

The distribution of littoral chironomids along an altitudinal gradient in High Tatra Mountain lakes: Could they be used as indicators of climate change?

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Abstract – We studied assemblages of littoral chironomids from three alpine lakes in the High Tatra Mountains (Slovakia) along an altitude range of 1725–2157 m. The study sites were selected in order to emphasize differences in their thermal regimes. Littoral samples were taken quantitatively in the ice-free seasons of 2000 and 2001. In total, 3468 chironomid larvae and pupae were collected and 29 taxa were identified. Some parameters of the littoral chironomid assemblages showed clear patterns along the altitude gradient. The number of taxa and Shannon diversity increased markedly with decreasing altitude. Density, however, did not show any correlation with altitude. Even though gatherers highly dominated in all sites, their relative abundance decreased with decreasing altitude. The ratio of scrapers and predators correlated negatively with altitude. According to the results of a Detrended Correspondence Analysis, *Pseudodiamesa arctica* and *Micropsectra radialis* were chosen as indicator species for alpine lakes > 2000 m a.s.l. Typical subalpine lake inhabitants are *Zavrelinyia* sp., *Prodiamesa olivacea*, *Corynoneura scutellata* group, *Cricotopus polaris*, *Micropsectra bavarica* and *Paratanytarsus austriacus*. A single species, *Micropsectra junci*, seemed to be characteristic of alpine lakes < 2000 m a.s.l. This “gradient lake concept” could be used to predict changes in mountain lake fauna under expected climate change scenarios. Generally, an upward shift of subalpine species would be expected. The thermal regime of lakes, however, also depends on several local factors. Consequently, the schemes outlined here would not be valid for the entire Tatra lake district.

Key words: Chironomidae / alpine lakes / climate change / bioindicators / Slovakia

Introduction

The ongoing debate about climate change and its impact on aquatic ecosystems has increased the need for knowledge about long-term changes and consequent effects on natural variability. According to both recent estimations and future simulations, global warming is and will be particularly pronounced in alpine and arctic areas (Houghton *et al.*, 1996; Beniston *et al.*, 1997). In addition, mountains are particularly susceptible to the impacts of a rapidly changing climate, and could be important locations for the early detection and study of the signals of climatic change and related impacts on hydrological, ecological and societal systems (Beniston, 2003). Indeed, mountain lakes at around 1500 to 2000 m in altitude are likely to be ultra-sensitive, as they are located in the elevation range where changes in both ice-cover and snow

cover duration will be particularly pronounced (Thomson *et al.*, 2005).

Even though alpine lakes are considered to be in pristine environments, their conditions have been changed in various ways, *e.g.* by the introduction of fish, acidification, long-range air pollution transport and global climate change (Pechlaner, 1984; Psenner and Schmidt, 1992; Psenner and Catalan, 1994; Camarero *et al.*, 1995). However, due to their remote and relatively undisturbed character, attention given to alpine lakes has increased recently in response to the recognition that they could be used as potential indicators of climate change. In remote mountain areas, altitude is considered the driving variable determining living conditions. Altitude is closely connected with the main climatic gradient, distinctly reflected in the increase of air temperature as elevation decreases (Lotter *et al.*, 1997).

The “gradient lake concept” of alpine lakes situated along an altitudinal/temperature gradient was suggested

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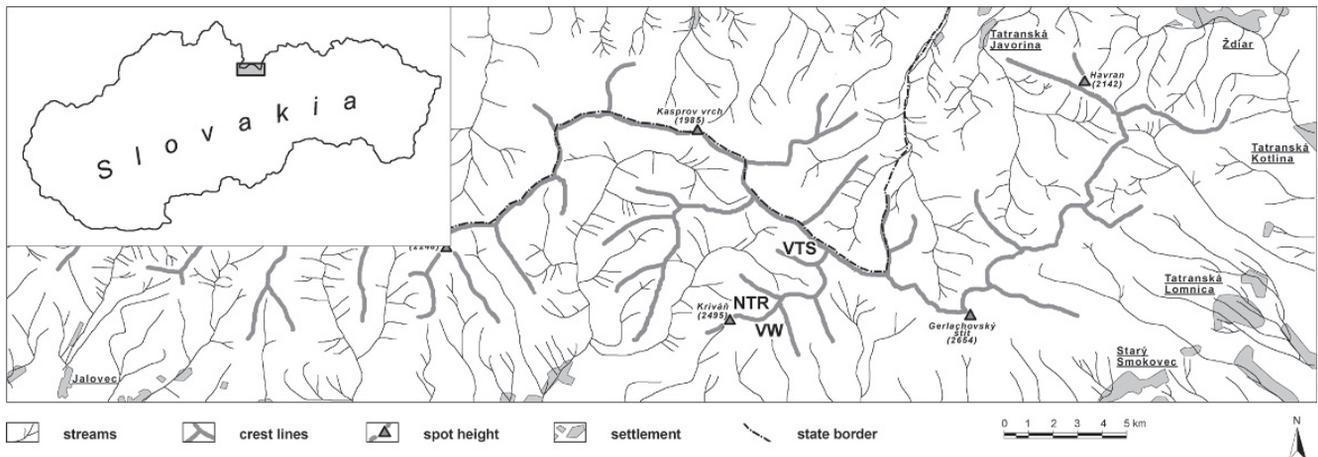


Fig. 1. Location of the High Tatra Mountains and the studied lakes. For lake names see Table 1.

within the framework of the EMERGE project (Patrick, 2003). The idea was that lakes at different elevations represent natural climate/altitude gradients and could serve as a model for predicting the possible impact of temperature change. Studies of the biota of similar lakes with different thermal regimes could contribute to the understanding of the ecological impacts of climate change as well as predict possible lake fauna development, in cases of both climate heating and/or cooling. It has been hypothesized that such conditions are fulfilled in alpine environments, where the main driving factor is climate and changes are clear even along short altitude gradients. Global, large-scale patterns of climate ultimately control the structure of the benthic invertebrate communities in lakes; however, at small scales site-specific factors dominate (Johnson and Goedkoop, 2002). Coupled with changes in temperature and climate are changes in other lake processes, including rates of catchment weathering, inputs of nutrients and organic material, and lake productivity, to name a few (Brodersen and Quinlan, 2006). Therefore, the gradient lakes for this study were selected using the following criteria: (i) a low degree of human disturbance in their catchments such as grazing or recreation; (ii) lake water quality influenced only by atmospheric pollution and/or natural variability; and (iii) localities belonging to the same catchment. Moreover, they were selected in order to minimize geological, chemical and morphological variability, as well as to emphasize differences in elevation and thus in their thermal regimes.

