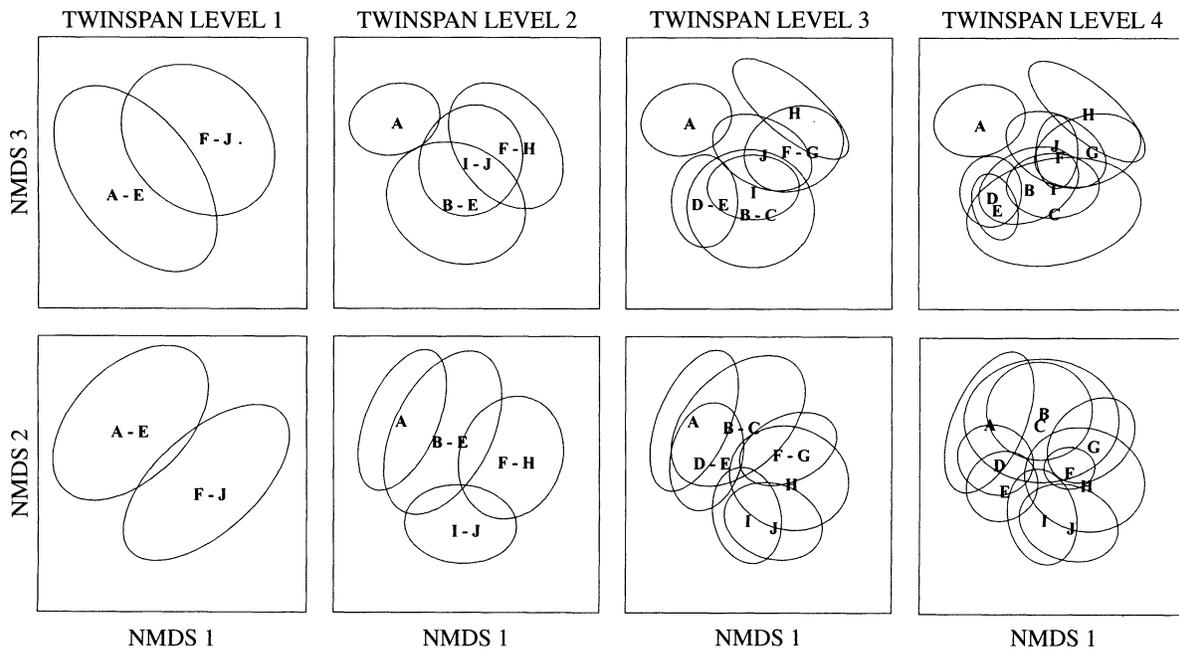


FIG. 2. An ordination diagram showing the distribution of the TWINSpan site groups in the NMDS space. The centroid of each TWINSpan group or group combination is denoted by capital letters (A–J). Ellipses encircle 90% of sites belonging to a given group.

TABLE 1. Results of indicator species analysis (INDVAL) at the fourth TWINSPAN division level.

Indicator taxon	TWINSPAN group									
	A	B	C	D	E	F	G	H	I	J
<i>Heptagenia sulphurea</i>	1	0	0	0	1	0	0	0	60	0
<i>Ephemera aurivillii</i>	13	18	12	29	13	0	0	0	0	0
<i>Onychogomphus forcipatus</i>	0	0	0	0	0	0	0	0	30	0
<i>Leuctra fusca</i>	55	0	0	10	1	0	0	0	0	0
<i>Capnopsis schilleri</i>	0	2	5	6	2	31	3	0	0	1
<i>Protonemura intricata</i>	28	0	0	0	1	0	0	0	1	0
<i>Rhyacophila fasciata</i>	0	0	0	0	0	14	0	0	35	0
<i>Cheumatopsyche lepida</i>	0	0	0	0	1	0	0	0	31	0
<i>Hydropsyche pellucidula</i>	2	0	0	0	0	0	0	0	65	14
<i>Hydropsyche siltalai</i>	0	0	0	0	0	0	0	0	51	31
<i>Potamophylax cingulatus</i>	0	1	0	1	0	43	2	0	2	1
<i>Chaetopteryx villosa</i>	30	0	0	0	0	0	0	0	1	0

Notes: Shown are indicator values for the top 12 species significantly discriminating (indicator value > 25, $P < 0.001$) among the 10 TWINSPAN site groups (A–J). The significance of the indicator values was tested using a Monte Carlo randomization test with 1000 permutations. The highest indicator value for each species is given in boldface.

