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ORIGINAL ARTICLE

Community structure of Ephemeroptera in Siberian streams

Mikhail A. BEKETOV

UFZ – Helmholtz Centre for Environmental Research, Department of System Ecotoxicology, Leipzig, Germany

Abstract

In recent decades, the relationships between environmental conditions and community structures of stream macroinvertebrates have been investigated in many parts of the world. However, knowledge about assemblages of mayflies and other stream macroinvertebrates in Siberia (northern Asia) and Asia is limited. In fact, the patterns in mayfly species richness and assemblage structure in relation to environmental parameters have not been previously examined in western Siberia. The aim of the present study was to examine the relationship between Ephemeroptera community structure and physical parameters along a river altitude/longitude gradient in Siberia. The results showed that maximum species richness was at relatively low altitudes, high water temperatures, slow current velocities, medium stream widths, medium-small substrate particle size, and the presence of macrophytes. The mayfly assemblage was separated using TWINSPAN classification into eight distinct groups, which differed significantly with respect to at least one measured environmental factor. Multivariate ordination (detrended correspondence analysis) revealed that mayfly assemblages are structured by a single dominant gradient of altitude-related environmental variables; altitude and water temperature were the best predictors. Ordination further revealed that mayfly assemblages are structured by altitude-related environmental factors at high elevations, whereas in the lowlands these factors are less important.

Key words: altitude, assemblage structure, macroinvertebrates, Siberia, species richness.

INTRODUCTION

The longitudinal distribution of macroinvertebrates within a river system is generally thought to be determined by a gradient of physicochemical parameters (Vannote *et al.* 1980). Although altitudinal/longitudinal patterns in the diversity and structure of macroinvertebrate communities are expected to be best explained by a large set of environmental factors, many studies have shown that just a few environmental variables explain most of the variability in assemblage structure. These factors include stream size (Bronmark *et al.* 1984; Wright *et al.* 1984), velocity (Malmqvist & Maki 1994), substrate (Minshall 1984), temperature (Jacobsen *et al.* 1997; Minshall & Robinson 1998), in-stream vegetation (Malmqvist & Maki 1994; Wright *et al.* 1994), and large-scale catchment characteristics (Corkum 1989; Carter *et al.* 1996).

In recent decades, relationships between the physicochemical environmental characteristics of a stream and the species richness and community structure of macroinvertebrates inhabiting it have been actively investigated not only in Europe and North America, but also in many other parts of the world (King 1981; Bunn & Davies 1992; Rundle *et al.* 1993). However, knowledge about mayflies and other stream macroinvertebrates in Siberia and Asia is extremely limited. For the temperate zone in Asia, only a monograph by Levanidova (1982) describes mayfly assemblage composition in relation to environmental parameters. However, this study is purely descriptive and does not analyze the general relationships between environmental factors and biological communities. Mayflies (Ephemeroptera) are an important and abundant component of stream macroinvertebrate communities (Ward 1992). The spatial distribution of these organisms is known to be

Correspondence: Mikhail A. Beketov, UFZ – Helmholtz Centre for Environmental Research, Department of System Ecotoxicology, Permoserstrasse 15, D-04318 Leipzig, Germany. Email: mikhail.beketov@ufz.de

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dependent on the natural altitude/longitude environmental gradient (Dodds & Hisaw 1925; Kamler 1967; Brodsky 1980; Levanidova 1982; Ward 1986) as well as influenced by anthropogenic factors or stressors (Beketov 2004).

Although the mayfly fauna has been recently investigated in western Siberia (Beketov & Kluge 2003; Beketov 2005, 2007; Beketov & Godunko 2005), the patterns of species richness and assemblage structure in relation to environmental parameters have not been examined. The aim of the present study was to investigate patterns in Ephemeroptera species richness and assemblage structure and test their correlation to physical parameters associated with a river altitudinal/longitudinal environmental gradient. Measured parameters were altitude, stream width, temperature, current velocity, bottom substrate and presence/absence of macrophytes. The samples used in the present analysis were collected exclusively in pristine, uncontaminated streams to exclude anthropogenic effects.

MATERIALS AND METHODS

Study area

The samples used in the present analysis were collected during 2002–2005 in three regions of southwestern Siberia: Novosibirsk Province, Altai Republic, and Khakassia (Fig. 1). Novosibirsk Province is in the southeastern corner of the West Siberia Plain and is mainly characterized by a flat relief (Fig. 1a). In the southeast of this province are found the low mountains of Salairskii Kryazh (up to 502 m a.s.l.), drained by the Berd River basin. All study sites in Novosibirsk Province were in the Ob River basin, except one site in the Om River basin far to the west (Fig. 1a). The climate of the region is moist continental, mid-latitude with cold winters (mean January temperature is –18°C, extreme temperatures can reach –40°C) and relatively warm summers (mean July temperature is 20°C). Precipitation is 500–800 mm per year (Davitaya 1960). During the long winter most water bodies are covered with ice (from November to April). Study sites in the province are mostly in the forest–steppe zone. In the south, patches of true steppes are a significant part of the landscape, whereas birch/aspen forests of the sub-taiga type with a minor component of spruce occur in the north. Watercourses are fed by a mixture of groundwater, rain and snow (Krivonogov 1969; Blazhenov & Khudyakova 2000).