Chironomid communities have proven to be good indicators of lake-ecosystem responses to different environmental and anthropogenic disturbances (Brodersen and Quinlan, 2006). In addition, chironomids are the most widely distributed insect family in freshwaters, comprising thousands of species corresponding to 25% of aquatic insects (Cranston, 1995). Freshwaters at high altitudes and latitudes are colonised mainly by chironomids (e.g. Brittain and Milner, 2001; Lods-Crozet *et al.*, 2001a, 2001b), but little was known about the chironomid communities of mountain lakes in the Tatra Mts. until the 20th century. Only recently, due to pan-European projects

(e.g. AL:PE, MOLAR, EMERGE), have intensive surveys of the composition and structure of chironomid communities, as well as the entire benthos, of high altitude Tatra lakes begun. For an overview of Tatra lakes research, see Bitušík *et al.* (2006a).

A previous study of benthic fauna from remote lakes across Europe (Fjellheim *et al.*, to appear) has shown that responses of faunal assemblages to an altitudinal gradient vary with latitude. Although there were some common species, there were also differences in chironomid taxonomic composition among lake districts. This study underlined the importance of having knowledge of the regional fauna in order to understand climate-driven processes on a broader geographical scale.

Čiamporová-Zaťovičová *et al.* (to appear) have already tested the validity of the gradient lake concept as a possible indicator of climate change in the High Tatra Mts. based on the entire littoral zoobenthos. Therefore, we focused on the chironomid assemblages of these gradient lakes and addressed the following questions: (i) Do the chironomid assemblages differ among the lakes?; (ii) Are these changes sufficiently significant to indicate climatic events?; (iii) Are we able to establish potential indicator taxa for each surveyed lake and lake groups they represent?; and (iv) Will it be sufficient to just monitor chironomids of gradient lakes instead of both/either a higher number of lakes and/or a higher number of other taxa for the purpose of tracing the effects of temperature changes in the Tatra lake district?

Study sites

The three selected gradient lakes Vyšné Temnosmrečinské pleso (VTS), Nižné Terianske pleso (NTR), and Vyšné Wahlenbenbergovo pleso (VW) are located in the High Tatra Mountains (the West Carpathians). They are situated above the timberline at altitudes 1724 m, 1940 m and 2155 m, respectively, and drain into the river Váh (Fig. 1). In the Tatra Mts., no lakes situated along one chain fulfilled the conditions for

Table 1. Basic characteristics of the studied High Tatra lakes (Kopáček *et al.*, 2004; Gregor and Pacl, 2005).

Lake name	Vyšné	Nižné	Vyšné
	Wahlenbergovo p. VW	Terianske p. NTR	Temnosmrečinské p. VTS
Location	49.1642 N 20.0271 E	49.1698 N 20.0143 E	49.1891 N 20.0395 E
Altitude (m)	2157	1940	1724
Lake area (m ²)	51 655	55 580	55 625
Volume (m ³)	392 078	871 668	414 713
Max. depth (m)	21	47	20
Mean depth (m)	5.3	15.7	7.5
Residence time (years)	1.01	0.65	0.36
Duration of ice cover (days)	217	203	189
Inlet/outlet	0/0	1/1	1/1
Littoral substrate type: rocks:sand:organic matter (%)	95:04:01	90:10:00	88:08:04
Maximum daily mean water temperature in 2001 (°C)	11.6	11.8	12.9
pH	6.26	6.73	7.19
Alkalinity (µg.L ⁻¹)	29.3	89	261.9
DOC (mg.L ⁻¹)	0.15	0.26	0.2
Catchment area (ha)	32	110	112
Orientation	S	W	NW
Bare rocks: moraine: alpine meadows (%)	37:51:12	40:32:28	40:34:26
Precipitation (mm.year ⁻¹)	1538	1446	1326

gradient lakes (differences in size, volume or chemistry were too large); consequently, the lakes selected are located in different valleys representing separate branches of the same river system. The distances between particular lakes vary from ~0.9 km (VW and NTR) to ~2.7 km (VW and VTS).

With respect to the altitudinal distribution of vegetation in the Tatra Mountains, VTS is situated in the subalpine zone, while NTR and VW are located in the alpine zone. All these lakes have relatively deep basins with small lake surfaces (~5 ha). The watersheds are formed of acid biotite-rich granitoides to tonalities. Bare rocks and screes are the dominant cover in the watersheds, with increasing percentage with altitude. Alpine meadows (dry tundra) on undeveloped soils occur in the remainder of the watersheds. Sparse bushes of dwarf pine (*Pinus mugo*) are present in the VTS watershed, while they are rare in NTR, and are absent in VW. The morphometric and geographic characteristics of the catchment areas and lake basins are given in Table 1.

The lake shores are formed in general by massive rocks; some dwarf pine shrubs grow on the shore of VTS, such that some branches reach the water. The littoral substrates consist mainly of gravel and pebbles. Small areas of sand with a high amount of fine organic matter were found in the littoral of VW. The two lower elevation lakes have inlets and permanent out-flowing streams. VW is a seepage lake without an apparent inflow or outflow.

Climate conditions of the Tatra Mts. are continental, reaching a maximum average air temperature of 9 °C (July) and minimum of -10 °C (January) at the altitude 1800 m. The average yearly precipitation is ~1280 mm (Smoleň and Ostrožlík, 1991). The maximum daily mean water temperature of lakes situated from 1580–2157 m a.s.l. varies from 10.2 to 17.8 °C (Šporka

et al., 2006). Ice-cover on the lakes persists for 190 to >200 days. For more hydrological characteristics, lake water chemistry and temperature conditions, see Gregor and Pacl (2005) and Bitušík *et al.* (2006a).

All lakes are fishless, and their watersheds have not been directly affected by anthropogenic disturbance or landscape use since the 1950s when the Tatra Mountains became a national park. Even though acid deposition in the second half of the 20th century had significant impact on many Tatra lakes including VW (Kopáček and Stuchlík, 1994), at the time of this survey, the lake was no longer considered acidified (Kopáček *et al.*, 2006).

