

Diversity and distribution patterns of benthic invertebrates along alpine gradients. A study of remote European freshwater lakes

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With 4 figures, 3 tables and 1 appendix

Abstract: Invertebrates inhabiting alpine water bodies are sensitive to environmental variability and lake faunal communities can therefore be important indicators of long-range airborne pollution, climate change and other human impacts. Information about the trophic structure and species composition of alpine lake ecosystems over space and time should therefore give important insights into environmental change effects. To explore the sensitivity of the faunal communities to environmental variability at local and regional scales we sampled biological and environmental variables from alpine lakes in seven different alpine lake districts in six European mountain regions. The fauna of the lakes was mainly com-

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posed of oligotrophic/ultraoligotrophic species, predominantly chironomids which made up more than 60% of all individuals. Species accumulation curves were used to explore patterns of species turnover and distribution, and the results indicated strong patterns in species diversity and also environmentally-driven patterns in species distributions among lake districts. We used ordination analyses to explore these patterns in more detail. The results showed that the over-riding patterns in faunal assemblages were found between the lake districts. Lake-water chemistry appeared to be the major driver of the faunal assemblages at this scale, but altitude and geography could also account for significant fractions of the variability. In addition to these broad-scale patterns, repeatable trends in the faunal assemblages could be found in the faunal assemblages within lake districts. At this scale, the strongest compositional trends were found along the altitudinal gradient, but the faunal communities also responded to within-district variability in lake-water chemistry. Lake size or maximum depth did not appear to have any statistically significant effect on the littoral faunal assemblages at either scale.

Key words: alpine lakes, Europe, littoral invertebrates, distribution, environmental gradients.

Introduction

Alpine lake ecosystems are well-suited for studying large-scale effects of long-range transported pollution of anthropogenic origin because 1) they are simple ecosystems having few species and less complex food webs than lowland lakes, 2) they respond rapidly to environmental change, and 3) the effects of local anthropogenic influence are normally negligible. Small lake size and a high turnover of surface waters make arctic and alpine catchments vulnerable to anthropogenic pollution. The watersheds have little capacity to neutralize acid deposition (except in lakes on limestone – MURI & BRANCELJ, 2002) and pollutants will rapidly reach water bodies due to bare rocks, thin soils and sparse vegetation cover (CUMMING et al., 1992; MOSELLO et al., 1995; BIRKS et al., 2004). Heavy metals and volatile organic compounds have a tendency to accumulate more readily in high altitude/high latitude lakes (CAMARERO et al., 1995; JØRGENSEN et al., 1999; DONAHUE et al., 2005). Arctic and alpine lake ecosystems are also uniquely suited for monitoring global change since they rapidly respond to climatic change (PSENNER & SCHMIDT, 1992; KOINIG et al., 1998; SMOL et al., 2005) and atmospheric deposition (ROSSELAND et al., 1986; ILYASHUK & ILYASHUK, 2001; WOLFE et al., 2001; RÜHLAND et al., 2003). Most alpine lakes also have undisturbed fossil records accumulated in sediments allowing reconstruction of the past conditions.

The ecology of the benthic fauna in alpine lakes is influenced by both local and regional factors. Bedrock characteristics, local climate and human impact in the form of changes induced in vegetation cover, grazing cattle or pollution from point sources are important local factors. On a regional scale, the biogeographic history of the lakes, climate and long-range transported airborne pollution are important factors. Benthic macroinvertebrates form a diverse group, of which the critical limits of many taxa to various environmental factors are known. They are therefore useful as indicators of environmental change and have been used as a tool in monitoring human impact upon ecosystems (FJELLHEIM & RADDUM, 1990; HODKINSON & JACKSON, 2005). Remains of some invertebrate groups, such as chironomids and cladocerans, are stored in the sediments and therefore form valuable data-series of historic ecosystem changes and succession (WARWICK, 1980; BRODERSEN et al., 1998; BRANCELJ et al., 2000).

Alpine lakes are situated in extreme environments where the amplitudes of climatic factors are relatively large. Ice cover normally lasts for a long period (7-9 months), and during

the ice-free season, thermal heating of the lakes may be substantial due to intense solar radiation, small lake areas and/or water volumes and poorly developed thermoclines. Even small climate-driven changes may lead to rapid responses in the benthic community structure. Studies of the dynamics of alpine lakes along gradients provide vital information for understanding the sensitivity and responses of such ecosystems to climate and environmental change.