In contrast to Novosibirsk Province, the Altai Republic (Fig. 1b) and Khakassia (Fig. 1c) are predominantly characterized by mountainous relief. These two regions are western components of the great South-Siberian Mountain System stretching from the Altai Mountains in the southwest and the Putorana Mountains in the northwest to the Pacific Ocean in the east. The majority of the mountains are below 2000 m a.s.l. (maximum elevation is 4506 m a.s.l, Belukha Mountain). Mean January temperatures are –18°C and –20°C, mean June temperatures are 12°C and 16°C, and mean precipitation values are 800 mm and 1600 mm per year in the Altai Republic and Khakassia, respectively (Davitaya 1960). Taiga is the predominant vegetation, being replaced by alpine meadows and alpine tundra at elevations higher than 2000 m a.s.l. Watercourses are predominantly fed by rain/snow (Blazhenov & Khudyakova 2000).

Sampling and data processing

In total, material from 1976 samples collected at 46 sites was used. Mayfly larvae were collected using D-frame nets (500 μm mesh) in pristine streams (width 0.5–185 m). Samples were taken from all major habitat types present in a stream (including stones, pebbles, submerged macrophytes and fine sediments). In large watercourses, only the littoral section was sampled to a depth of 1 m. Collected macroinvertebrates were preserved in 95% ethanol and identified in the laboratory. Sampling methods were not fully uniform for all samples. In particular, sampling area varied between 0.125 and 0.25 m^2, and highly abundant species were not quantified in some samples. Hence a species presence/absence table was created for the present analysis and the abundance of each species was not considered in the analysis. Large plain rivers (e.g. the Ob River) were not included in the analysis, as they were contaminated and not relevant to the present study. Slow-flowing plain rivers, which are typical of swampy territories of the Western Siberian Plain, were also excluded.

Taxonomy used here is based on Kluge (1997). Thus, the genus *Baetis* is considered "broadly" according to revisions made by Novikova and Kluge (1987) and Novikova (1987), with *Acentrella*, *Baetiella*, *Labiobaetis Nigrobaetis*, and *Pseudocloeon* considered as subgenera. The genus *Ecdyonurus* includes *Afghanurus* and *Afronurus* as subgenera.

Environmental parameters

The following environmental characteristics were considered in this study: altitude, mean summer water temperature, current velocity, stream width, and dominant