Material and methods

Field and laboratory

Field work was performed during the ice free seasons in 2000 and 2001 (June–October) at monthly intervals. VW (two sampling sites) was sampled nine times, NTR (three sampling sites) eight times and VTS (one sampling site) 13 times.

Quantitative benthic samples from the littoral zones were taken with a modified Hess sampler with sampling area 0.1 m² and mesh-size 500 µm (Helan *et al.*, 1973) modified by Krno (1988) for using in standing waters. To obtain representative and comparable littoral samples, all sites were located near lake outlets and far from inlets (if present) to avoid their influence (different water temperature, rheophilic to rheobiont fauna). Sampling locations reached from the shore to a water depth of ~0.4 m and covered an area of 0.3 m².

Even though pebbles were the dominant substrate type, the substrate size varied from fine gravels to small

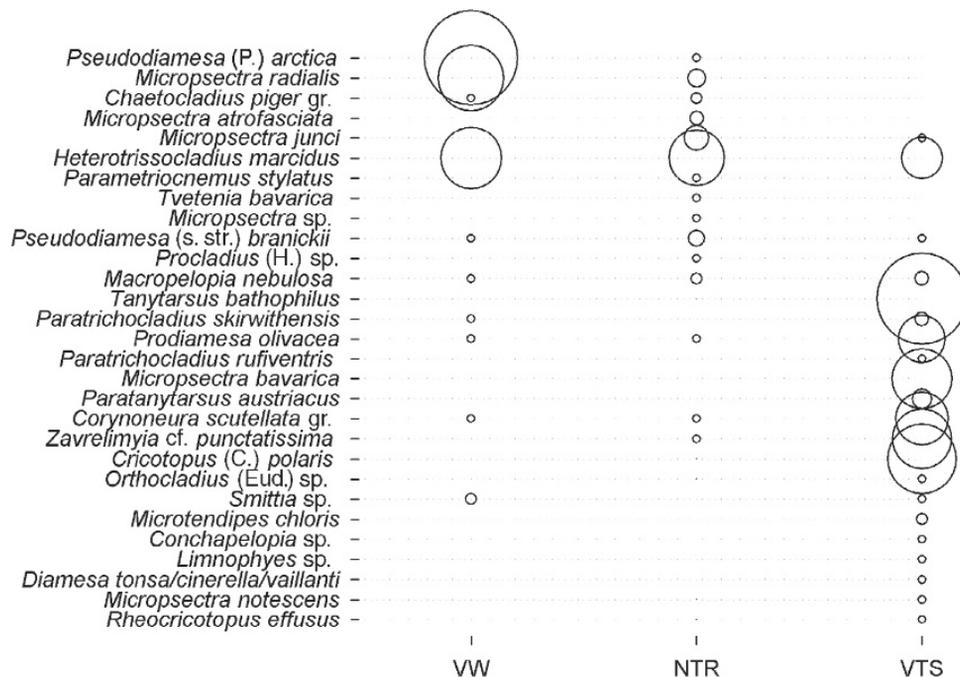


Fig. 2. Diagram of the distribution of chironomid species/taxa in the littorals of the studied lakes. Circles represent square root transformed densities. Lakes are arranged in order of decreasing altitude, species according to axis 1 scores in DCA.

cobbles (Allan, 1995) at all sites. In the uppermost VW, an additional substrate-type consisting of sand mixed with a high amount of soft organic matter was sampled. However, this substrate was excluded from the between-lake analysis and was only used for in-lake comparisons.

The material collected was placed in plastic bottles and fixed *in situ* with formalin to a final concentration of 4%. In the laboratory, chironomids were sorted, counted and mounted on a slide under a low-power stereomicroscope (7–40 \times). Identification was done under high magnification (400 \times) to genus, species or group of species using the following taxonomic keys for larvae: Wiederholm (1983), Schmid (1993), Stur and Ekrem (2006); and for pupal exuviae and pharate adults: Schlee (1968), Hirvenoja (1973), Simpson *et al.* (1983), Wiederholm (1986), Langton (1991) and Ekrem (2004).

Chironomid taxa were divided into feeding groups mainly according to Moog (1995), with some additional taxa according to Bitušík and Hamerlík (2003).

Data analysis

Shannon's diversity index (H') (Shannon and Weaver, 1949) was calculated for every sample using Species Diversity and Richness 4.0 software (Seaby and Henderson, 2004). The T-test was used to compare the relative abundance of dominant species between two different sediment-types in the littoral of VW. Values of $P < 0.05$ were considered significant.

Detrended Correspondence Analysis (DCA) (Hill, 1979) was used to visualize the distribution of data along a main environmental gradient using the CANOCO 4.5 package (ter Braak and Šmilauer, 2002). The data

matrix included 29 taxa from 36 samples. Species abundance data (ind. m^{-2}) were $\log_{10}(x + 1)$ transformed prior to analyses. To reduce random noise, taxa found in just one sample were omitted from the data set. In the ordination diagram, only taxa with species weight range $\geq 10\%$ are shown.

Chironomid data of 34 Tatra lakes situated between 1579–2145 m a.s.l. (Krno *et al.*, 2006) were used for verifying the correlation of altitude and the abundance of taxa considered characteristic in this paper, which enabled us to establish indices of characteristic taxa for particular altitude zones. SigmaStat for Windows was used for regression analysis.

Results

Overall, 3468 chironomid larvae and pupae were collected and 29 taxa were identified in the littoral of the investigated lakes (Fig. 2).

In the subalpine VTS, the subfamily Chironominae, especially Tanytarsini, dominated with 44% of the total abundance. Despite the low frequency (recorded in only one sample) the *Tanytarsus lugens* group was the most abundant taxon (26%), followed by *Micropsectra bavarica* (Stur and Ekrem, 2006) ($\sim 16\%$). Orthoclaadiinae represented 34% of the total abundance; the most abundant and frequent species were *Cricotopus* (s. str.) *polaris* (Kieffer, 1926) along with the *Corynoneura scutellata* group comprising 24% of the total abundance.

The most abundant species in the littoral of the lower located alpine NTR was *Heterotrissocladius marcidus* (Walker, 1856), representing 62% of the total abundance.