Polycentropus flavomaculatus (Pictet) (38) and *Hydropsyche siltalai* Döhler (37). At the fourth TWINSPAN division level, INDVAL detected relatively few good indicators for the 10 site groups (Table 1). Species typical of group A were the stoneflies *Leuctra fusca* (Linnaeus) and *Protonemura intricata* (Ris), and the caddisfly *Chaetopteryx villosa* (Fabricius). Group D was characterized by the mayfly *Ephemera aurivillii*. The stonefly *Capnopsis schilleri* (Rostock) and the caddisfly *Potamophylax cingulatus-latifennis* were the type species of group F, whereas no significant indicator species were found for groups G and H. Group I was characterized by the mayfly *Heptagenia sulphurea* (Müller), the dragonfly *Onychogomphus forcipatus* (Linnaeus), and the caddisflies *Rhyacophila fasciata* Hagen, *Cheumatopsyche lepida* (Pictet), *Hydropsyche pellucidula* (Curtis), and *Hydropsyche siltalai*. *H. siltalai* also characterized streams of group J. Albeit significant, indicator values remained low (<50) even for most of these major indicator taxa (Table 1).

The first TWINSPAN division paralleled geographical separation of streams into a northern (A–E) and a southern (F–J) subgroup (Fig. 1). Further divisions were related to local environmental factors (Tables 2 and 3). The prediction success of DFA decreased with increasing TWINSPAN division level and number of groups: the proportion of correct predictions was 91.9, 85.5, 68.1, and 59.6% for the first to fourth division level, respectively. At the first TWINSPAN level, eight variables were included in the DFA model, in order of importance: latitude, longitude, [TN], percentage deciduous trees, depth, particle size, alkalinity, and conductivity. At the fourth division level, the DFA model incorporated latitude, pH, longitude, water color, moss cover, particle size, and percentage deciduous trees (Table 3). Using this reduced set of variables, DFA predicted correctly 59.6% of the streams, the percentage of correct classifications ranging from 0 to 96 (Table 4). No streams in group H were correctly predicted, and streams in groups D, E, and F were poorly predicted

TABLE 2. Mean values of environmental variables important in discriminating among the TWINSPAN groups at the fourth division level.

Variable	TWINSPAN group									
	A	B	C	D	E	F	G	H	I	J
North coordinates	7131	7476	7639	7465	7307	7050	7046	7089	6919	6919
East coordinates	3650	3411	3456	3497	3528	3427	3358	3439	3450	3531
Deciduous trees (%)	42	74	87	65	65	41	52	61	72	70
Current velocity (cm/s)	29	39	38	36	45	45	34	29	41	31
Depth (cm)	23	24	19	22	25	23	21	22	24	16
Moss cover (%)	40	46	15	41	46	31	18	19	31	29
Particle size	7.1	5.6	6.7	6.4	6.1	6.5	4.9	5.0	5.9	5.1
pH	5.5	7.0	7.3	7.1	7.2	5.9	5.8	6.1	6.6	6.5
Alkalinity (mmol/L)	0.05	0.34	0.32	0.53	0.54	0.10	0.10	0.17	0.23	0.18
Conductivity (mS/m)	2.38	4.76	4.52	6.80	6.77	4.20	3.35	4.71	5.24	4.91
Total N ($\mu\text{g/L}$)	263	249	165	230	301	838	712	776	444	417
Color (mg Pt/L)	161	69	35	81	98	204	275	151	89	80

TABLE 3. Wilks' lambda from stepwise DFA for variables best discriminating among groups at the first and the fourth TWINSpan division level.

Step	TWINSpan division level			
	1		4	
	Variable	Lambda	Variable	Lambda
1	latitude	0.502	latitude	0.277
2	longitude	0.457	pH	0.155
3	[TN]	0.426	longitude	0.087
4	% deciduous	0.403	color	0.062
5	depth	0.384	moss	0.048
6	particle size	0.375	particle size	0.040
7	alkalinity	0.365	% deciduous	0.034
8	conductivity	0.357		

Note: The variable minimizing the overall Wilks' lambda is entered at each step.