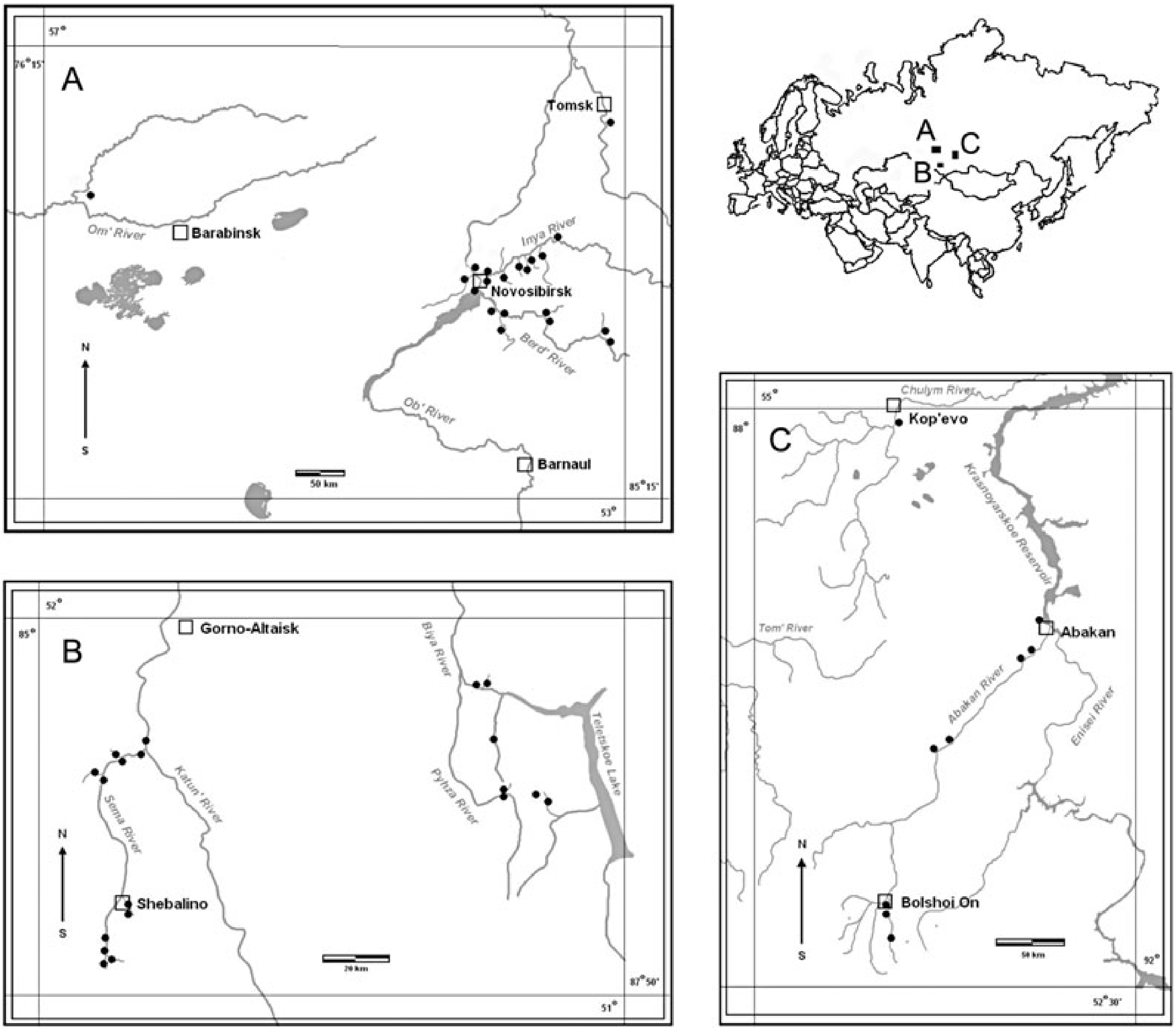

Figure 1 Study area: (a) Novosibirsk Province, (b) Altai Republic, and (c) Khakassia. (●), Sampling points; (□), cities.

substrate particle size. Absolute altitude was measured using a geographic positioning system (GPS) device (e-Trex; Garmin, Olathe, KS, USA) or using available maps. Water temperature was measured using a mercurial thermometer. Mean summer temperature for each site was calculated as the arithmetic mean of all measurements made during the ice-free period. Winter temperatures were not measured due to technical difficulties, although under-ice winter water temperatures are relatively similar in the different watercourses. Stream width was measured using a tape measure, and for large watercourses by GPS. Substrates were assigned to seven different size classes according to the method of Hering *et al.* (2003) and a "semi-continuous" variable called dominant substrate mean particle size was used in the analysis. Surface current velocity was assessed by timing a bobber ($n = 3$) over 5 m of stream. Last, the presence/absence of aquatic macrophytes was recorded.

Statistical analyses

Relations between environmental variables and species richness were analysed by fitting nonlinear regression models. The following nonlinear models were used: one-phase exponential equation ($Y = \mathrm{A} \times \exp(-\mathrm{B} \times X) +$

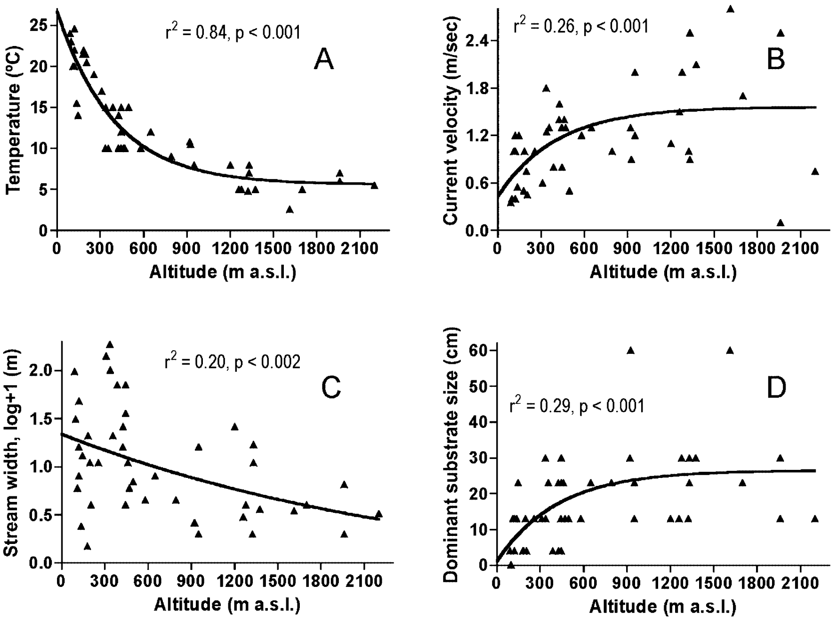

Figure 2 Environmental parameters of the studied watercourses in relation to absolute altitude (m a.s.l.): (a) temperature (°C), (b) current velocity (m/s), (c) stream width (log + 1 transformed, m), and (d) dominant substrate particle size (cm). One-phase exponential regression curves and squared Pearson's correlation coefficients (r^2) are given.