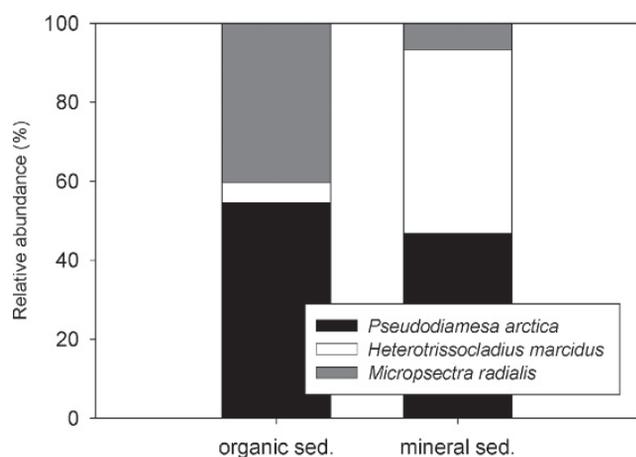


Fig. 3. Relative abundance of dominant species/taxa in different substrate types in Vyšné Wahlenbergovo pleso (VW). Organic sed. – soft sediment with a high amount of organic matter, mineral sed. – coarse sediment composed of stones and pebbles.

Pre-imaginal stages of *Micropsectra junci* (Meigen, 1818) represented ~14% of the chironomid abundance and were slightly less frequent than the previous species. The remaining taxa represented less than 10% of total abundance; however, some such as *Macropelopia nebulosa* (Meigen, 1804) and *Zavrelimyia* sp. occurred with high frequency.

Pseudodiamesa (*Pachydiamesa*) *arctica* (Malloch, 1919), *Heterotrissocladius marcidus* and *Micropsectra radialis* (Goetghebuer, 1939) were the dominant taxa in the littoral of the uppermost lake (VW) representing together ~99% of the chironomid assemblages.

In this lake, the structures of chironomid communities from the organic-rich fine substrate and coarse mineral substrate were also compared. There was no significant difference in the relative abundance of *P. arctica*, with larvae representing ~50% (Figs. 3 and 4A). However, significant differences in the proportion of *H. marcidus* ($P < 0.005$) and *M. radialis* ($P = 0.01$) were found (Figs. 4B and 4C). In the site with soft organic sediment, *M. radialis* dominated (40%) along with *P. arctica*, while *H. marcidus* made up only 5% of the total abundance. On the contrary, *H. marcidus* was more common (47%) in the site with coarse mineral substrata, and the relative abundance of *M. radialis* was markedly lower (6%) (Figs. 3 and 4).

Some parameters of chironomid littoral assemblages showed clear patterns with altitude. The number of taxa and Shannon diversity increased with decreasing altitude (Figs. 5A and 5B). While only five taxa were found in the uppermost VW, 14 and 25 taxa were recorded in NTR and VTS, respectively. Density did not show any correlation with altitude, as the lowest density was observed in the intermediate NTR (Fig. 5C).

Various trends along the altitude gradient were also clear when analysing the qualitative structure of chironomid assemblages. Differences were evident even on the subfamily level; in every lake, a different subfamily dominated and their relative abundance markedly changed with altitude (Fig. 6A). Diamesinae dominated in VW and then

its proportion decreased with decreasing altitude. In the subalpine VTS, Chironominae (especially the Tanytarsini tribe) was the most abundant subfamily, with a trend opposite to the Diamesinae. NTR was dominated by Orthoclaadiinae and its proportion was higher than in both the lower and higher situated lakes. The proportion of Tanytarsinae and Prodiamesinae slightly increased with decreasing elevation; however, the abundance of taxa in these subfamilies was only marginal in the studied lakes.

Various trends along the altitude gradient were evident in the chironomid trophic structure (Fig. 6B). Gatherers highly dominated at all sites; however, their relative abundance decreased with decreasing altitude. In contrast, the ratio of scrapers and predators correlated negatively with altitude. The numbers of filter-feeders in the surveyed lakes was very low, and independent of altitude.

The first two axes of the DCA explained 40.5% of the overall variability in species data. Sampling sites were scattered along the first axis, but samples of particular lakes were separated from each other and the three lakes clearly identified (Fig. 7A). It can be assumed that the main axes represents temperature-altitude gradient, with temperature increasing and altitude decreasing from left to right. Indicator species for each altitude zone were selected according to their location in the DCA diagram. In the left part of the diagram, cold-stenothermal species such as *Pseudodiamesa arctica* and *Micropsectra radialis*, the indicators of high alpine lakes, are located. The right part of the diagram is represented by taxa generally common in the subalpine lake (VTS), such as *Zavrelimyia* sp., *Prodiamesa olivacea* (Meigen, 1818), the *Corynoneura scutellata* group, *Cricotopus polaris*, *Micropsectra bavarica* and *Paratanytarsus austriacus* (Kieffer, 1924). Species widely distributed and common in nearly all Tatra lakes, such as *Heterotrissocladius marcidus*, *Macropelopia nebulosa* but also a species typical for NTR (*Micropsectra junci*), are located in the central part of the diagram (Fig. 7B).

To verify if these indicators based on the gradient lakes could be used throughout the Tatra lakes generally, indexes were assigned to each of the indicator taxa (Fig. 8). Littoral chironomid data of 34 Tatra lakes at altitudes ranging from 1579 to 2145 m (Krnó et al., 2006) were used for the validation procedure. Using just the proposed indicator species/taxa, an index for the altitude of each lake was calculated by multiplying the abundances of each indicator species/taxa with the appropriate index and dividing by total abundance. Some of the indicator taxa, however, had to be excluded from the analysis due to their absence in the 34-lake taxa list (e.g. *Micropsectra bavarica*, *Cricotopus polaris*). Regression analysis of the average index of littoral chironomid assemblages and altitude of the lakes showed a close relation: 42% of the variability in the index could be explained by altitude ($n = 34$, $P < 0.001$) (Fig. 9). Subalpine lakes as well as alpine lakes above 2000 m a.s.l. were clearly identified using the indicator species/taxa. However, alpine lakes at altitude 1800–2000 m could not be identified using these indicators.