(<50%) to their actual groups. Groups B and J showed moderate prediction success, with more than half of the streams being correctly classified. Finally, classification success was high for groups A, C, G, and I, with >70% of streams correctly classified (Table 4).

Eigenvalues and species-environment correlations for the first three CCA axes were all significant (Monte Carlo test, $P < 0.01$). Forward selection of environmental variables incorporated 15 variables (Table 5) in the final model (Monte Carlo test, 100 permutations at each step, $P < 0.05$). Axis 1 was strongly related to latitude, whereas axis 2 represented a water quality gradient with clear-water, high pH streams, and brown-water, acid streams being the endpoints of this gradient (Fig. 3a). Axis 3 mainly described variation in assemblage structure along the east-west gradient (Table 4). Overall, CCA reinforced the main results of DFA: assemblage structure varied along a geographical gradient and, secondarily, along a water chemistry gradient. Nevertheless, TWINSpan groups showed considerable overlap in the CCA space (Fig. 3b), as did also the distributions of the top 12 INDVAL indicator taxa along the first two CCA axes (Fig. 4). Thus, even taxa that were identified as indicators of their respective groups exhibited wide ranges of environmental toler-

ance. Gradient lengths for the first three DCA axes were 3.304, 2.716, and 3.059, respectively, implying that species turnover among sites at the opposite ends of the gradients were incomplete.

DISCUSSION

Given the obvious advantages of community-level conservation (see Angermeier and Schlosser 1995), it would be highly desirable if macroinvertebrate assemblage types could be clearly identified and predicted based on environmental variables. For boreal headwater streams, however, this proved to be difficult. While MRPP did find significant differences among the macroinvertebrate assemblage types at each TWINSpan division, the associated MRPP R statistics were overall very low (<0.09), indicating that there was wide variability within each TWINSpan group. Therefore, accepting these results as indicative of disjunct assemblage types incurs a risk of mixing statistical and biological significance (McCune and Mefford 1999, see also Van Sickle and Hughes 2000). Furthermore, INDVAL found few, if any, effective indicator taxa for most of the assemblage types defined by TWINSpan. In fact, only the division of streams into a northern and southern subgroup provided some indication of the existence of clearly definable assemblage types. Variation in assemblage structure was mainly related to geographical location, stream acidity, and water color, factors formerly identified as major correlates of macroinvertebrate distribution and assemblage structure in boreal streams (Malmqvist and Mäki 1994, Hämäläinen and Huttunen 1996, Malmqvist and Hoffsten 2000, Sandin and Johnson 2000, Paavola et al. 2000).

The absence of discrete macroinvertebrate assemblage types in boreal headwater streams may be attributable to a number of reasons. In general, systems characterized by unpredictable disturbances and high extent of dispersal should exhibit highly variable assemblage structure (Palmer et al. 1996). In such systems, random extinctions and recolonizations may lead to assemblage structure deviating from that expected based on water chemistry and physical habitat

TABLE 4. Prediction of TWINSpan group (A-J) membership for the 235 stream sites using discriminant function analysis on environmental variables.

Actual	Predicted										Correct classifications (%)	
	A	B	C	D	E	F	G	H	I	J		
A	24				1							96.0
B		16	4	3	2		2					59.3
C			34	6	3		1					77.3
D		4	6	6	3	1	1					28.6
E		3	1	3	8	3			1			42.1
F	2					3	3	2	2			25.0
G	1	1				1	24		1	2		80.0
H		2		1	1	3	4	0	1	4		0
I	1				1					14	4	70.0
J	1						3		6	11		52.4

Note: The number of correctly classified streams is given in boldface.

TABLE 5. Summary of the canonical correspondence analysis.

Variable	Axis 1	Axis 2	Axis 3
Eigenvalue	0.245	0.177	0.134
% variance of species data	4.2	3.0	2.3
Species–environment correlation	0.918	0.853	0.795
Latitude	-0.921	-0.062	-0.009
Longitude	0.040	0.285	0.673
Riparian integrity	-0.156	-0.092	-0.313
Deciduous trees	-0.238	0.341	-0.302
Shading	0.232	-0.471	-0.197
Stream width	-0.224	0.533	0.258
Velocity	-0.156	0.215	-0.044
Depth	-0.253	0.001	0.318
Moss cover	-0.196	0.102	0.345
Particle size	-0.268	0.067	0.321
pH	-0.556	0.620	-0.339
Conductivity	-0.136	0.418	-0.327
Total phosphorus	0.384	-0.379	0.029
Color	0.325	-0.496	0.309
Iron	0.236	-0.494	0.200