The overall aim of this study is to disentangle the relative contributions of different potentially important causal factors to the assembly of faunal communities in European alpine lakes. Specifically, we hypothesize that (1) strong gradients in faunal community composition can be found over short distances in alpine lakes, with climate (i.e. altitude) being the most important driver of such local faunal gradients, but also that (2) faunal assemblages differ among mountain regions. While climate is assumed to be a strong driver of compositional patterns in these habitats, other environmental variables (e.g., bedrock and soils), or historical factors could also play a role. We address these questions by surveying the faunal community composition of European alpine lakes along geographic and altitudinal gradients.

Material and methods

Study areas and lake selection

The EMERGE survey (PATRICK, 2003) has produced a unique database of biological and environmental information for mountain lakes across Europe. Approximately 350 remote mountain lakes were sampled within the EMERGE programme. The Project had two thematic programmes: first, the up-scaling of knowledge from individual sites to regions (lake-districts); and second, the evaluation of regional data to enable the formulation of effective policies and sustainable management strategies (PATRICK, 2003). This paper presents data from two subsets (see below) of littoral invertebrate data from the EMERGE lakes. The lakes were selected to study patterns in species turnover and community composition along comparable local environmental gradients (lakes that are closely situated and physically linked along altitudinal gradients). Seven alpine lake districts (PATRICK, 2003) in Europe were included in the study; Central Norway (CN), the Italian Alps (PT), the Julian Alps (JA), the Polish Tatras (TAP), the Slovakian Tatras (TAS), the Retezat Mountains in Romania (RE), and the Rila Mountains in Bulgaria (RI) (Fig. 1, Table 1). The lakes are all situated close to or above the local tree-line, at altitudes ranging from 728 m a.s.l. (CN) to 2535 m a.s.l. (RI). Surface water chemistry ranges from the extremely mineral-poor waters of the Norwegian reference sites (conductivity 6 – 7 $\mu\text{S cm}^{-1}$) to the mineral rich lakes of the Julian Alps (conductivity 90 – 150 $\mu\text{S cm}^{-1}$). Calcium concentrations reflected the lithology and ranged from 0.4 (CN) to >20 mg l^{-1} (JA), and pH ranged from 6.1 (several locations) to 8.5 (JA). Additional information on the chemistry of surface waters is provided by the MOLAR WATER CHEMISTRY GROUP (1999), MARCHETTO et al. (2004), BOGGERO et al. (2006) (CN, PT, JA), KOPÁČEK et al. (2004) (TAP, TAS), CURTIS et al. (2005) (RE) and BOTEV (2000) (RI).

The first data subset consisted of data from 126 lakes in seven lake districts: 29 lakes in the Italian Alps, 24 in Central Norway, 11 in the Polish Tatras, 14 in the Retezat Mountains, 34 in the Slovakian Tatras and 14 in the Julian Alps. This dataset was used for a preliminary exploratory analysis of species richness and species turnover based on species accumulation and rarefaction curves. The second subset consisted of 25 lakes in seven lake districts which were selected on the following criteria: 1) Lake catchments should experience a low degree of disturbance by human activities such as animal grazing or human recreation. 2) Changes in lake water quality should only be due to atmospheric pollution and to natural variability. 3) Each lake district subset includes a gradient of lakes within the same watershed. This data subset was used for a more detailed analysis of patterns in community composition among lakes (Fig. 1).

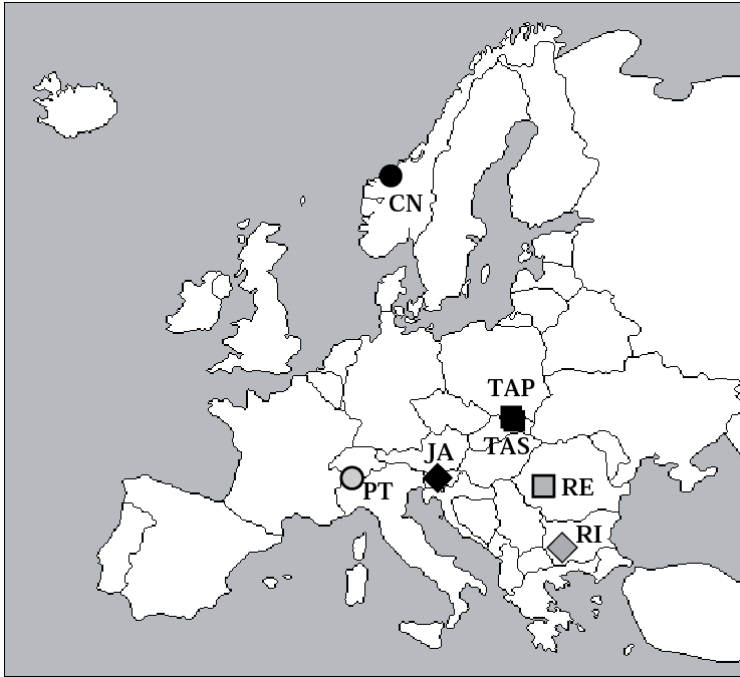


Fig. 1. Map showing the geographical situation of the studied lake areas. CN: Central Norway, PT: Italian Alps, JA: Julian Alps, RI: Rila Mountains, RE: Retezat Mountains, TAP: Polish Tatra Mountains, TAS: Slovakian Tatra Mountains.