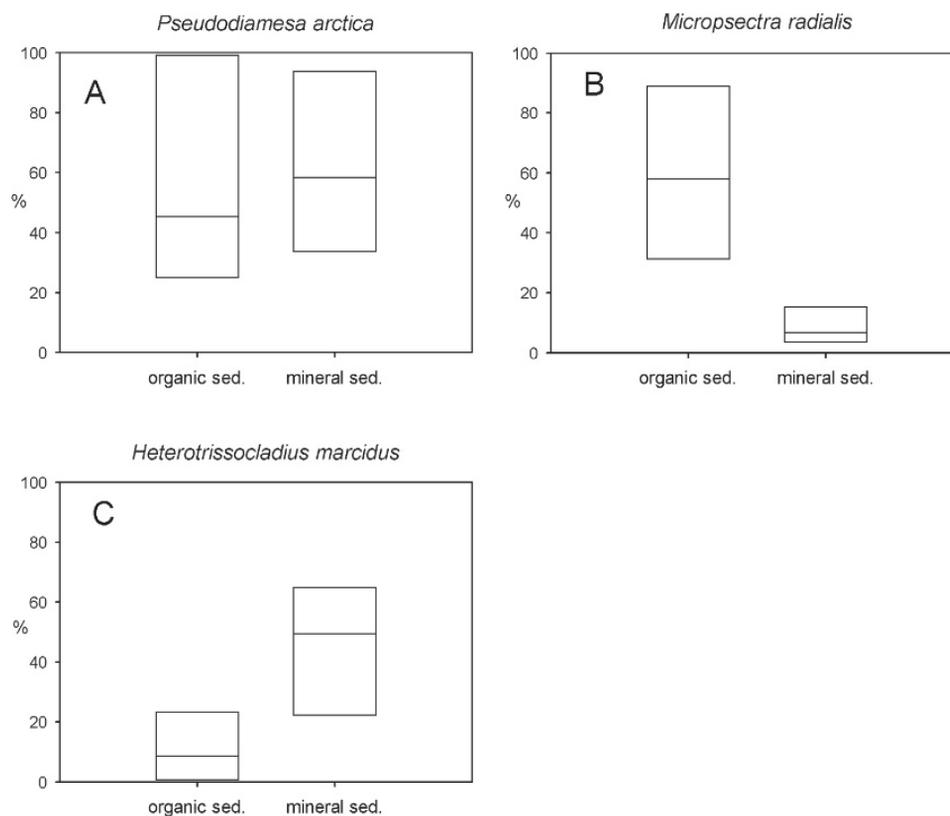


Fig. 4. Box & Whisker plots showing the variability in relative abundance of dominant species in different substrate types in the littoral of Vyšné Wahlenbergovo pleso (VW). A – *Pseudodiamesa arctica*, B – *Micropsectra radialis*, C – *Heterotrissocladius marcidus*.

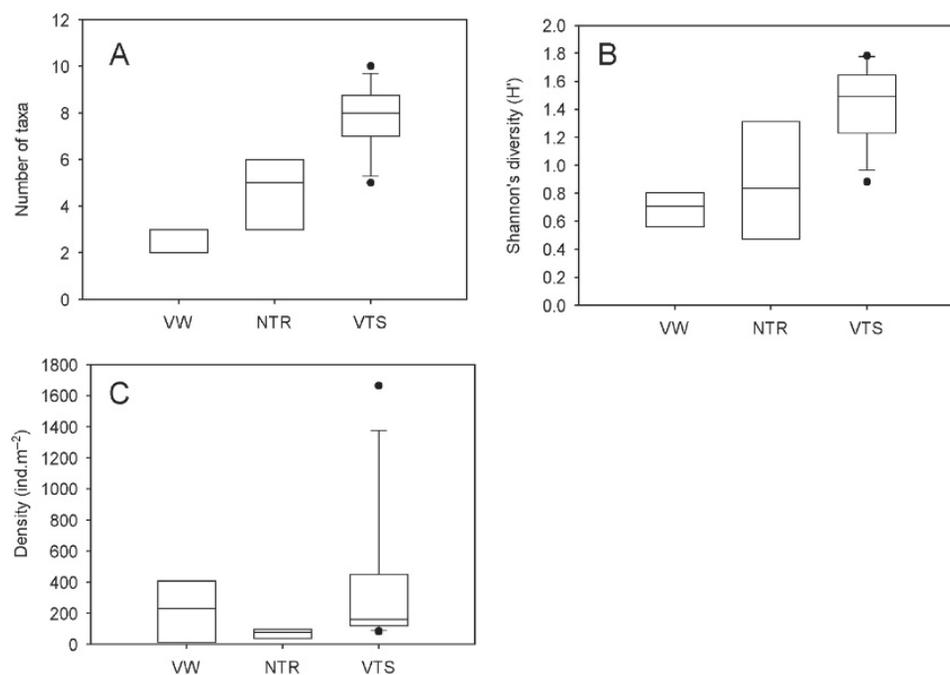


Fig. 5. Box & Whisker plots showing the variability of biotic scores in the littoral of the surveyed lakes. A – number of taxa, B – Shannon's diversity, C – density.

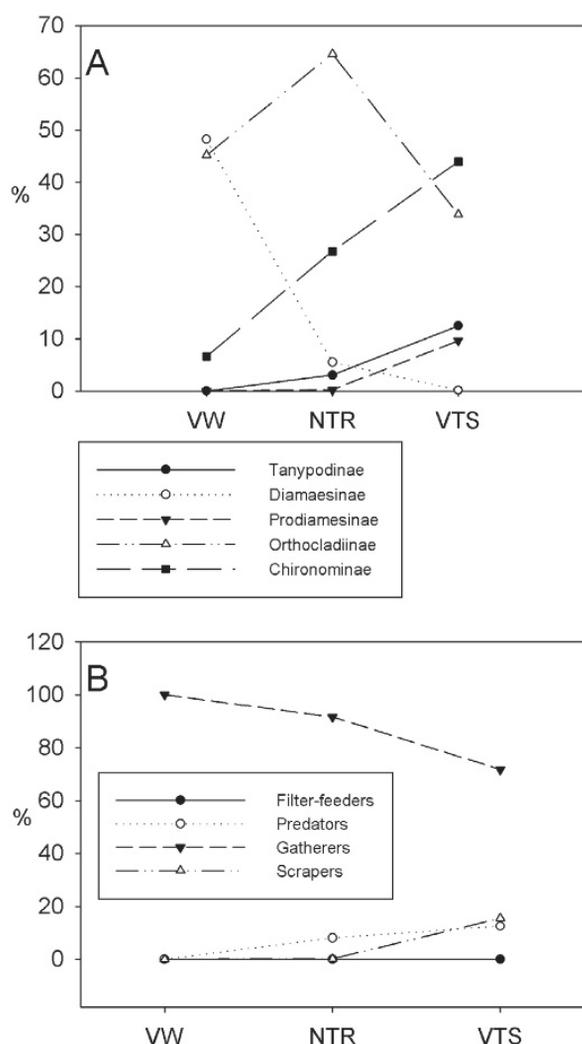


Fig. 6. Changes in the ratios of chironomid subfamilies (A) and feeding groups (B) with decreasing altitude.

