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Littoral benthic macroinvertebrates of alpine lakes (Tatra Mts) along an altitudinal gradient: a basis for climate change assessment

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Abstract Littoral benthic macroinvertebrates were studied in three alpine lakes in the High Tatra Mountains (Slovakia) located at different elevations: 2157, 1940 (alpine zone) and 1725 m (sub-alpine zone). The study sites were selected in order to obtain a gradient in thermal regimes and particular organic matter (POM). Differences in the faunal composition of lakes were tested for the ability of these differences to indicate climatic changes, and species/taxa were identified that could be used for the purposes of monitoring and climate change assessment. Macroinvertebrates were sampled quantitatively during the ice-free seasons of 2000 and 2001, and lake surface water temperature (LSWT) and POM were measured. LSWT and POM were negatively correlated with elevation, whereas ice cover was positively correlated with elevation. A total of 60 oligostenothermic macroinvertebrate species/taxa were collected belonging to ten higher taxonomic groups. Statistical analysis showed trends in several biotic metrics with altitude. More specifically, there was a clear increase in the number of species/taxa, genera, and higher taxonomic groups, as well as an increase in the Shannon–Wiener diversity with decreasing altitude. On the contrary, evenness and density of benthic macroinvertebrates did not show any clear relationship with altitude. Gatherers of detrital particles dominated the assemblages' trophic structures, but no distinct changes in the proportion of functional feeding groups along the altitudinal gradient were found. While the non-insect fauna of the lakes was rather uniform across the elevational gradient, the insect fauna composition was highly correlated with altitude, as confirmed by Detrended Correspondence Analysis. Aquatic insects, in particular chironomids and caddisflies, can therefore be used as good indicators of temperature changes. Our results suggest that under warmer conditions, non-insect benthic macroinvertebrates will remain more or less stable, while aquatic insects will undergo an increase in the number of thermophilic species typical for lower altitudes. These colonizers will increase the diversity of alpine lakes, while the extinction of cold stenothermal species will lead to impoverishment of the native fauna. An indirect impact on benthic macroinvertebrates through changes in food sources is likely, and changes in trophic structure of the littoral assemblages can be expected.

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Introduction

Global warming is one of the major issues currently confronting mankind, with vital ecological and economic consequences. The climate is changing rapidly, possibly at a faster rate than at any time in the last ten thousand years (Thompson et al., 2005). Global warming is particularly pronounced in alpine and arctic ecosystems, where changes in temperature and precipitation regimes are more evident. During the past few decades, air temperatures in these areas have increased by about 1.5–2°C on average compared to 0.5°C globally (Beniston et al., 1997). Moreover, General Circulation climate Models (GCMs) simulating presumable future climatic scenarios (Livingstone et al., 1999) predict continuing climate warming mainly in alpine and northern areas (Houghton et al., 1996; Beniston et al., 1997). Even though extensive monitoring of climate change is ongoing, links between alpine aquatic biota and increased temperature are still not sufficiently described.

Alpine lakes of glacial origin are among the most remote and undisturbed aquatic environments in Europe. Compared with lakes at lower altitudes, these lakes are generally much less influenced by pollution from agriculture and wastewater (Skjelkvåle & Wright, 1998). Alpine lakes are known as extremely sensitive indicators of global issues such as acid atmospheric deposition (Psenner & Catalan, 1994), long-range transport of toxic and radionuclide pollutants (Camarero et al., 1995) as well as global climatic change (Psenner & Schmidt, 1992; Battarbee et al., 2002). Furthermore, these lakes also serve as 'early warning' systems for the whole mountain ecosystem (The MOLAR Water Chemistry Group, 1999).

Altitude is considered to be the most important variable determining living conditions in remote mountain areas. Ice cover, snow cover and water temperatures in alpine catchments are controlled by air temperatures, and thus climate is the main driving factor determining changes in alpine environments. These effects can be seen even along short altitude gradients (Whiteman, 2000). Recently, alpine lakes situated along an altitudinal/temperature gradient (gradient lakes) have begun to be studied as potential indicators of climate change (e.g. the EMERGE project, Patrick, 2003). Lakes at different elevations represent a natural climatic gradient and could serve as models for predicting the possible impacts of temperature change. This 'gradient lake concept' could contribute to an understanding of the ecological impacts of climate change as well as predict the possible development of lake fauna under scenarios of climate warming and/or cooling.

Benthic invertebrates of remote glacial lakes are excellent indicators of local as well as global temperature changes (Fjellheim et al., 2000). The aquatic biota of such areas are adapted to persistent low temperatures and hence react very sensitively to even slight changes in the environment (Skjelkvåle & Wright, 1998). A previous study on benthic fauna of remote lakes across Europe (Fjellheim et al., 2009) has shown that the response of faunal assemblages to altitudinal gradients varied with latitude. Despite the fact that lakes at different latitudes had common species, differences in taxonomic composition were found among lake districts. That study underlined the importance of detailed knowledge of the regional fauna for an understanding of climate-driven processes on a broader geographical scale.

In order to validate the gradient lake concept as a possible indicator of climate change, the structure of littoral aquatic invertebrates of three High Tatra Mountain lakes was studied. The main objectives were to (i) assess the selection of the gradient lakes by studying surface water temperature and particulate organic matter, (ii) examine the ability of differences in the faunal composition of these lakes to indicate climatic events and finally (iii) identify taxa that could be used for the purposes of monitoring and climatic change assessment.

Materials and methods

Study sites

The three study sites are lakes of Quaternary glacial origin in the High Tatra Mountains in northern Slovakia (49°10′ N and 20°10′ E). This mountain range is characterized by steep changes in temperature and precipitation with altitude. The average annual air temperature decreases with elevation by 0.6°C (Lajczak, 1996) or 1.4°C (Šporka et al., 2006) per 100 m, being 1.6 and −3.8°C at elevations of 1778 and 2635 m, respectively (Konček & Orlicz, 1974). The amount of precipitation varies from ~1.0 to 1.6 m year^{-1} between 1330 and 2635 m a.s.l., but reaches >2.0 m year^{-1} in some valleys (Chomitz & Šamaj, 1974). Snow cover usually lasts from October to June at elevations >2000 m. The duration of ice cover in the Tatra lakes increases with altitude at a mean rate of 10.2 days every 100 m.

The main criterion for gradient lake selection was their location above the natural tree line along an altitudinal gradient, with approximately equal elevation differences among lakes. When possible, the effect of other variables (geology, lake morphometry, chemistry) was minimized in order to emphasize differences in thermal regimes due to different elevations. The lakes selected are located relatively close to each other (Fig. 1) within the same catchment (the Váh river basin). They are situated above the timber line at 2157 (Vyšné Wahlenbergovo pleso—VW), 1940 (Nižné Terianske pleso—NTR) and 1725 m a.s.l. (Vyšné Temnosmrečinské pleso—VTS), respectively, so that elevation differences between adjacent lakes are ~200 m. NTR and VW are in the alpine zone, VTS in the sub-alpine zone. The lake basins are formed mostly of acid metamorphic and magmatic rocks (gneis and granitoides). They are relatively deep with small lake surface areas (~5 ha). All lakes contain soft water, are oligotrophic, and are fishless. Substrates of the littoral zones are characterized mainly by a large amount of rocks with a small proportion of sand and gravel. Dominant vegetation of the lake catchments changes with increasing altitude from sub-alpine bushes with dwarf pine (*Pinus mugo*) to alpine meadows (dry tundra) with an increase in the percent of bare rocks and screes. There have been no significant direct human activities occurring in the lake catchments since the 1950s when the Tatra Mountains became a national park. Even though acid deposition in the second half of the twentieth century had a significant impact on many Tatra lakes including Vyšné Wahlenbergovo pleso (Kopáček & Stuchlík, 1994), at time of our survey, this lake was no longer considered acidified (Kopáček et al., 2006). For more details on hydromorphology and water chemistry of the lakes, see Table 1; additionally Gregor & Pacl (2005) and Bitušík et al. (2006a).