Benthic invertebrate sampling and identification

Lake sampling took place during late summer or early fall according to a common sampling protocol (FJELLHEIM et al., 2000). Samples were taken from the littoral and sieved through a net with 250 μm mesh size, and preserved in 70% ethanol. In each lake, samples from the range of available habitats were amalgamated to one sample prior to analysis. Benthic animals were identified to species using a binocular and/or a microscope. Chironomid larvae were mounted in Hoyer's solution on microscopic slides and identified to the lowest taxonomic level possible. Most animal groups were identified to the species level. In cases of differences in taxonomic precision between the participating institutions, the highest taxonomic level was chosen to facilitate comparison between regions (see SCHNELL et al., 1999).

Environmental data

Water chemistry was analyzed by the participating institutions following the protocol of MOSELLO & WATHNE (1997). Parameters included in the multivariate analyses were pH, conductivity, Ca^{2+} , Mg^{2+} , Na^+ , alkalinity, SO_4^{2-} , Cl, total nitrogen and total phosphorus. Geographical and morphometric parameters included were latitude, longitude, altitude, lake area and maximum depth. The variables were log-transformed when necessary to normalize variances.

Statistical analysis

We used species accumulation curves and rarefaction curves to explore species turnover among lakes within and among regions. We computed expected species accumulation curves and individual-based rarefaction curves for chironomids (the dominant benthic taxa group). The rarefaction curve represents the statistical expectation for the corresponding accumulation curves, and differences between the two types of curves indicate a heterogeneous and clumped distribution of species within the study area. Both types of curves were computed using EstimateS 7.5 (COLWELL, 2005).

We analysed all the lake districts and in particular the Italian Alps district due to the high difference between number of individuals and number of species found. Sample order was randomized 50 times and mean richness estimate was computed for each sample accumulation level. This removes the effect of sample order and generates a smoother curve. Individual-based rarefaction curves (Coleman curves) computed for sample-based abundance data according to COLEMAN (1981) showed the number of species/taxa expected in the pooled samples as a mean among runs, assuming individuals are distributed at random among samples. Species accumulation curves (sample-based rarefaction curves in the terminology of GOTELLI & COLWELL, 2001, named Mao Tau curves) indicate the number of species expected in the pooled samples and were computed according to COLWELL et al. (2004). Based on the species accumulation curves we compared species richness within regions using the t-test based on the number of individuals, species richness and standard deviation of species richness provided by the output of EstimateS. Five regions were compared at a minimum sample size of 14 lakes (TAP was not included since the maximum number of lakes sampled was 11). The software used was R, version 2.6.0 (The R Foundation for Statistical Computing).

Ordination methods were used to explore the patterns of species turnover in more detail. Specifically we used the partial ordination approach to quantify the explanatory power of different groups of environmental variables (climate, lake water chemistry) for species composition in lakes at the within-region and among-regional scales using the computer program CANOCO version 4.5 (TER BRAAK & ŠMILAUER, 2002). The benthic faunal assemblages of lakes from which < 100 individuals had been sampled were considered insufficiently sampled, and these lakes were excluded from the analyses. All analyses were performed using log-transformed species counts, down-weighting of rare taxa, and default CANOCO 4.5 settings unless otherwise stated. Unimodal-based methods were selected on the basis of a preliminary detrended correspondence analysis (DCA; HILL & GAUCH, 1980) with detrending by segments and nonlinear rescaling which found that the main gradient in the species data was ca. 3.7 standard deviation units (LEPŠ & ŠMILAUER, 2003).