Discussion

The taxonomic structure found in the lakes is generally consistent with the distribution patterns at higher altitudes and/or latitudes described by Thienemann (1932) and since confirmed many times (e.g. Laville, 1971; Kownacki *et al.*, 2000; Boggero *et al.*, 2006; Füreder *et al.*, 2006). When comparing the chironomid fauna composition of the Tatra lakes (Bitušík, 2004) with the fauna of remote lakes across Europe (Fjellheim *et al.*, 1997; Schnell, 1998), high similarity with some French and Austrian Alps and Pyrenees lakes can be found on the generic and species level. However, taxa occurring in some remote lakes in the Italian Alps, Scotland, and especially in Scandinavia, such as the genera *Protanypus*, *Mesocricotopus*, *Monodiamesa*, *Heterotanytarsus*, *Corynocera*, probably do not occur in the Tatra lakes. Furthermore, it seems that some species with broad geographical distribution across Europe are specific for particular mountain ranges. For example, *Paracladius alpicola* (Zetterstedt, 1850) and *Micropsectra contracta* (Reiss, 1965) are widespread in the Alps and

Pyrenees, but they are rare or entirely absent in the Tatra Mountains (Bitušík, 2004; Bitušík *et al.*, 2006b).

The species collected in this present study are all of Palaearctic and/or Holarctic origin (Sæther and Spies, 2004) and no endemic species were identified. With respect to the distribution of some species, the Tatra Mts. can be seen as “islands” above the surrounding landscape. It is reasonable to suppose that the occurrence of such species as *Pseudodiamesa arctica* and *Micropsectra radialis* in Slovakia is restricted to just a few lakes created by the last glaciation, where they have remained isolated in high-elevation lakes until the present. Our investigation has resulted in new insights into the previous debate on the autecology of *Heterotrissocladius marcidus* larvae (Walker and Mathewes, 1987; Warwick, 1989). In soft sediments with high amount of organic matter, *M. radialis* dominated and *H. marcidus* represented only a small percentage in density, while the reverse was true in mineral substrates. This observed microdistributional pattern supports Warwick’s (1989) opinion that the driving force behind chironomid community changes in Holarctic lakes appears to be the interplay between mineral sediment accumulation and the availability of organic food resources rather than direct temperature change. As the amount of organic matter in substrates increases, larvae of *Heterotrissocladius* can no longer compete and are replaced by species like *Micropsectra* which require stable soft bottom sediments and readily accessible food resources.

A number of authors have found changes in the structure of aquatic organisms of remote lakes along the altitude/temperature gradient (e.g. Walker and Mathewes, 1989; Lotter *et al.*, 1997; Larocque *et al.*, 2001; Füreder *et al.*, 2006; Krno *et al.*, 2006). The approximately linear decrease in littoral water surface temperature with increasing altitude has been shown in various mountain ranges (e.g. Lotter *et al.*, 1997; Šporka *et al.*, 2006). In our study, some parameters of the chironomid assemblages showed clear trends with altitude. The number of species/taxa and Shannon diversity decreased with elevation; however, abundance did not show obvious correlation with altitude. Generally, with increasing elevation, species richness and abundance of aquatic invertebrates declines (Janetschek *et al.*, 1977; Krno *et al.*, 1986; Ertlová, 1987; Füreder *et al.*, 2006) and species structure changes (Mani, 1968, 1990). However, Boggero *et al.* (2006) did not find any clear relationship between chironomid taxa number and altitude in Alpine lakes. Füreder *et al.* (2006) observed trends similar to ours in the abundance of aquatic invertebrates in lakes of the Alps. A decline in taxa numbers and diversity was seen with an increase in abundance up to elevation 2600 m, after which the abundance clearly decreased. According to their interpretation, the increase of densities up to 2600 m could be caused by the fact that few but well adapted species find a richer environment due to increased solar radiation and consequently somewhat higher water temperatures despite the higher elevation.

The Orthoclaudiinae generally became more frequent with increasing altitude while Chironomidae decreased

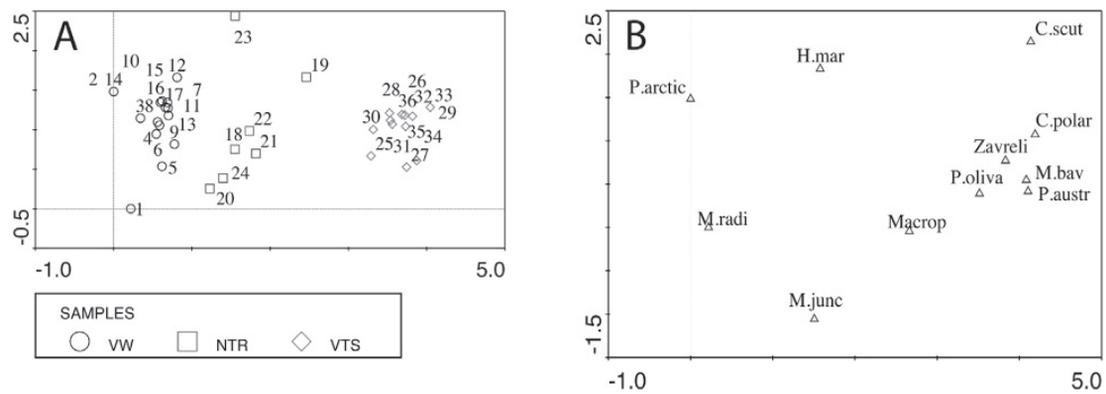


Fig. 7. DCA diagram of sites (A) and chironomid species/taxa (B) based on quantitative data (29 species/taxa and 36 samples). Eigenvalues: first axis 0.765, second axis 0.196. Percentage variance of the species data explained: first axis 32.2, second axis 8.3. Only species/taxa with species weight range > 10% are shown. List of species/taxa names abbreviations in alphabetic order: C.scut – *Corynoneura scutellata* group, C.polar – *Cricotopus cf. polaris*, H.mar – *Heterotrissocladius marcidus*, Macrop – *Macropelopia nebulosa*, M.bav – *Micropsectra bavarica*, M.junc – *M. junci*, M.radi – *M. radialis*, P.austr – *Paratanytarsus austriacus*, P.oliva – *Prodiamesa olivacea*, P.arctic – *Pseudodiamesa arctica*, Zavreli – *Zavrelimyia* sp.