Notes: Shown are the eigenvalues for and percentage variance explained by the first three axes, as well as the intraset correlations among the axes and environmental variables. Only variables selected through forward selection procedure are presented. The variable with the highest correlation for each axis is given in boldface. Total inertia of species data was 5.819.

at the time of sampling. While the role of disturbance (floods, droughts, bottom freeze) in shaping the biotic communities of boreal headwater streams is well established (Malmqvist and Hoffsten 2000), not much is known about the dispersal rates and distances of lotic invertebrates in general. Indirect evidence suggests, however, that most species possess considerable dispersal capacity. For example, Malmqvist et al. (1991) documented an astonishingly rapid colonization by most invertebrate taxa of a man-made stream in southern Sweden. Importantly, this stream originated from a lake, so colonization by lotic taxa must have been mainly via aerial dispersal. Furthermore, as taxa inhabiting boreal streams tend to have wide environmental tolerances and geographic distributions (Malmqvist and Hoffsten 2000), it appears that local filters in these systems are relatively weak, resulting in poorly distinguishable assemblage types. This was also observed in our study, regardless of the fact that the environmental gradients sampled were fairly long.

The relatively low distinctiveness of macroinvertebrate assemblage types in our study streams may also reflect the fact that, due mainly to historical reasons (e.g., glaciation), northern European macroinvertebrate fauna is known to be depauperate compared to many other regions of the world (Jacobsen et al. 1997). Such low diversity clearly reduces our ability to detect distinct assemblage types (see also Reynoldson et al. 2001). It should be remembered, however, that our data are stratified by habitat type (only headwaters), season (only autumn), and taxonomic resolution (chironomids not included), and therefore likely capture only a portion of the regional species pool. Therefore, our estimate of regional taxon richness is not directly comparable to most other regional analyses of lotic mac-

roinvertebrate diversity (e.g., Wright et al. 1984, Reynoldson et al. 2001).

Obviously, increasing the environmental scope of the study by including other types of stream habitats, e.g., large rivers and lake outlets, would have revealed patterns different from those observed here. Our sampling was stratified by stream type; we concentrated on headwater streams (mostly orders 1 and 2). Stratification by the size of the water body was also recommended by Tonn (1990; “lake type filter”), and we believe this is indeed to be recommended for many reasons. First, from a biodiversity perspective, headwater streams comprise a valuable and unique resource, supporting a number of taxa absent from larger rivers (Wright et al. 1998, Furse 2000, Malmqvist and Hoffsten 2000). Second, including streams of different sizes almost certainly results in a predominant size-related axis in any multivariate analysis of lotic assemblages (e.g., Malmqvist and Mäki 1994, Angermeier and Winston 1999), thus potentially obscuring the detection of other biologically relevant trends. Therefore, while the inclusion of multiple habitat types would almost certainly produce easily definable assemblage types, this incurs a loss in our ability to identify assemblage types within one important freshwater habitat type, headwater streams.

From a bioassessment perspective, our data portray a reference condition for boreal headwater streams, because all material was collected from near-pristine environments. Human-induced changes, whether in the surrounding terrestrial landscape or in the stream channel, may create a novel “anthropogenic filter,” resulting in assemblage types rarely found in more natural settings. For example, Muotka et al. (2002) found that streams dredged in Finland to facilitate timber transport provide a unique type of filter (simplified substratum