Macroinvertebrates

Sampling of macroinvertebrates was performed during the ice-free seasons of 2000 and 2001 (June–October) in 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

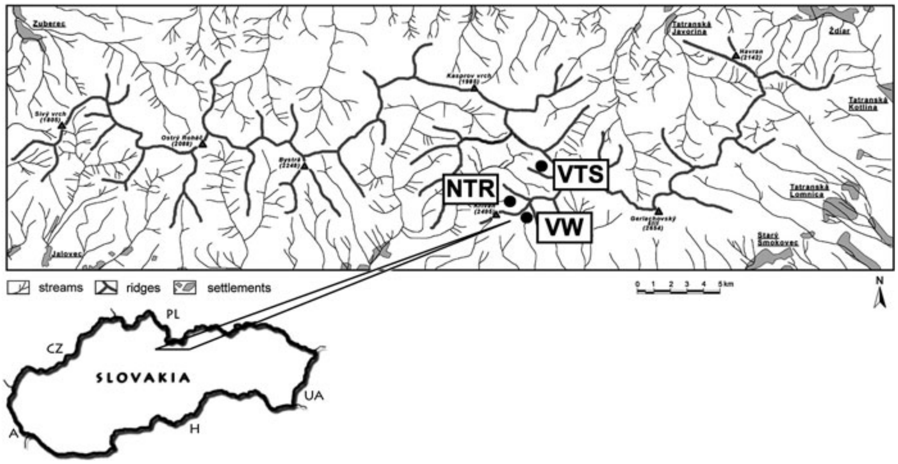

Fig. 1 Map of the studied area: location of the High Tatra Mts and the surveyed gradient lakes Vyšné Wahlenbergovo pleso (VW), Nižné Terianske pleso (NTR) and Vyšné Temnosmrečinské pleso (VTS)

Table 1 Basic environmental characteristics of the studied High Tatra lakes

Lake	Vyšné Wahlenbergovo pleso (WV)	Nižné Terianske pleso (NTR)	Vyšné Temnosmrečinské pleso (VTS)
Zone	Alpine	Alpine	Sub-alpine
Latitude N	49°09′51.12	49°10′11.28	49°11′20.76
Longitude E	20°01′37.56	20°00′51.48	20°02′22.20
Altitude (m a.s.l.)	2157.0	1940.4	1724.8
Lake area (m^2)	51,655	55,580	55,625
Maximal depth (m)	20.6	47.3	20.0
Lake volume (m^3)	392,078	871,668	414,712
Littoral substrate—R:SG:DP:MD (%)	95:4:0:1	90:10:0:0	88:8:2:2
Presence of inlet/outlet	0/0	1/1	1/1
Part within lake chain	1	2	1
Land cover in catchment—R:M:A (%)	37:51:12	40:32:28	40:34:26

R rocks, *SG* sand and gravel, *DP* dwarf pine submerged, *MD* mud or detritus, *M* moraines, *A* alpine meadows (Kopáček et al., 2004; Gregor & Pacl, 2005; EMERGE project DB)

(Helan et al., 1973) with sampling area 0.1 m^2 and mesh size 500 µm (use in standing water followed Krno, 1988). Sampling locations reached from the shore to a water depth of ~0.4 m. Each sample consisted of three partial sampling units with a total area of 0.3 m^2. The material collected was placed into plastic bottles and fixed in situ with formalin to a final concentration of 4%.

In the laboratory, all animals were sorted and counted under a low-power stereomicroscope (×7–40). Oligochaetes and chironomid larvae were mounted on slides and identified under high magnification (×400). Invertebrates were identified to the lowest possible taxonomic level (with the exception of Nematoda and Acarina) following the taxonomic keys for Oligochaeta (Brinhurst & Jamieson, 1971; Hrabě, 1981; Kasprzak, 1981, 1986), Ephemeroptera (Bauernfeind & Humpesch, 2001), Plecoptera (Lillehammer, 1988), Coleoptera (Galewski & Tranda, 1978; Nilsson & Holmen, 1995), Trichoptera (Szczęsny, 1978; Waringer & Graf, 1997) and larvae of Chironomidae (Hirvenoja, 1973; Wiederholm, 1983; Schmid, 1993; Ekrem, 2004; Stur & Ekrem, 2006).

Temperature and organic matter

Miniature thermistors with integrated data loggers (8-TR Minilogs, Vemco Ltd., Shad Bay, Nova Scotia, Canada) were used to measure lake surface water temperatures (LSWTs) of the studied lakes in 1-h intervals from June 2000 to October 2001. The thermistors were inserted into the underside of floats consisting of rectangular styrofoam blocks (13 cm × 13 cm × 5 cm). The thermistor sensors were approximately 5 cm under the lake surface and the styrofoam blocks shaded the sensors from direct solar radiation. The thermistors were anchored either near the lake outflow to ensure a continual flow of epilimnetic water around them (VTS and NTR) or in deep central region, far enough from shore (VW) to avoid any local littoral effects and to minimize disturbance. Unfortunately, the thermistor in VTS was lost after 3 months of measurement and was replaced in July 2001; however, the available data still represent the temperature regime of this lake for an entire ice-free period. The temperature data from data loggers were downloaded in the field and daily averages were used for subsequent analyses. Automatic temperature measurements were supplemented with point measurements (mercury thermometer) during benthos sampling dates.

The amount of particulate organic matter (POM) from the lake littorals were measured using benthic samples taken in 2001. The minimum size of the particles gathered was determined by the mesh size of the sampler. Particles smaller than 0.5 mm passed through the sampler; therefore, only two fraction sizes were considered: coarse—CPOM (>1 mm) and partly fine—FPOM (1–0.5 mm). In the laboratory, fractions of POM were separated, dried at 105°C for 3.5 h and weighed. The weight loss upon combustion at 550°C (3.5 h) was taken as the amount of organic matter in the sample. Values of POM are given as g m^{-2} of ash-free dry mass (AFDM).

Data analysis

The autoecological characteristics of invertebrate taxa were obtained from Moog (1995) and Šporka (2003). The Shannon–Wiener diversity index (H′) and evenness (Simpson's E) were calculated for each littoral and sampling date using Species Diversity & Richness 4.0 software (Seaby & Henderson, 2006). Samples taken on the same day from VW or NTR (with multiple sampling sites) were averaged. Subsequently, one-way analysis of variance (ANOVA) was used to compare selected biotic metrics of the littoral zones (numbers of species/taxa, genera, and higher taxonomic groups, diversity, evenness, density); values of $P < 0.05$ were considered significant. The ANOVA and all graphs, excluding ordination diagrams, were done in SigmaPlot for Windows 9.0 software.