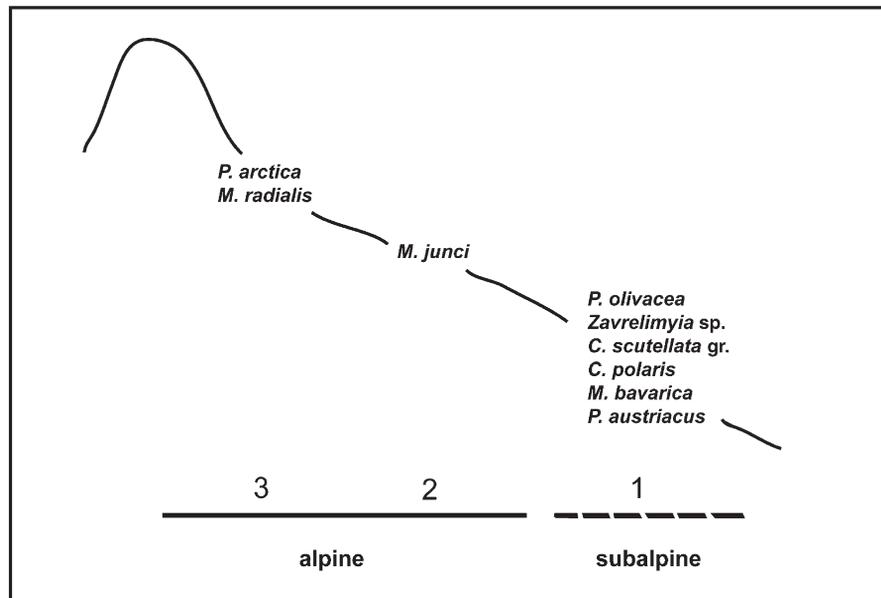


Fig. 8. Scheme of the distribution of indicator chironomid species/taxa with altitude and their index values: 3 – species of alpine lakes above 2000 m a.s.l., 2 – species of alpine lakes below 2000 m a.s.l., and 1 – subalpine lake species/taxa.

with elevation. This agrees well with the current literature (Lindegaard and Brodersen, 1995; Lotter *et al.*, 1997; Bitušík *et al.*, 2006b; Boggero *et al.*, 2006; Krno *et al.*, 2006). The results from our surveyed lakes corresponded with this pattern only partially. The relative abundance of the Chironominae (mainly Tanytarsini), Tanypodinae and Prodiamesinae showed a clear negative correlation with altitude, while the ratio of Diamesinae correlated positively with altitude. However, there was no clear relation between the relative abundance of Orthoclaadiinae and altitude. Hamerlík (2004) found similar trends, with the highest ratio of Orthoclaadiinae in the littoral of alpine Tatra lakes situated at altitudes from 1800–2000 m, and declining with increasing and decreasing elevation.

The most common factors influencing the feeding behaviour of larval midges are larval size, food quality and sediment composition (Berg, 1995). The amount of particulate organic matter (POM) in ultra-oligotrophic alpine lakes plays an important role in the trophic systems of aquatic fauna (Galas and Dumnicka, 1998). The majority of POM in high mountain lakes has allochthonous origin (Galas, 1993; Füreder *et al.*, 2006). As the amount of POM in the littoral of the study lakes decreased noticeably with elevation (Krno *et al.*, 1986; Čiamporová-Zaťovičová *et al.*, to appear), a considerable change in particular feeding groups along an altitude was expected. Gatherers dominated in the littoral of the three studied lakes, but their relative abundance decreased with

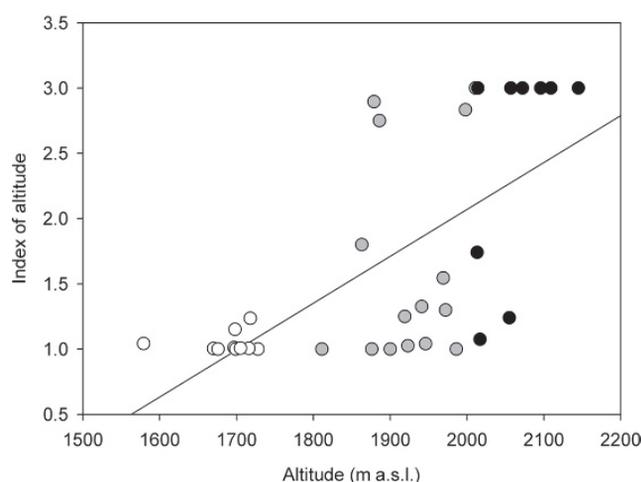


Fig. 9. Results of regression analysis between the index of altitude calculated based on indicator species and the actual altitude of 34 Tatra lakes; $r^2 = 0.42$, $P > 0.001$. Open circles represent subalpine lakes, grey circles alpine lakes below 2000 m a.s.l., and black circles alpine lakes above 2000 m a.s.l.

decreasing altitude. In contrast, the ratio of scrapers and predators correlated negatively with altitude. Number of filter-feeders in the surveyed lakes was very low and was independent of altitude. The opposite trend was found by Boggero *et al.* (2006) in lakes in the Alps, where scrapers became more frequent and gathering collectors decreased with increasing altitude. However, their analysis was based on the simplified assumption that Orthoclaadiinae are scrapers and Chironominae are collectors, which is not always true (e.g. Moog, 1995). However, identification of the trophic status of some species is often problematic due to considerable feeding mode flexibility and may lead to misinterpretations. Furthermore, Zah *et al.* (2001) claimed that aquatic invertebrates are more plastic in utilizing food resources in extreme environmental conditions (e.g. alpine and arctic streams and lakes).