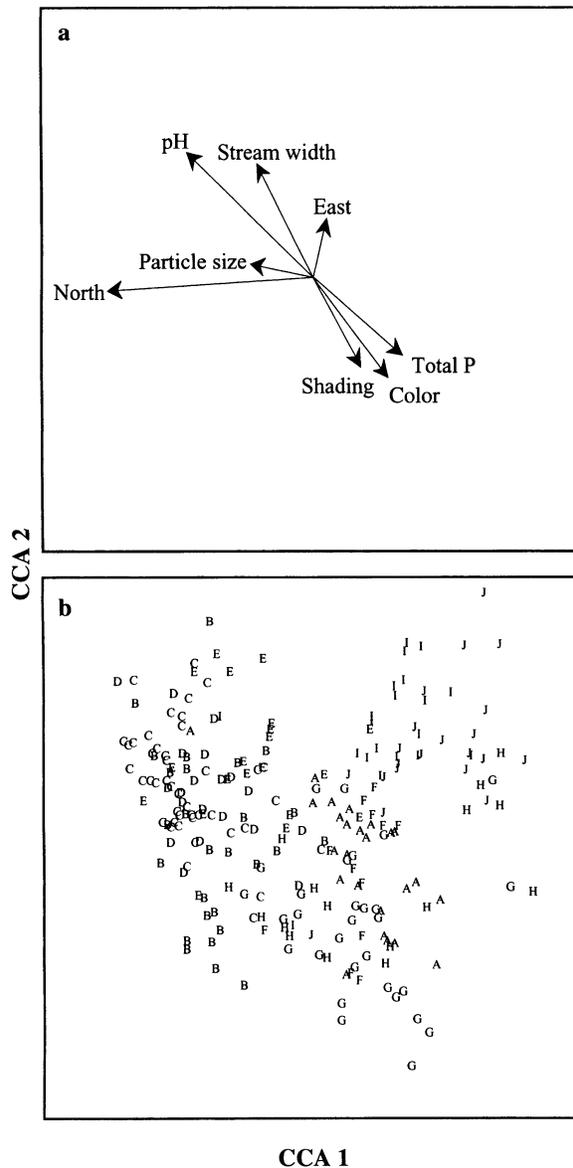


FIG. 3. A CCA biplot defined by the first two axes of the ordination of environmental variables and TWINSPAN site groups (denoted by capital letters). For clarity, only the eight most important variables are shown.

structure, homogeneous flow patterns, reduced retention potential) favoring species traits that might not be as beneficial in more complex and retentive natural channels. Because the very objective of stream bioassessment is to evaluate whether a stream is impaired or not, relative to regional reference conditions, such modified streams are obviously unsuitable as reference sites for bioassessment.

The strong latitudinal patterns in macroinvertebrate assemblage structure suggest that regional-scale filters (e.g., temperature; Tonn 1990, Poff 1997) have a major influence on the distribution of taxa across headwater streams. This pattern may have been further accentu-

ated by covariation of geographical location and water chemistry across the study area (Heino et al. 2002). Therefore, it seems obvious that geographical stratification would improve stream bioassessment programs in boreal areas. Regional stratification might allow mastering part of the natural variation in assemblage structure, simply because adjacent headwater streams should resemble each other more than those farther away, and should thus respond similarly to large-scale environmental variation. However, neither regional delineations (Whittier et al. 1988, Sandin and Johnson 2000) nor biological classifications (Wright et al. 1984, 1998, Ormerod and Edwards 1987, Marchant et al. 1997, Reynoldson et al. 2001) alone perform well for boreal headwater streams, because assemblage types are far from discrete and not readily predictable based on environmental variables. A combination of regional stratification and biological characterization of assemblage types might provide a better framework for the bioassessment of boreal streams. Such a combination could increase the robustness of predictive models, leading to more parsimonious models than those generated for larger, more heterogeneous areas (Johnson and Goedkoop 2000). Moreover, acknowledging that macroinvertebrate assemblages exhibit continuous variation across environmental gradients, predictive models should not rely too heavily on methods that produce distinct site groupings (e.g., cluster analysis), whether these were biologically meaningful or not (see also Chessman 1999).

Since the characterization of macroinvertebrate assemblage types seems to be of limited value in the conservation evaluation of boreal headwater streams, how should their conservation value be assessed? Obviously, approaches based on species richness, rare species hotspots, or unusual species combinations warrant consideration in this regard. Ultimately, however, conservation efforts should guarantee that biologically valuable assemblages remain viable, i.e., that they retain their value in the future (Angermeier and Schlosser 1995). To be successful, such efforts will require that the regional and landscape context of biological assemblages be preserved by enhancing the terrestrial-aquatic linkages and by providing possibilities for the biota for intersite dispersal throughout entire stream networks (Naiman et al. 1993, Winston and Angermeier 1995, Ward 1998). Finally, conservation assessment should not be based on a single taxonomic group, e.g., macroinvertebrates or fish, at least not until the potential applicability of such "indicator taxa" in preserving lotic biodiversity is more fully explored.