Visualization of the samples and species/taxa distribution along the main environmental gradient was done using indirect gradient analysis (CANOCO for Windows Package 4.5, Ter Braak & Šmilauer, 2002). Detrended Correspondence Analysis (DCA; Hill, 1979) of insect density data (ind. m^{-2}) was used since the initial Correspondence Analysis (CA) resulted in an arch effect (due to the long gradient of first axis: 4.052). The data matrix included 48 species/taxa and 29 samples; data were log transformed and rare taxa downweighted prior to analysis.

Results

Environmental factors

Results of the LSWT measurements in the surveyed lakes are shown in Figs. 2 and 3. LSWTs of all lakes reached their maxima in summer months (July–August), and differences between lakes clearly reflected their elevation: the highest elevation VW had the lowest maximum temperatures, and the lowest elevation VTS the highest. During the simultaneous temperature measurements in all three lakes, the average temperatures were 6.1, 7.2 and 8.0°C in VW, NTR and VTS, respectively. In the same periods, the highest daily average temperatures of the alpine lakes were similar (11.6°C in VW and 11.8°C in NTR), in contrast with the sub-alpine lake (13.5°C in VTS). During the winter ice cover, temperatures of all lakes were around zero. The ice cover period lasted 205 days in the highest VW,

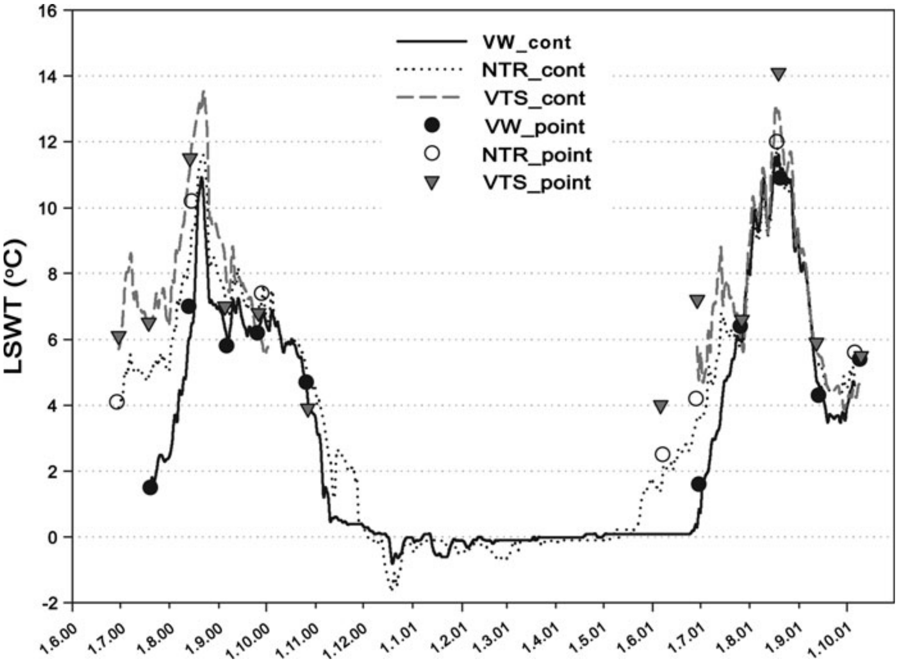

Fig. 2 Lake surface water temperature (LSWT) of the studied High Tatra lakes in 2000 and 2001. Data results from automatic (*lines*) and point (*symbols*) measurements. Points are consistent with the dates of the benthic macroinvertebrate sampling (VW, NTR, VTS—see Table 1)

185 days in NTR and 160 days in the lowest VTS. Thus, the duration of ice-free period ranged from 161 days (44% days of the year) in VW to 181 days (49%) in NTR, and 206 (56%) in VTS. The differences in ice-free period duration resulted in a 45-day difference between the furthermost lakes (VW and VTS). These differences in maximum summer temperatures and ice-free periods resulted in clear trends of higher water temperature with decreasing altitude for both the whole period of measurement and the warmest summer months (Fig. 3A, B).

Figure 4 presents the amount of coarse (CPOM), partly fine (1–0.5 mm, FPOM), and total obtained POM of the lake littorals, and shows that the amount of organic matter increases as elevation decreases. The average amount of total POM in the highest elevation VW was 0.9 g m^{-2}, about ¼ of that in NTR (3.5 g m^{-2}). In the lowest elevation VTS, the POM was highest and reached 6.6 g m^{-2}. There is also a clear trend in the increase of both the CPOM and FPOM fractions with decreasing altitude. This increase in POM was ~2.5–3 g m^{-2} per each ~200 m of decreasing altitude.

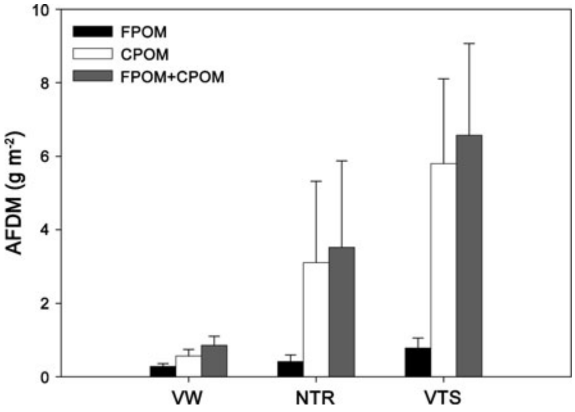

Fig. 4 Average values and standard deviations of AFDM (g m^{-2}) of >1 mm = coarse (CPOM), 0.5–1 mm = part of fine (FPOM) and total particulate organic matter (POM) in the littorals of the studied lakes in 2001 (VW, NTR, VTS—see Table 1)

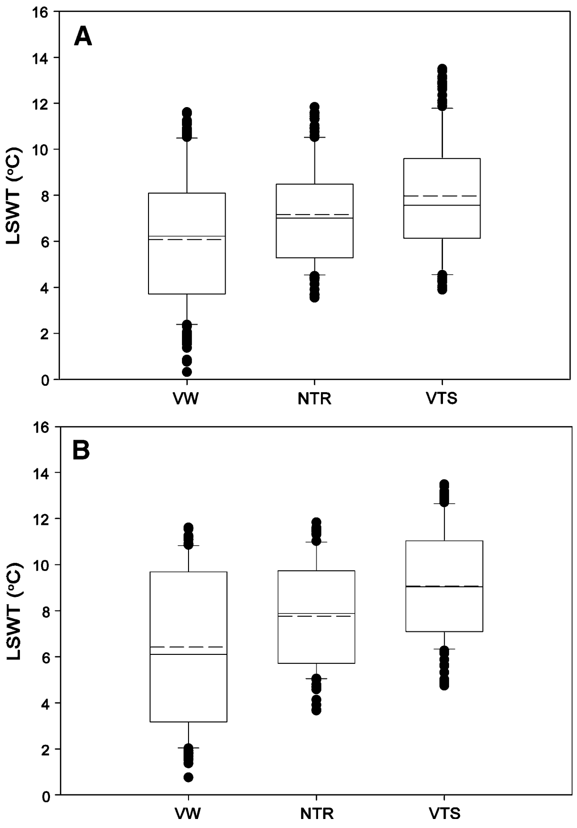

Fig. 3 Variability of lake surface water temperature (LSWT) during the simultaneous measurement of temperature at all the studied lakes in 2000 and 2001 (**A**) and in summer months—July and August (**B**) (*solid line* median, *dash line* average; VW, NTR, VTS—see Table 1)