Plateau) and two-phase exponential equation ($Y = A1 \times \exp(-B1 \times X) + A2 \times \exp(-B2 \times X) + \text{Plateau}$) (Motulsky 2003; Motulsky & Christopoulos 2003). The non-parametric Mann–Whitney test was used to assess the significance of differences in species richness between the stream sites with and without macrophytes. These analyses were performed using the program Prism 4.0c for Macintosh (GraphPad Software, San Diego, USA).

Classification of stream sites according to mayfly assemblage structure was carried out using two-way indicator species analysis TWINSPAN (Hill 1979). This divisive technique separates sites using species data (in this case presence/absence data), and at each step the site-by-species matrix is divided dichotomously. Three division levels resulting in eight site-groups were used. This level was chosen as that giving a reasonable number of groups among which significant differences in environmental variables could be found (Van Tongeren 1987). This analysis was performed using the program WinTWINS 2.3 (Centre for Ecology and Hydrology/University of South Bohemia, Huntingdon/Ceske Budejovice, Czech Republic) according to the guide by Hill and Smilauer (2005). Comparison of environmental parameters of the site-groups classified by TWINSPAN was performed using one-way ANOVA followed by Tukey's post hoc test. Levene's test was used to estimate the homogeneity of variances. Differences in the proportions of sites with and without macrophytes were assessed using the χ^2 test. These analyses were performed using SPSS 11.0 for Macintosh (SPSS, Chicago, USA) and Prism 4.0c for Macintosh (GraphPad Software).

Analysis of assemblage structure in relation to environmental factors was carried out using unconstrained unimodal multivariate ordination techniques such as detrended correspondence analysis (DCA). The unconstrained ordination with passive projection of environmental variables was chosen to understand actual variability in the biological data. The unimodal method was chosen because of the relatively long gradients (>0.3) found by preliminary DCA. The detrended form of correspondence analysis (CA) was used to accommodate the marked arch effect (quadratic dependence of the second axis on the first one) found in preliminary CA. This analysis was performed using CANOCO 4.5 for Windows (Wageningen, the Netherlands) according to available guides (Ter Braak & Smilauer 2002; Leps & Smilauer 2003).

RESULTS

Environmental parameters

The study streams ranged in altitude from 90 to 2200 m a.s.l. and had a wide range of environmental conditions. The environmental parameters measured are shown in relation to altitude (Fig. 2). Dependencies of all parameters with altitude were best explained by a one-phase exponential model. Therefore, the one-phase exponential regression curves are shown in Figure 2 with respective correlation coefficients (r^2). Among the measured factors, only temperature was strongly correlated with altitude (Fig. 2a; $r^2 = 0.84$). The relations of other factors to altitude were weak, but stream width reached maximum values and current velocity and substrate size reached minimum values at low altitudes (Fig. 2b–d).

Species richness

A total of 55 species were found (Table 1), with 1–24 species present per site. Dependencies of species richness on the five environmental factors are shown in Figure 3. Maximum species richness was found at low altitudes (Fig. 3a) and where there were high water temperatures (Fig. 3b), relatively slow current velocities (Fig. 3c), medium stream widths (Fig. 3d), and medium-small particle sizes (microlithal according to Hering *et al.* 2003) (Fig. 3e). The one-phase exponential model provided a better fit than the two-phase model for all relations except stream width (Fig. 3). Species richness was significantly higher at stream sites with aquatic macrophytes than at sites where macrophytes were absent ($P < 0.05$, Mann–Whitney test).

Assemblage structure

The first three divisions of TWINSPAN yielded eight groups of sites, each containing 3–12 sites (Table 2). Groups differed significantly from each other with respect to at least one environmental factor (Table 2). The groups varied from small alpine cold-water streams (groups 1 and 2) to plain and relatively warm-water watercourses (groups 6–8). The species compositions of the eight TWINSPAN groups are given in Table 1.

Ordination analysis of assemblage structure in relation to environmental factors was conducted using the DCA technique with all the recorded species incorporated into the ordination model (Fig. 4). Environmental parameters were passively projected on the ordination model (Fig. 4). A summary of the analysis is given in Table 3. The first gradient is the longest, explaining 13.7% of the total variability. The second and higher axes explain much less. Only the first ordination axis is well correlated with the environmental data ($r = 0.96$, Table 3). A correlation matrix (inter-set weighted correlations) of the environmental parameters and ordination axes is given in Table 4. All the environmental factors are better correlated with the first ordination axis than with all other axes (Table 4). This result suggests that the whole data set is governed by a single dominant gradient that corresponds to the altitudinal/longitudinal gradient.