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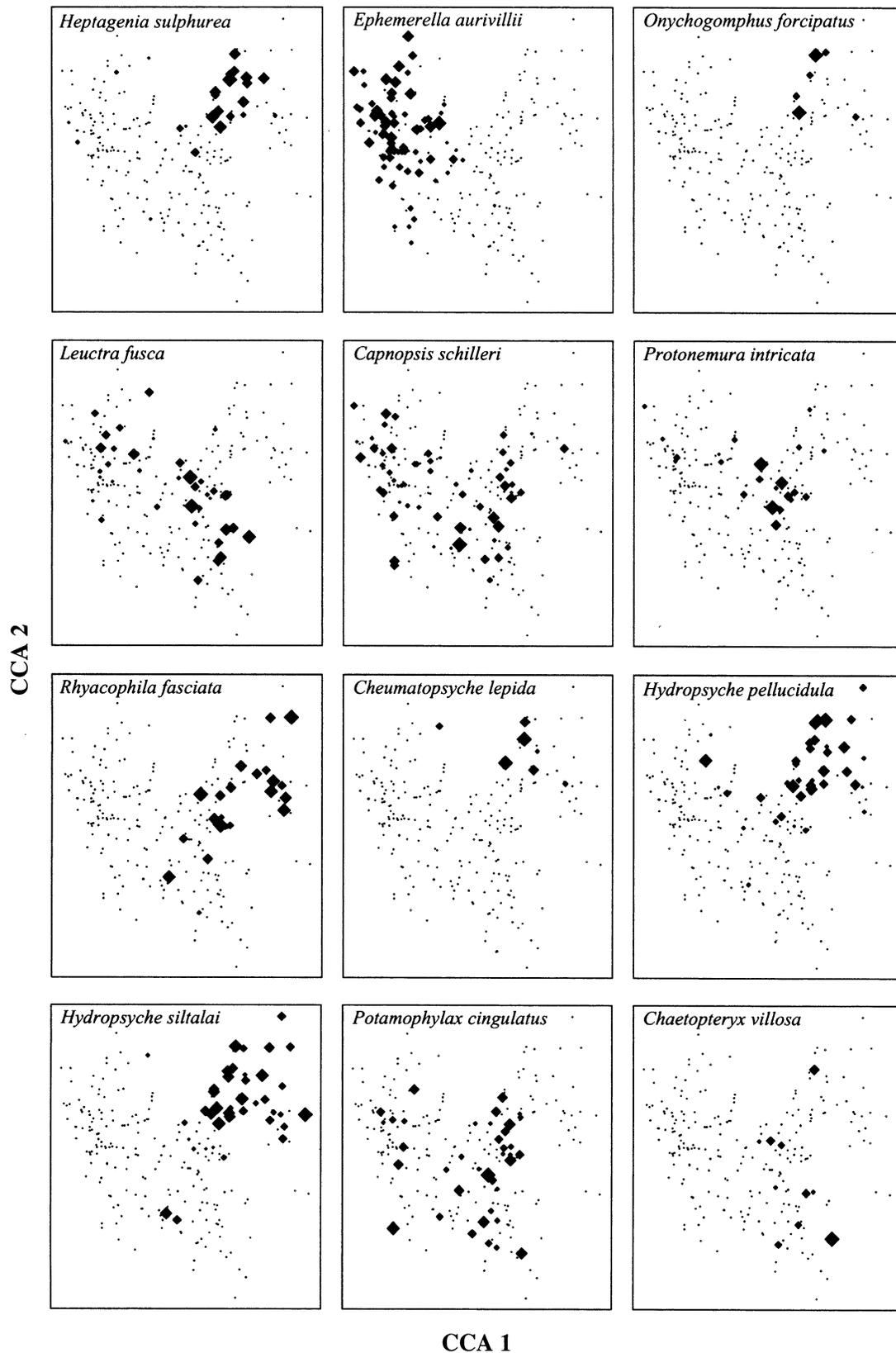


FIG. 4. Distribution and abundance of the 12 top indicator species (see Table 1) for the 10 TWINSpan groups along CCA axes 1 and 2. The smallest symbols indicate the absence of a species at a site, whereas the largest symbol size indicates the peak abundance for that species.

stream invertebrates, especially worms, with us. This study is part of the Finnish Biodiversity Research Programme (FI-BRE). Financial support was also provided by the Maj and Tor Nessling Foundation.

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