Littoral macroinvertebrates

A total of 12,700 specimens were identified to 60 species/taxa belonging to ten higher taxonomic groups (Appendix 1 in Electronic supplementary material). The richest group was Diptera (31 Chironomidae species/taxa, 1 Tipuliidae), followed by Oligochaeta (9), and Trichoptera (6). Other groups were less diverse: Plecoptera (4), Coleoptera (3), Ephemeroptera (2), Tricladida and Bivalvia (each with one species only). Nematoda and Acarina were not determined to the species level. In terms of abundance, Chironomidae and Oligochaeta dominated in all the lake littorals.

Only ten species/taxa were found to be present in all the surveyed lakes. Five of them (*Crenobia alpina*, *Cernosvitoviella atrata*, *Haplotaxis gordioides*, *Nais variabilis* and *Stylodrilus heringianus*) represented almost 40% of all taxa belonging to the non-insect macroinvertebrate benthic fauna. In contrast, five insect species/taxa (*Capnia vidua*, *Acrophylax zerberus/sowai*, *Pseudodiamesa branickii*, *Prodiamesa olivacea* and *Heterotrissocladius marcidus*) constituted only about 10% of all insect species/taxa. 34

species/taxa (57%) were found in only one of the three lake littorals.

Numbers of species/taxa, genera, and higher taxonomic groups increased significantly with decreasing altitude (ANOVA, $P < 0.001$) (Fig. 5A–C). Even though there was no statistically significant difference between the Shannon–Wiener diversity (H′) of the two alpine lakes (VW, NTR), there was a clear tendency to increase with decreasing elevation (Fig. 5D). On the contrary, the evenness and density of benthic macroinvertebrates did not show any consistent trends with altitude (Fig. 6A, B); both metrics increased moderately from NTR to the higher (VW) and lower (VTS) elevation lakes.

Different patterns along the altitudinal gradient were evident when the species/taxa of non-insect macroinvertebrate fauna and aquatic insects were analysed separately. The species/taxa richness of non-insect fauna showed no significant differences between lakes. However, richness of aquatic insects increased markedly with decreasing elevation, with significant differences (ANOVA, $P < 0.001$) between adjacent lakes (data not shown). This altitudinal trend in species/taxa richness of aquatic insects was similar to the trend in total number of taxa, with the strongest difference between alpine and sub-alpine lakes (Fig. 7). The composition of the non-insect fauna did only slightly change along the altitudinal gradient.

The proportion of different functional feeding groups did not show any distinct changes along the altitudinal gradient (Fig. 8). Gatherers highly dominated in all lake littorals (60–70%), but no relation to altitude was found. The high percentage of predators in VW was due to the dominant species *Crenobia*

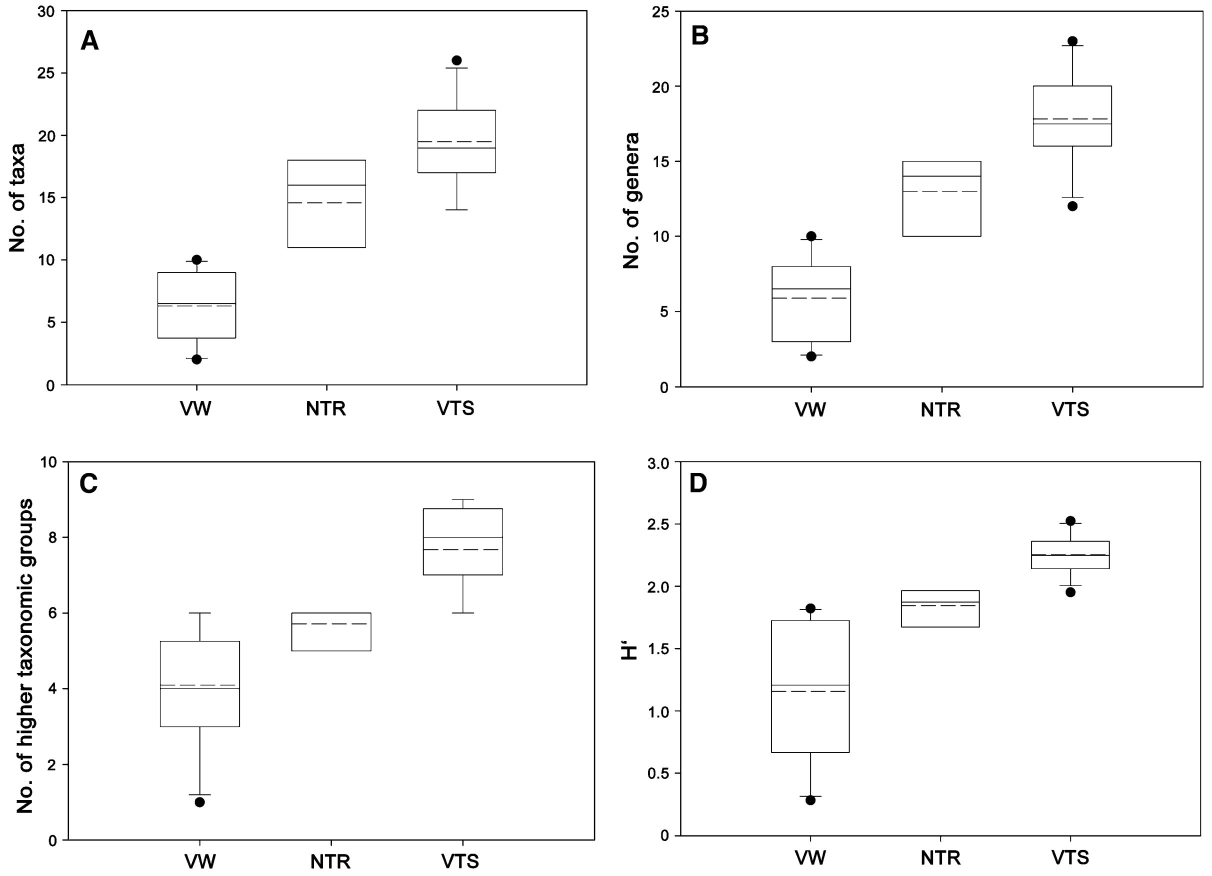

Fig. 5 Box and whisker plots of variability of biotic metrics in the littorals of the studied lakes: number of taxa (**A**), number of genera (**B**), number of higher taxonomic groups (**C**), Shannon–Wiener diversity index (H′) (**D**) (VW, NTR, VTS—see Table 1; *solid horizontal lines* medians, *dash lines* means, *boxes* 25th and 75th percentiles, *whisker extending from boxes* 10th and 90th percentiles, *outliers* 5th and 95th percentiles)