DISCUSSION

Species richness

According to recent faunistic investigations, the mayfly fauna of western Siberia includes 57 species (Beketov & Kluge 2003; Beketov 2005, 2007; Beketov & Godunko 2005). In the present study, 55 species were recorded (Table 1), comprising approximately 96% of the overall species list known for the territory investigated. Over a relatively large range of altitudes (90–2200 m a.s.l.) and variations in related environmental factors, maximum species richness was found at low altitudes; at places with high water temperatures, relatively slow current velocities, medium stream widths, and medium-small particle sizes of the dominant substrate (microlithal); and in the presence of macrophytes (Fig. 3).

The trends in Ephemeroptera species richness found in the present study in western Siberia are in accordance with previously reported results for temperate-zone streams. A number of empirical studies have shown that taxonomic richness of ephemeropterans, and stream macroinvertebrates in general, increases with a decrease in absolute altitude and corresponding changes in related environmental factors (Allan 1975; Ward 1986; Perry & Scheffer 1987; Brussock & Brown 1991; Cereghino *et al.* 2003; Paller *et al.* 2006). When an entire river system is considered, the dependence of taxonomic richness on altitudinal/longitudinal river gradient is usually hump-shaped, with maximum taxonomic richness observed near (but not at) the lowland end of the river system (Minshall *et al.* 1985; Grubaugh *et al.* 1996). The "river continuum concept", a well-known ecological theory, predicts that the taxonomic richness of benthic communities will change with stream size, reaching a maximum in mid-order streams; whereas in headwaters or large rivers taxonomic richness will be relatively low (Vannote *et al.* 1980; Minshall *et al.* 1985).

The high level of taxonomic richness observed in medium-size watercourses is frequently attributed to the pronounced habitat heterogeneity of these water bodies because heterogeneous conditions can support species with different ecological preferences (Thienemann 1954). Several studies have shown that spatial heterogeneity of the stream bottom is the prime factor governing the taxonomic richness of stream invertebrates (Giller & Malmqvist 1998; Vinson & Hawkins 1998; Beisel *et al.* 2000). Other factors, such as temperature (Minshall & Robinson 1998), flow, substrate stability (Stanford & Ward 1983; Death & Winterbourn 1994) and substrate type (Minshall 1984) have also been

Table 1 Mayfly species present in the eight TWINSPAN groups of stream sites

Species	TWINSPAN group 1	2	3	4	5	6	7	8
Ameletus sp.	+	+	+	+				
Epeorus maculatus (Tshernova, 1949)		+	+					
Rhithrogena sp. (*hirasana*?) (Imanishi, 1935)	+	+						
Rhithrogena cava (Ulmer, 1927)	+	+	+	+				
Ephemerella aurivillii Bengtsson, 1908		+	+	+		+		
Baetis sp. *rhodani* group		+						
Baetis khakassikus Beketov et Godunko, 2005		+						
Baetis bicaudatus Dodds, 1923	+	+	+	+				
Leptophlebia chocolata (Imanishi, 1937)				+				
Epeorus alexandri Kluge et Tiunova, 1989			+	+				
Ephemerella nuda Tshernova, 1949		+	+					
Ephemerella mucronata (Bengtsson, 1909)			+					
Baetis sp. 1			+					
Baetis pseudothermicus Kluge,1983			+	+		+		
Baetis feles Kluge, 1980			+	+				+
Ecdyonurus aspersus Kluge, 1980				+	+			
Ephemerella lepnevae Tshernova, 1949			+	+				+
Ephemerella triacantha Tshernova, 1949		+	+	+		+	+	+
Choroterpes sp. (*altioculus*?) Kluge, 1984				+	+		+	
Epeorus pellucidus (Brodsky, 1930)			+	+	+	+	+	+
Heptagenia sulphurea (Müller, 1776)				+		+	+	
Potamanthus luteus (Linnaeus, 1767)						+	+	
Leptophlebia marginata Linnaeus, 1768						+		
Ephemera orientalis McLachlan, 1875						+	+	
Ecdyonurus joernensis Bengtsson, 1909						+	+	
Heptagenia flava Rostock, 1878						+	+	
Ephemerella ignita (Poda, 1761)						+	+	+
Baetis sp. 2						+		
Baetis ursinus Kazlauskas, 1963						+		+
Baetis vernus Curtis, 1834						+		+
Baetis tuberculatus (Kazlauskas, 1963)					+	+		
Baetis fuscatus (Linnaeus, 1761)				+		+	+	+
Siphlonurus alternarus Say, 1824							+	
Ephoron virgo (Olivier, 1791)							+	
Leptophlebia submarginata (Stephens, 1835)							+	
Isonychia ussurica Bajkova, 1970							+	
Ephemera vulgata Linnaeus, 1758							+	+
Rhithrogena lepnevae Brodsky, 1930				+		+	+	+
Ecdyonurus vicinus Demoulin, 1964							+	
Ecdyonurus abracadabrus Kluge, 1983							+	+
Heptagenia fuscogrisea (Retzius, 1783)							+	
Ephemerella lenoki Tshernova, 1952						+	+	+
Caenis robusta Eaton, 1884							+	
Caenis pseudorivulorum Keffermuller, 1960							+	+
Caenis miliaria (Tshernova, 1952)							+	
Caenis lactea (Burmeister, 1839)							+	
Caenis horaria (Linnaeus, 1758)							+	+
Brachycercus harrisella Curtis, 1834							+	
Cloeon simile Eaton, 1870						+	+	
Cloeon macronyx Kluge et Novikova, 1992							+	
Cloeon dipterum Linnaeus, 1761							+	
Cloeon bifidum Bengtsson, 1912							+	+
Baetis tricolor Tshernova, 1928							+	
Baetis sibiricus (Kazlauskas, 1963)						+		+
Baetis bacillus Kluge, 1983				+			+	+