The detrended correspondence analysis allowed the identification of three more-or-less distinctive chironomid assemblages distributed along the axis that can be considered to be an altitude/temperature gradient. This confirms the suitability of the choice of these three lakes in the gradient concept. Dissimilarities in the structure of assemblages are clear, despite the fact that the altitude difference between the lowest and highest elevation lakes spans only ~430 m. The major shift in the structure of assemblages was found between the VW and VTS littorals. From the relatively poor littoral assemblage of VW, *Pseudodiamesa arctica* and *Micropsectra radialis* were selected as indicators not only of this lake, but also of all Tatra lakes situated in alpine zone above 2000 m a.s.l. (Bitušík *et al.*, 2006b). *Pseudodiamesa arctica* is adapted to harsh physical environments, including freezing and drying, and indicative for ultra-oligotrophic conditions and extremely low water temperature, without respect to altitude (Serra-Tosio, 1972, 1976; Sæther, 1975; Lindegaard, 1980). *Micropsectra radialis* can be

considered a characteristic species of lakes situated both at high altitudes and at high latitudes (Larocque *et al.*, 2001; Boggero *et al.*, 2006). Its absence in warmer subalpine lakes in the Tatra Mountains is typical, with the exception of some deep lakes with a cold and well-oxygenated hypolimnetic zone (Bitušík *et al.*, 2006b). The littoral of VTS was inhabited by a rich chironomid assemblage, consisting mainly of species widespread in subalpine but also in montane lakes, and even in water bodies at lower elevation (*Microtendipes chloris*, *Prodiamesa olivacea*, *Tanytarsus bathophilus*). A similar taxonomic composition has already been reported from previous studies on the macroinvertebrate fauna the Tatra Mts. lakes (Kownacki *et al.*, 2000; Krno *et al.*, 2006) and analogous biotopes in Europe (e.g. Boggero and Nobili, 1998; Füreder *et al.*, 2006). The littoral assemblage of VTS was characterized by the presence of *Zavrelimyia* sp., *Prodiamesa olivacea*, the *Corynoneura scutellata* group, *Cricotopus polaris*, *Micropsectra bavarica* and *Paratanytarsus austriacus*. These species/taxa were identified as indicators of subalpine Tatra lakes. *Microtendipes chloris*, known as a typical inhabitant of subalpine lakes (Bitušík *et al.*, 2006b) was not considered here as a characteristic species due to its low abundance and frequency of occurrence in the VTS littoral. In this study, *Paratanytarsus austriacus* was found only in the subalpine VTS, but its pre-imaginal stages have been found in a majority of Tatra lakes below 2000 m a.s.l. (Hamerlík, 2004; Bitušík *et al.*, 2006b). The chironomid subfossil record has revealed a relatively recent colonization of VTS by *P. austriacus*, which corresponds with warmer climatic conditions and increased lake productivity since the end of the 19th century (Bitušík *et al.*, 2009). This suggests that its future presence in Tatra lakes situated in the higher alpine zone could be a signal of changes to their temperature regimes.

The littoral assemblage in NTR was dominated by *Heterotrissocladius marcidus* and *Micropsectra junci*. Although our results suggest that larvae of *M. junci* plays an important role in the NTR littoral, the importance of this species as an indicator of alpine lakes located at 1800–2000 m a.s.l. remains questionable. Besides the problem with identification of larvae mentioned above, the ecology and distribution of *M. junci* is very poorly known (e.g. Bitušík and Hamerlík, 2003) and its potential as an indicator should be reviewed by future research. *Heterotrissocladius marcidus* is the most widely distributed chironomid in the Tatra lake district (Bitušík *et al.*, 2006b; Krno *et al.*, 2006), and is therefore not applicable for characterizing lakes situated at different altitudes.

According to our results, Tatra lakes situated at 1800–2000 m a.s.l. represent a transition zone between lower and higher elevations, where subalpine species reach their uppermost high alpine species their lowermost boundary of altitude distribution, and thus these lakes have no indicator species. A recent investigation on chironomid pupal exuviae (Bitušík *et al.*, 2006b) also supports this hypothesis. One could ask if the taxonomic composition of the NTR littoral (and other lakes situated at equivalent altitude) might be the result of recent effects of

climate warming. However, palaeolimnological analysis of NTR sediment showed a relatively stable taxonomic composition of chironomid assemblages over the past few centuries, with no colonisation events by species present at lower altitudes (Bitušík *et al.*, 2009).

The gradient lake concept demonstrated how climate-related factors affect the modern composition of littoral chironomid assemblages. Our results suggest that differences in modern littoral chironomid fauna are sufficient to separate lakes situated at the extremes of the Tatra altitude/temperature gradient: subalpine lakes and alpine lakes above 2000 m a.s.l. Based on this simplified scheme, an upward shift of subalpine species could be expected under warmer conditions. Consequently, chironomids of the lakes situated at the lower alpine zone (1800–2000 m) would resemble the subalpine fauna in the future. Site diversity (α diversity) would increase due to successful colonisations of more thermophilic species. Similarly, the chironomid species richness of subalpine lakes could increase due to the presence of species from lowland lentic habitats. The relict late-glacial fauna composed of the most cold-stenothermic species could go extinct, and consequently, regional diversity (γ diversity) would decrease. The gradient lake concept has made the scenario of expected changes in mountain lake fauna more predictable. However, it is clear that this general scheme will not be applicable general to the entire Tatra lake district. Lake thermal cycles depend on several local factors such as lake orientation, landscape morphometry, mean lake depth and lake surface to volume ratio (Brodersen and Anderson, 2000). Šporka *et al.* (2006) demonstrated a high degree of variability in the timing of the ice-cover period in Tatra lakes as a consequence of individual lake morphometry, lake setting, and rate of inflow. The importance of lake setting was also emphasised by Łajczak (1982), who showed ice cover duration to be dependent on whether the lake faces north or south. This suggests that the thermal characteristics of some Tatra lakes differ from the scheme of linear changes along the altitude gradient (Šporka *et al.*, 2006). Features of external (landscape) lake filters (Blenckner, 2005) could reduce the effect of climatic change, and make these lakes refuge for relict chironomid fauna. Recognition and a more detailed study of these lakes should be a focus of future research.

Our results also confirm the importance of more detailed identification of chironomids, as has been stressed in previous studies (*e.g.* Rossaro *et al.*, 2006). The known fact that species within a genus often have different ecological requirements was clear in our gradient lakes: three different species of the genus *Micropsectra* were characteristic for lakes at different elevations.

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