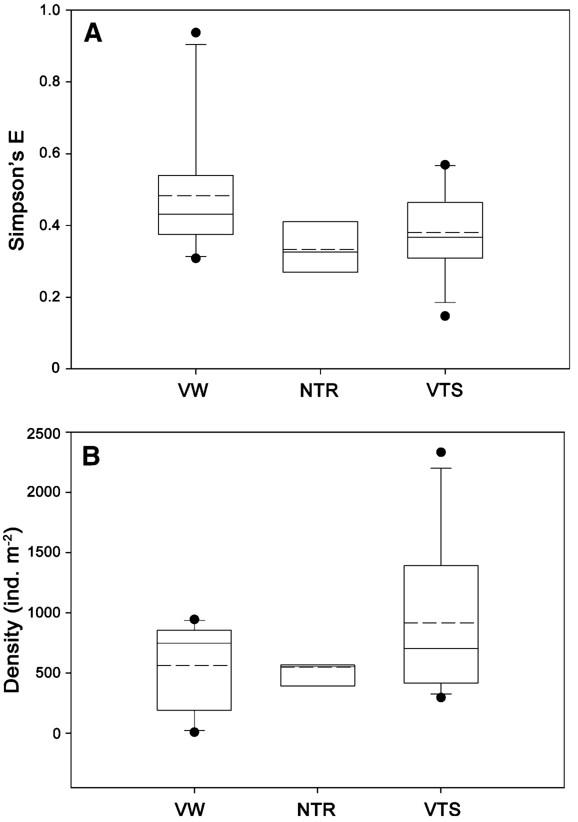

Fig. 6 Box and whisker plots of variability of biotic metrics in the littoral of the studied lakes: evenness (Simpson's E) (**A**), density (ind. m^{-2}) (**B**) (VW, NTR, VTS—see Table 1; *solid horizontal lines* medians, *dash lines* means, *boxes* 25th and 75th percentiles, *whisker extending from boxes* 10th and 90th percentiles, *outliers* 5th and 95th percentiles)

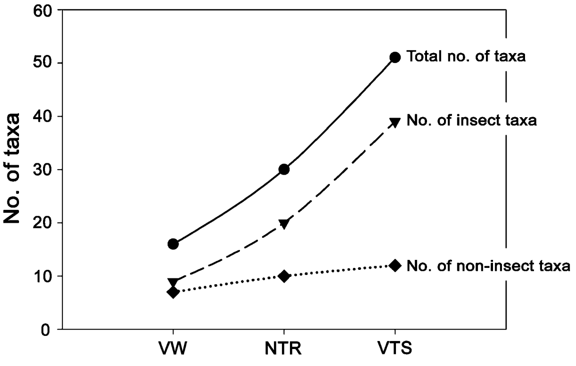

Fig. 7 Comparison of taxa number of non-insect fauna, aquatic insect fauna and total macroinvertebrate fauna in the studied lake littorals (VW, NTR, VTS—see Table 1)

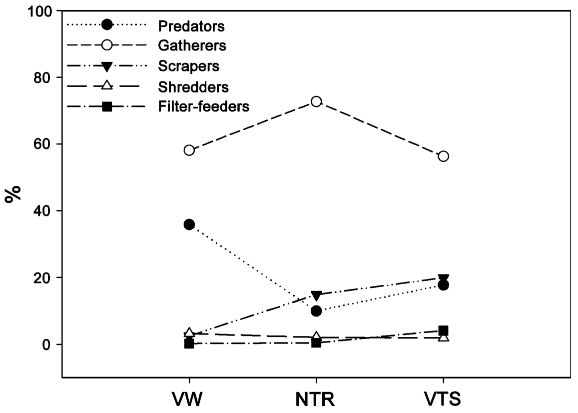

Fig. 8 Proportions of functional feeding groups in the studied lake littorals (VW, NTR, VTS—see Table 1)

alpina, whose density decreased markedly in the lower lakes. Only the proportion of scrapers showed a slight increase with decreasing altitude; the relative abundance of shredders and filter-feeders was very low in all the studied lake littorals.

Insect fauna along an altitudinal/temperature gradient

Results of the cluster analysis based on presence/absence data resulted in similar final dendrograms both for total macroinvertebrate data and insect data only, confirming distinct heterogeneity in species composition of the different altitudinal zones (not shown). When the data of non-insect fauna were used, no similar clustering reflecting an altitudinal gradient was found. For this reason, only aquatic insect data were used in the subsequent analysis.

Detrended correspondence analysis (DCA) was performed to explore the distribution of species/taxa among the lake littorals, taking into account the density data. Eigenvalues of axes 1 and 2 of the DCA were 0.724 and 0.246, respectively, and explained 37.1% of the overall variance of the species data (Table 2). All samples were scattered along the first axis and were organized into three groups corresponding with the three lake littorals (Fig. 9A). It can be assumed that the main axis represented the altitudinal/temperature gradient, reflected in increases in air and water temperatures with decreasing altitude from the left to the right side of the ordination diagram. Samples from VW and VTS were grouped at both poles of the gradient (VW on the left; VTS on the right); samples from NTR were located in the middle part of the diagram closer to the VW samples,

Table 2 Summary table of DCA based on quantitative insect data—eigenvalues and percent of variance of the first four ordination axes

Axes	1	2	3	4	Total inertia
Eigenvalues	0.724	0.246	0.141	0.094	2.612
Lengths of gradient	4.052	1.970	2.187	1.580	
Cumulative percentage variance of species data	27.7	37.1	42.5	46.1	
Sum of all eigenvalues					2.612