Taxonomic classification according to Kluge (1997).

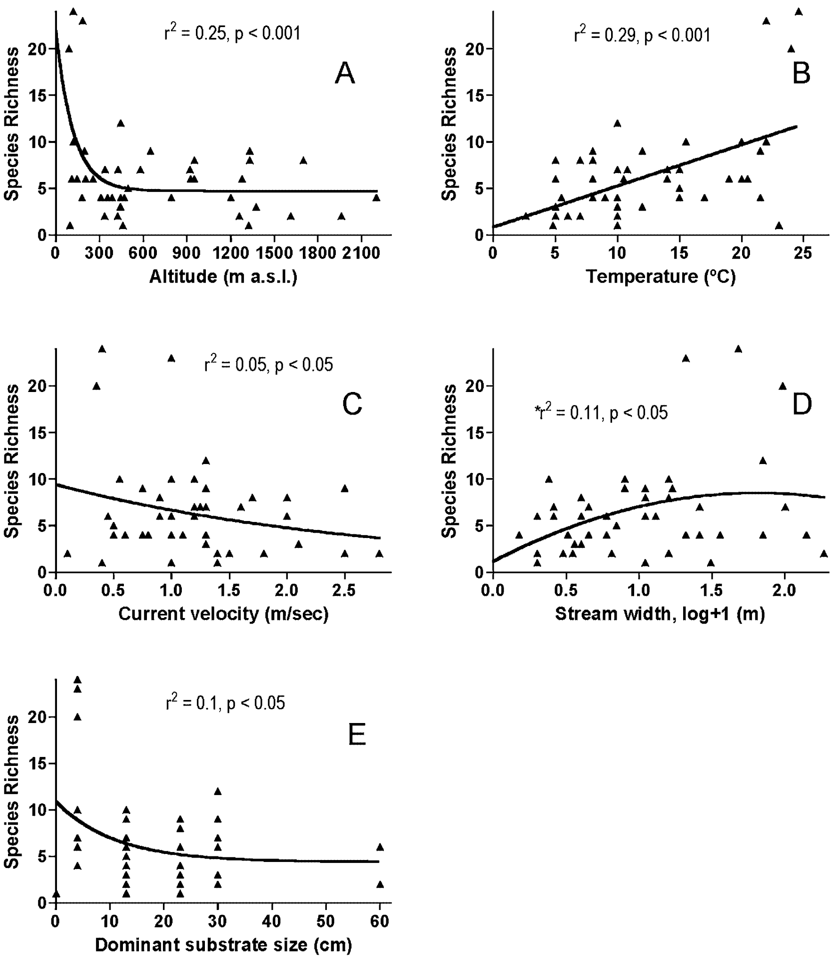

Figure 3 Ephemeroptera species richness (number of species per site) in relation to the main environmental parameters: (a) absolute altitude (m a.s.l.), (b) temperature (°C), (c) current velocity (m/s), (d) stream width (log + 1 transformed, m), and (e) dominant substrate particle size (cm). One-phase (a–c,e) and two-phase (d) exponential regression curves and squared Pearson's correlation coefficients (r^2) are given ($*r^2$ indicates the value for the two-phase model).

Table 2 Environmental parameters and species richness in the eight TWINSPAN groups of stream sites

	TWINSPAN group							
Variable	1	2	3	4	5	6	7	8
Number of sites	6	4	6	4	3	12	4	7
Altitude (m a.s.l.)	1728 (151)^{a}	1408 (98)^{a}	916 (101)^{b}	811 (166)^{b}	413 (39.7)^{c}	273 (41.6)^{c}	123 (21.3)	325 (48.8)^{c}
Temperature (°C)	5.18 (0.6)^{a}	5.45 (0.52)^{a}	9.38 (0.5)^{b}	9.5 (0.96)^{b}	10.7 (0.7)^{b}	16.4 (1.3)^{c}	23.4 (0.6)	15.5 (1.4)^{c}
Current velocity (m/s)	1.63 (0.43)^{a}	1.4 (0.27)^{a}	1.35 (0.24)^{a}	1.43 (0.2)^{a}	1.5 (0.15)^{a}	0.88 (0.1)	0.54 (0.16)	1.13 (0.11)
Stream width (m)	2.64 (0.62)	4.25 (1.97)^{a}	4.53 (2.33)^{a}	29.3 (14)^{b}	66 (59.5)^{ab}	23.8 (12)^{b}	48.3 (17) ^{b}	28.1 (13)^{b}
Substrate size (cm)	26.5 (7.51)^{a}	22.3 (3.5)^{a}	28.2 (7.09)^{a}	22.3 (3.5)^{a}	25.3 (2.33)^{a}	11.7 (1.9)^{b}	3 (0.98)	11.9 (2.5)^{b}
Macrophytes (% sites)	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	16.7^{b}	100	14.3^{b}
Species richness	2.5 (0.34)^{a}	5.7 (1.65)^{b}	6.5 (0.67)^{b}	8.2 (1.65)^{b}	2 (0.58)^{a}	5.7 (0.82)^{b}	17 (5.4)	6.14 (0.7)^{b}

Data are means with standard errors in parentheses. Within rows, values marked with the same letters are not significantly different ($P > 0.05$, ANOVA followed by Tukey's post-hoc test and the χ^2 test).

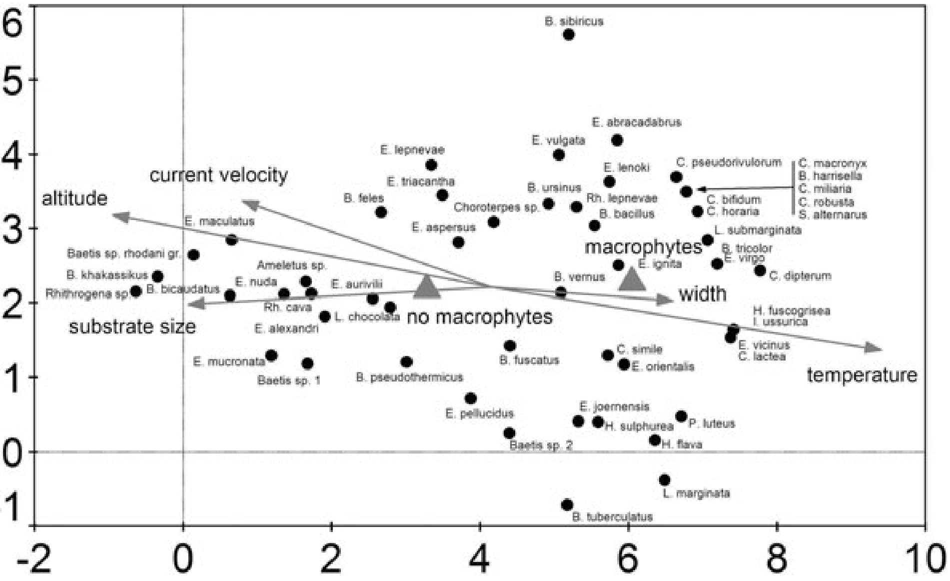

Figure 4 Ordination diagram constructed using detrended correspondence analysis. Species and environmental factors are shown. For full species names see Table 1.

Table 3 Summary of the detrended correspondence analysis performed with all the recorded species and passively projected environmental variables

	Axis				
	1	2	3	4	Total inertia
Eigenvalue	0.836	0.389	0.265	0.205	6.098
Length of gradient	7.772	4.321	4.106	3.319	
Species-environment correlation	0.956	0.294	0.338	0.446	
Cumulative percentage variance					
Of species data	13.7	20.1	24.4	27.8	
Of species-environment relation	47.4	49.4	0.0	0.0	
Sum of all eigenvalues					6.098
Sum of all canonical eigenvalues					1.556

found to be important parameters influencing the taxonomic richness of stream macroinvertebrates. However, it is difficult to understand the importance of separate environmental factors, as the factors are normally inter-correlated.