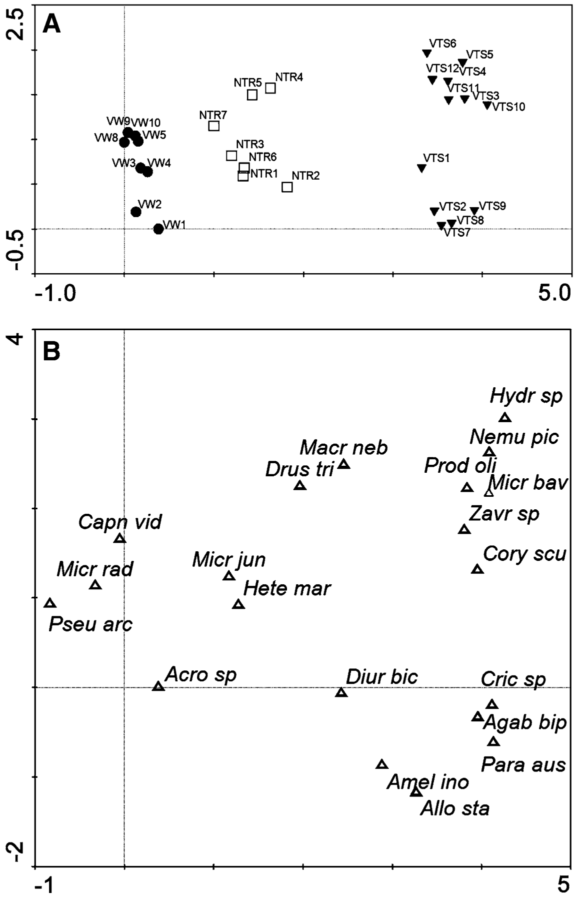

Fig. 9 DCA diagram of samples (**A**) and species/taxa (**B**) based on quantitative insect data. Only species with species weight range >10% are figured (*black circle* VW, *empty square* NTR, *black down-triangle* VTS—see Table 1; Pseu arc, *Pseudodiamesa arctica*; Micr rad, *Micropsectra radialis*; Capn vid, *Capnia vidua*; Acro sp, *Acrophylax zerberus/sowai*; Micr jun, *Micropsectra junci*; Hete mar, *Heterotrissocladius marcidus*; Drus tri, *Drusus trifidus*; Diur bic, *Diura bicaudata*; Macr neb, *Macropelopia nebulosa*; Amel ino, *Ameletus inopinatus*; Allo sta, *Allogamus starmachi*; Zavr sp, *Zavrelimyia* sp.; Prod oli, *Prodiamesa olivacea*; Cory scu, *Corynoneura scutellata* gr.; Agab bip, *Agabus bipustulatus*; Micr bav, *Micropsectra bavarica*; Nemu pic, *Nemurella pictetii*; Cric sp, *Cricotopus polaris*; Para aus, *Paratanytarsus austriacus*; Hydr sp, *Hydroporus* sp.)

confirming the higher similarity of macroinvertebrate fauna in the alpine lakes.

In the species/taxa diagram (Fig. 9B), only taxa with species weight range >10% were displayed (20 of total 48 taxa). Insects were organized according to their presence in particular lakes—species/taxa predominating in VW were located on the left side of the diagram, taxa occurring almost exclusively in VTS were situated on the right side. The central part of the diagram was filled by the taxa common to all lakes, or those that were found to be most abundant in NTR.

Most of the aquatic insect species/taxa defined by DCA (Fig. 9B) are considered to be indicative for the respective altitudinal zones. The distribution and density of these species are shown in Fig. 10, ordered according to their first axis species scores in the DCA. The littoral insect assemblage in VW consisted of only five species. Three of them could be identified as indicative for this lake littoral: chironomids *Pseudodiamesa arctica* and *Micropsectra radialis*, and the stonefly *Capnia vidua*. The highest densities of these three species occurred in VW, though they were also found at low densities in lower elevation lakes. The assemblage from the littoral zone of NTR was characterized by higher taxa richness, and no taxon was found exclusively in this lake littoral. The chironomid *Micropsectra junci* and caddisfly *Drusus trifidus* reached their highest density in NTR. Larvae of the caddisfly genus *Acrophylax* were common and abundant in both alpine lakes, while the stonefly *Diura bicaudata*, and chironomid *Macropelopia nebulosa* occurred at the same density in NTR and VTS. A diverse and species-rich insect assemblage was found in the littoral of the lowest elevation VTS. *Agabus bipustulatus*, *Hydroporus* sp. (Coleoptera), *Nemurella pictetii* (Plecoptera), *Micropsectra bavarica*, *Paratanytarsus austriacus*, *Cricotopus polaris*, *Zavrelimyia* sp., *Prodiamesa olivacea* and *Corynoneura scutellata* group (Chironomidae) characterized this assemblage in terms of presence and density.

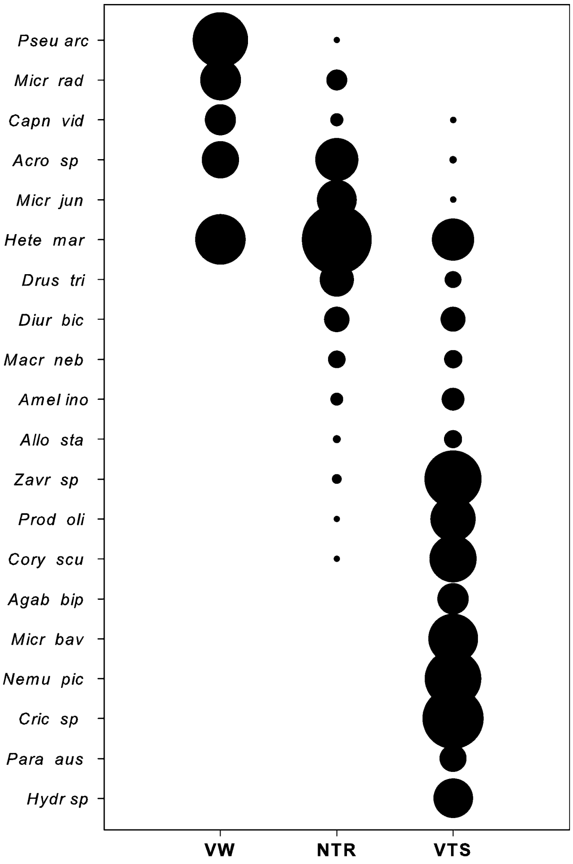

Fig. 10 Distribution of insect species/taxa (DCA species weight range > 10%) in the littorals of the studied lakes. Lakes are ordered by decreasing altitude (VW, NTR, VTS—see Table 1); species are ordered by DCA axis 1 species scores; *circles* symbolize log-transformed densities (for taxa abbreviations see Fig. 9)

Larvae of *Heterotrissocladius marcidus* were abundant in all the lake littorals.

Discussion

Environmental factors

Altitude and the closely linked parameters temperature and POM were considered in this study as determining environmental factors with respect to changes in the littoral macroinvertebrate assemblages of high mountain glacial lakes. Up until now, studies on the benthos of Tatra lakes have focused on a whole complex of environmental parameters with the variables of thermal regime, pH and altitude plus additional factors such as lake area, dissolved carbon, TP, and chlorophyll-*a* used to explain macroinvertebrate fauna structure and changes (see Krno et al., 2006 for more details). Other surveys (e.g. Jacobsen et al., 1997; Lotter et al., 1997; Fjellheim et al., 2000; Larocque et al., 2001; Di Sabatino et al., 2004; Füreder et al., 2006) have resulted in similar results from other mountain districts.

Altitude is closely connected with a climatic temperature gradient in the Tatra Mts, distinctly reflected in an increase of air temperature as elevation decreases (e.g. Lotter et al., 1997). This gradient in mean annual air temperature has been variously reported as 0.6°C (Lajczak, 1996) or 1.4°C (Šporka et al., 2006) per 100 m of elevation. As there is a close correlation between air and water temperature, gradients in LSWT of the studied lakes were expected. Our results confirmed this, as LSWT (average and maximal) increased with decreasing elevation, in agreement with the data of Livingstone et al. (1999), Lotter et al. (1997) and Šporka et al. (2006). Differences between the two alpine lakes were less marked than between alpine and sub-alpine lakes, confirming stronger relationship between alpine lakes. Seasonal fluctuations in the LSWTs of studied lakes also corresponded well with those from comparable studies of alpine and arctic lakes of Europe (Mosello et al., 1993; Raddum & Fjellheim, 2002), as well as for other lakes in the Tatra area (Šporka et al., 2006). A negative linear relationship between LSWT of a set of 19 Tatra lakes (including our gradient lakes) and altitude was found not only in summer, but also in spring and late autumn.

A variety of climate-related factors influence the limnological conditions (and hence biota) of high-latitude and altitude lakes, but changes in ice- and snow cover are often overriding controllers. Moreover, many other physical, chemical and biological changes occur in lakes that are either directly or indirectly affected by snow- and ice cover (Smol, 1988). The length of the ice-free growing season also determines habitat availability for benthic macroinvertebrates, especially pre-imaginal stages of aquatic insects. According to Catalan et al. (2009), an ice cover duration the 190 days was found to be the most significant ecological threshold affecting lake biota. Šporka et al. (2006) found an increasing trend in the duration of ice cover with altitude at a mean rate of 10.2 days every 100 m in the Tatra Mts. The increase in ice cover period with increasing altitude was also evident in our set of gradient lakes.

Particulate organic matter (POM), one of the main food sources for benthic macroinvertebrates, was also assessed in the studied lakes in relation to the altitudinal gradient. Compared to lower situated lakes, the majority of POM is allochthonous in alpine lakes (Galas & Dumnicka, 1998) and its input into water is very low at high elevations (Füreder et al., 2001). The extent of vegetation cover and soil pools in the catchments are essential sources of organic matter in oligotrophic lakes (Füreder et al., 2006). Not surprisingly, the amount of POM in the surveyed lakes changed along the altitudinal gradient; both CPOM and FPOM increased as elevation decreased. Moreover, noticeable differences in the amount of both POM fractions were observed. The sub-alpine VTS differed significantly in amount of POM, and especially FPOM, from both alpine lakes. Interestingly, Kopáček et al. (2004) observed a lower proportion of vegetation in the catchment of VTS than in that of NTR. This could be partly explained by the fact that they considered only alpine meadows and overlooked dwarf pine patches in the lake catchments. However, the presence of dwarf pine shrubs in the catchment of VTS is obvious. Historical data (Bohuš, 2005) show human impact in the valley of VTS at the beginning of the seventeenth century, with the dwarf pine belt and forests around the tree line being converted into pastures. Consequently, the current extent of dwarf pine is largely reduced, though it is still higher than in the NTR catchment and could be considered an important source of CPOM to VTS. This is also supported by the high amount of dwarf pine segments such as branches, cones and needles found in VTS sediment samples. Faster decomposition of CPOM in warmer conditions of the sub-alpine zone and input from soil pools likely resulted in the greater amount of FPOM in this lake.

Littoral macroinvertebrates

Due to remoteness and harsh climatic conditions, the majority of alpine lakes in European mountain regions have been sampled just qualitatively or semiquantitatively, and only a few times per season (e.g. Füreder et al., 2006; Krno et al., 2006). This study is among the first to study littoral macroinvertebrates using quantitative sampling with relatively high frequency throughout the whole growing season of 2 years.

The number and density of macroinvertebrate species/taxa of the studied lake littorals were low, as the extreme climatic, water chemistry and trophic conditions can be tolerated by only a reduced number of oligostenothermic species that are well adapted to this environmental stress. Similar patterns have been found elsewhere in Europe in alpine lakes above the tree line (Fjellheim et al., 2000, 2009). Chironomids and oligochaetes dominated in the studied lake littorals in terms of species/taxa richness ($>65\%$ of the total species/taxa number) as well as density. The number of chironomids could even have been underestimated, since the 500-µm mesh sampler used might not catch the youngest larvae instars. The macroinvertebrate fauna consisted mostly of species/taxa typical for high mountain lakes (Kownacki et al., 2000; Füreder et al., 2006; Krno et al., 2006). Most are cold stenothermic species which are distributed throughout the coldest areas of Europe. However, the caddisflies *Acrophylax sowai*, *Allogamus starmachi* and *Drusus trifidus* have a more narrow biogeographical distribution and are only found in the Carpathians and Central Europe (Krno, 2006).

Our results showed apparent trends of several biotic metrics with altitude. There were clear increases of the number of species/taxa, genera, higher taxonomic groups, as well as the Shannon–Wiener diversity with decreasing altitude. Comparable studies from high mountain lakes have also demonstrated an increase of species richness, diversity, abundance and biomass of benthic fauna with the improvement of environmental conditions (climatic, light and trophic) as altitude decreases (Krno et al., 1985, 2006; Ertlová, 1987; Fjellheim et al., 2000; Lencioni, 2004; Füreder et al., 2006).

However, evenness and density were lowest in NTR and increased in both lower and higher elevation lakes. In alpine lakes of the Alps, a decline of benthic macroinvertebrate diversity and number of taxa with rising elevation was followed by an increase of abundance up to 2600 m a.s.l., above which it then decreased markedly (Füreder et al., 2006). This phenomenon could be explained by the ability of a few well-adapted species to use time-restricted input of food resources under extreme climatic conditions. In the littoral of VW such mass-occurring species were

Crenobia alpina, *Cernosvitoviella atrata*, *Stylodrilus heringianus*, *Pseudodiamesa arctica* and *Heterotrissocladius marcidus*. Nevertheless, the reason for the lowest macroinvertebrate density in the littoral of NTR remains unclear.

The proportion of macroinvertebrate functional feeding groups (FFG) did not show any distinct trends along the altitudinal gradient. The dominance of gatherers (about 60–70%) in all the studied littorals, due mostly to gathering oligochaetes and chironomids, indicated a dependence of the macroinvertebrate assemblages on FPOM. The high percentage of predators in the uppermost lake VW was mainly due to *Crenobia alpina.* In both lower elevation lake littorals, predators were more diverse but their proportions were lower. Only scrapers showed an increasing proportion with a decline in altitude. It might be suggested that longer light availability due to earlier ice melt and higher nutrient inputs could favour littoral benthic algae and support the higher proportion of scrapers in the littoral of lower elevation lakes. However, we did not study the relationship between the amount of epilithic algae and elevation. The low number of shredders, even in the VTS littoral, indicates that CPOM is almost not utilized as a food resource in the studied lakes.

FFG metrics have a long history, and have recently begun to be applied to lake macroinvertebrate analyses. However, the use of these functional characteristics in biological assessment is still undeveloped (e.g. Solimini et al., 2008). The application of the FFG metrics in this study should therefore be considered informative only. Differences between the results presented here and the studies of other authors (e.g. Boggero et al., 2006) might have arisen from different approaches in the species/taxa allocation to the functional feeding groups. Species living in extreme conditions are generally assumed to be more flexible in the utilization of available food sources (Zah et al., 2001). Consequently, a more detailed recognition of benthic macroinvertebrate trophic preferences combined with taxonomic expertise is needed.

Different responses were observed for the non-insect and insect macroinvertebrate fauna to the altitudinal gradient. While the density of both these macroinvertebrate groups showed very similar patterns that were independent of altitude, clear differences in species/taxa richness and taxonomic composition were seen. Non-insect fauna was rather uniform, with many common species in all studied lake littorals (e.g. *Crenobia alpina*, *Stylodrilus heringianus*, *Haplotaxis gordioides*, Enchytraeidae, Naididae); therefore this group would seem to be a poor indicator of temperature changes. In contrast, insect fauna distinctly increased in number of species/taxa with declining elevation, and species structure also differed among lakes. Aquatic insects, primarily chironomids, dominate the littoral fauna in alpine lakes of Europe (Fjellheim et al., 2009). In the surveyed Tatra lakes, insects comprised from 30–40 to >50% of the total benthic macroinvertebrate density in the alpine and sub-alpine lakes, respectively.