The high level of mayfly species richness observed in the present study in the medium-size plain rivers (stream width 20–96 m) can probably be explained by the relatively high level of habitat heterogeneity in these watercourses. However, spatial heterogeneity was not directly quantified and related to species richness patterns. Among the analyzed environmental parameters, altitude and temperature were better predictors of species richness than other recorded variables (Fig. 3), although the

Table 4 Correlation matrix of environmental parameters and the detrended correspondence analysis ordination axes (interset weighted correlations, axes based on the species data set)

	Ordination axes (species data set)			
	1	2	3	4
Altitude	−0.8875	0.0871	0.1900	−0.2290
Temperature	0.9126	−0.0669	−0.2247	0.2404
Current velocity	−0.5812	0.1299	0.1094	−0.1311
Stream width	0.4257	−0.0022	−0.0002	−0.0091
Substrate size	−0.7137	−0.0713	0.3033	−0.4078
Macrophytes	0.6743	0.0624	−0.1470	0.1692

environmental characteristics considered were all more or less inter-correlated (Figs 2,4). Hence, it is only possible to conclude that taxonomic richness of mayflies is strictly dependent on the entire altitudinal/longitudinal gradient of environmental factors.

Assemblage structure

The results of the present study have shown that the mayfly assemblage over the relatively large range of altitude-related environmental factors can be separated by TWINSPAN into eight distinct groups. These groups differ significantly with respect to at least one of the considered environmental factors (Table 2). The most drastic changes in species composition of mayfly assemblages were observed between the two second-division TWINSPAN groups (third-division groups 1–4 and 5–8, Tables 1,2). The altitudinal border between these two groups is approximately within the range 400–800 m a.s.l. (Table 2). If these two groups are compared with the classical zonation system developed by Illies and Botosaneanu (1963), they can be roughly classified as rithral (groups 1–4) and a group comprising metarithral and epipotamon (groups 5–8), that is, the lowest zone of rithral and highest zone of potamal. According to the physical parameters, only TWINSPAN group 7 can be unequivocally referred to as potamal, as it is characterized by a mean summer temperature of 23°C (Table 2). On the basis of such biological characteristics as the considerable presence of the families Heptageniidae, Ephemerellidae, and Leptophlebiidae (Table 1), group 7 can be assigned to rithral. Similar difficulties with the applicability of the system of Illies and Botosaneanu (1963) for watercourses of the Russian Far East and eastern Siberia have already been discussed by Levanidova (1982). In this previous study, in these regions, many watercourses were characterized by a combination of high summer water temperature with rithron benthic elements, which is comparable to the present results.

The TWINSPAN classification given here does not cover all types of watercourses present in western Siberia. As mentioned before, large plain rivers (e.g. the Ob River) and slow-current plain rivers, which are typical of swampy territories of the Western Siberian Plain, were not included in the analyses. These types of habitats are quite different from any of the groups defined here by TWINSPAN: they are characterised by low mayfly abundance and species richness and typical potamal biological communities (e.g. prevalence of *Caenis* spp. and *Cloeon* spp. in Ephemeroptera assemblages).

In the present study, multivariate ordination revealed that mayfly assemblages are structured by a single dominant gradient of altitude-related environmental factors. Among the environmental factors considered in the present analysis, altitude and water temperature were the best predictors determining significant structural changes in mayfly assemblages. The amount of variability in mayfly assemblages that can be explained by the second ordination axis in DCA (i.e. explained by environmental factors other than the altitudinal/longitudinal gradient) increases with a decrease in absolute altitude (Fig. 4). This means that at relatively high elevations mayfly assemblages are uniquely structured by the altitudinal gradient of environmental factors, whereas in the lowlands a more diverse set of factors (including altitude-independent factors) may structure the assemblages.

Structural changes in lotic macroinvertebrate communities including mayflies that are associated with an altitudinal/longitudinal gradient of environmental factors are well known in freshwater ecology. Studies that describe in detail the altitude-dependent structure of mayfly assemblages are more rare than those broadly focused on entire macroinvertebrate communities and using relatively high levels of taxonomic identifications (e.g. genus or family; but see Dodds & Hisaw 1925; Kamler 1967; Brodsky 1980; Levanidova 1982; Ward 1986). For Asia, knowledge about the ecology of Ephemeroptera is particularly limited, and for the temperate zone in Asia only the monograph by Levanidova (1982) describes mayfly assemblage compositions in relation to environmental parameters. A reference should also be made to the detailed study by Brodsky (1980) that was conducted near the region investigated in the present study, but in the specific desert-mountain climate zone of Tian Shan, Central Asia. Nevertheless, these two studies are purely descriptive; analysis revealing clear correlations between physical factors and assemblage structural changes was not performed. Furthermore, environmental conditions and species composition of mayfly assemblages in the Russian Far East and, in particular, in Tian Shan differ significantly from those in the region considered in the present study. All this precludes direct comparison of the present results with these two investigations.

Undoubtedly, the present paper provides only baseline information on patterns in the community structure of Ephemeroptera in Siberian streams. Further investigations focused on stream macroinvertebrates in this extremely large and poorly investigated territory are necessary to develop a detailed understanding of the relationships between biological communities and environmental factors.

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