Apparently, the altitudinal gradient of the studied lakes is reflected in changes to the aquatic insect fauna. Environmental temperature is critical to the ecology and evolution of aquatic macroinvertebrates (e.g. Ward, 1992). Nearly all aspects of the life history and distribution of aquatic insects are influenced by temperature. The more sensitive response of aquatic insects to altitudinal/temperature gradient is caused by the fact that most aquatic insects (with the exception of the Coleoptera and Heteroptera) are subjected to extreme temperature conditions not only in the aquatic (immature) stage but also in the terrestrial (mature).

Insect fauna along an altitudinal/temperature gradient

The DCA based on quantitative insect data confirmed that the choice of the three surveyed lakes could successfully represent a gradient model. In spite of the fact that the altitude difference between the lowest elevation and highest elevation lakes was only ~430 m, three more or less distinctive littoral insect assemblages were distinguished.

The assemblage of VW consisted of a low number of oligostenothermic species often occurring in high densities (e.g. *Pseudodiamesa arctica*, *Heterotrissocladius marcidus*). This species composition seems to be a general feature of alpine Tatra lakes situated above 2000 m a.s.l. (Krno et al., 2006) and in some aspects resembles the fauna of other European lakes under extreme conditions (Lindegaard, 1992; Lotter et al., 2000; Larocque et al., 2001). We could not find any other water bodies in Slovakia where these species occur (perhaps with the exception of a small and extremely cold lake in the Low Tatra Mountains).

A decrease in density or extinction of the species (especially *Pseudodiamesa arctica*, *Micropsectra radialis* or *Capnia vidua*) could be a reliable signal of warming of the alpine lakes in the Tatra Mountains.

The littoral insect assemblage of VTS was the most species/taxa rich, consisting mainly of species that are widespread in the sub-alpine zone (e.g. *Cricotopus polaris*, *Paratanytarsus austriacus*, *Micropsectra bavarica*) as well as at lower elevation (e.g. *Prodiamesa olivacea*, *Agabus bipustulatus*, *Nemurella pictetii*). A similar taxonomic composition has previously been observed for Tatra Mts lakes (Kownacki et al., 2000; Krno et al., 2006) and analogous biotopes in Europe (e.g. Boggero & Nobili, 1998; Füreder et al., 2006). The littoral assemblage of NTR did not contain species that were markedly different to those in the VW and VTS littorals. Only two species (the chironomid *Micropsectra junci* and caddisfly *Drusus trifidus*) were selected by DCA as indicative, based on their highest density in this lake littoral. However, data on the occurrence of both species in Tatra lakes are so scarce that their value as indicators should be considered with caution.

Only two taxa were clearly restricted to lake littorals in the alpine zone: larvae of the caddisfly genus *Acrophylax* and the chironomid *Micropsectra radialis* were common and abundant in both NTR and VW. These strictly cold-stenothermal, polyoxybiontic taxa occur in sub-alpine lakes only rarely. For example, larvae of *M. radialis* have mostly been found in deep alpine Tatra lakes, and their presence in shallow lakes indicates extremely low temperature conditions. The species is generally absent in sub-alpine Tatra lakes with the exception of some deep lakes with a cold and well-oxygenated hypolimnetic zone (Bitušík et al., 2006b). The absence of *M. radialis* in alpine lakes could indicate higher temperatures not only in the littoral but also in the profundal zone (see Hofmann, 1988). This species has high indicative value, as demonstrated in Lake Paione Superiore where its abundance decreased markedly over the last 100 years due to climate changes (Guilizzoni et al., 1996).

A number of species/taxa were present in both sub-alpine VTS and alpine NTR. While some of them (e.g. *Allogamus starmachi*, *Zavrelimyia* sp., *Coynoneura scutellata* group) have their optima in the sub-alpine and lower alpine zone of the Tatra Mountains, others such as *Diura bicaudata*, *Ameletus inopinatus* and *Macropelopia nebulosa* have wider ecological valence and also occur below the tree line (Kownacki et al., 2000; Bitušík et al., 2006b; Krno et al., 2006, unpublished data). It is notable that these species/taxa and some other species mentioned above (e.g. *Paratanytarsus austriacus*) are confined to lakes situated at lower altitude, generally below 2000 m a.s.l. Thus, their regular appearance in lakes above ~2000 m a.s.l. could indicate changes in temperature. The final species selected by DCA—*Heterotrissocladius marcidus*—is one of the most widespread species in the Tatra lakes (Bitušík et al., 2006b). Consequently, its indicative value for temperature change is negligible.

The DCA revealed a high degree of similarity among the littoral benthic samples throughout the whole growing season in terms of both taxonomic composition and density. This is especially true for the littorals of the alpine lakes and suggests that the insect assemblage structures were not significantly affected by the seasonal dynamics of larvae, their life histories, or the emergence of adults. This finding could be important for the sampling design of future investigations.

Chironomids dominated the macroinvertebrate fauna of the surveyed lakes. Despite the fact that larval identification is time consuming and requires special taxonomic expertise, chironomids may provide valuable information relevant to various environmental variables. Our results support the use of chironomids and caddisflies as flagship indicators in the assessment of climatic change in mountain areas.

Concluding remarks

This study, based on the investigation of the gradient lake model, contributes to the understanding of changes in the littoral macroinvertebrate fauna induced by climate warming. In the Tatra Mts., mean summer temperatures have recently decreased, while mean winter temperatures have increased (Šporka et al., 2002). As lake ice melt and ice formation is controlled by spring and autumn temperatures (Agustí-Panareda & Thompson, 2002), a decrease in the duration of ice cover in Tatra lakes can be expected. Recently, an ice cover duration of 190 days, the most important ecological threshold for alpine lake biota, has been recognized in sub-alpine lakes in the Tatra Mountains.

If temperatures of these lakes increase, what changes in the littoral macroinvertebrate fauna could be expected? While the non-insect benthic macroinvertebrate fauna will remain more or less stable, the aquatic insects will be affected. The higher number of developmental degree days may play an important role in allowing the existence of more thermophilic species through conditions of a longer ice-free period with warmer water in the littoral zone. The local macroinvertebrate fauna will be affected by species currently present only at lower altitudes (below the tree line and in sub-alpine zone), leading to higher biodiversity. At the same time, the higher ambient air temperature will be favourable for the survival and dispersal of insect adults. On the other hand, cold stenothermal species will be subject to extinction. An indirect impact on benthic macroinvertebrates through food sources can also be expected. The epilithic algal biomass could be enhanced by the change of light availability resulting from earlier ice melt. Consequently, there could be a higher proportion of scrapers in the trophic structure of the littoral assemblages.

Of course, the magnitude of a climate-driven response of benthic macroinvertebrates will vary. Many other factors such as watershed characteristics, lake morphometry, orientation and local meteorology modify the linear relationship between altitude and thermal regime of lakes (Brodersen & Anderson, 2000). Nevertheless, the strongest response of macroinvertebrate fauna will likely be in shallow alpine lakes above 2000 m a.s.l. when the duration of ice cover shortens below the 190-day threshold.

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