Variation partitioning is a multivariate statistical approach that overcomes the problems of collinearity in observational data by allowing the decomposition of the total variability in the response variable(s) into independent components reflecting the unique contributions of each (group of) explanatory variables as well as their joint effects (BORCARD et al., 1992; LIU, 1997; HEIKKINEN et al., 2005). This is done by means of a series of (partial) (canonical) correspondence analyses [(p)(C)CA] (TER BRAAK & ŠMILAUER, 2002). While the approach was originally presented as a means of partitioning variation onto two sets of variables, typically 'space' and 'environment' (BORCARD et al., 1992), it can be generalized to any number of explanatory variables (VANDVIK & BIRKS, 2002; ØKLAND, 2003). In this paper, we use the variation partitioning approach to quantify how the community assemblies of benthic invertebrates in alpine lakes respond to four sets of potentially important environmental variables - lake water chemistry (WC), lake size (LS), altitude (A) and geography (G). In particular, we focus on the explanatory power of these different sets of environmental variables at two different spatial scales; within lake districts and among lake districts:

- i) A CCA run with the matrix of the categorical (or dummy) variables representing the geographical regions (R) partitioned the total variation in the faunal assembly into a within-region and between-region component.
- ii) A series of four CCA runs with forward selection and the associated Monte-Carlo permutation test (999 permutations) of each added explanatory variable was performed separately for each of the environmental variable groups WC, LS, A, and G to exclude explanatory variables that did not contribute significantly ($p > 0.05$ after Bonferroni correction) to the variation explained by each of these groups (BORCARD et al., 1992). This was done to avoid overestimation of the explained variation in the data (BORCARD et al., 1992), and all subsequent analyses are based on these subsets of significant variables.

Table 1. Physical and chemical characteristics of the investigated lakes. The lakes are coded according to lake district (Fig. 1). TA0007, TA0009 and TA0010: Polish lake district (TAP), TA0011, TA0017 and TA0022: Slovakian lake district (TAS). Methods of chemical analysis are described by The MOLAR Water Chemistry Group (1999).

SiteCode	Name	Alt. m a.s.l.	L. area ha	Depth m	Catchment area (ha)	Latitude N	Longitude E	pH	Cond $\mu\text{S cm}^{-1}$	Ca ²⁺ mg l ⁻¹	Mg ²⁺ mg l ⁻¹	Na ⁺ mg l ⁻¹	Alk $\mu\text{eq l}^{-1}$	SO ₄ ²⁻ mg l ⁻¹	Cl ⁻ mg l ⁻¹	TN $\mu\text{g l}^{-1}$	TP $\mu\text{g l}^{-1}$
CN0016	Øvre Neådalssvatn	728	50.0	18	1600	62.77778	8.98237	6.2	6	0.4	0.09	0.70	17	0.5	0.80	62	1.0
CN0017	Fallbekktjøttna	1043	27.0	12	370	62.74996	9.03719	6.1	7	0.4	0.10	0.68	13	0.6	0.90	41	1.0
TA0007	Zielony Staw	1672	3.8	15.1	33	49.22890	20.00100	6.8	17	2.1	0.16	0.42	88	2.0	0.17	344	4.4
TA0009	Długi Staw	1784	1.6	10.6	65	49.22730	20.01070	6.2	14	1.4	0.08	0.33	22	2.2	0.17	534	1.4
TA0010	Zadni Staw	1852	0.5	8	72	49.22550	20.01190	6.4	16	1.9	0.12	0.37	37	2.2	0.18	688	1.3
TA0022	Vyšné Temnosmrčinské pleso	1716	5.0	20	112	49.18910	20.03950	7.2	33	4.8	0.29	0.36	262	2.0	0.16	392	1.8
TA0011	Nížné Terianske pleso	1941	4.9	43.2	110	49.16980	20.01430	6.7	17	2.6	0.10	0.32	89	1.7	0.17	466	1.6
TA0017	Vyšné Wahlenbergovo pleso	2145	5.0	21.1	32	49.16420	20.02710	6.3	11	1.3	0.07	0.22	29	1.3	0.17	416	2.2
PT0026	Lago Paione inferiore	2002	0.9	13	121	46.16889	8.19083	6.6	13	1.3	0.13	0.36	38	2.1	0.14	350	2.0
PT0028	Lago Paione dimezzo	2147	0.7	4	84	46.17222	8.19194	6.5	13	1.2	0.13	0.40	35	2.0	0.18	440	5.0
PT0027	Lago Paione superiore	2269	0.7	10	51	46.17583	8.19083	6.1	9	0.7	0.08	0.24	3	1.6	0.18	430	6.0
JA0007	Jezero Čmo	1325	0.9	6	140	46.29889	13.80000	8.5	137	23.4	2.20	0.32	1504	1.9	0.67	1659	78.0
JA0005	Jezero Dvojno (5.)	1669	1.0	7.8	90	46.31750	13.78417	7.8	150	23.1	3.91	0.29	1624	1.7	0.44	1576	10.1
JA0006	Jezero Dvojno (6.)	1669	0.7	5.6	90	46.31583	13.78417	8.0	140	21.9	3.94	0.05	1611	1.5	0.32	1473	21.9
JA0004	Jezero v Ledvicah	1830	2.2	15	175	46.34028	13.78667	7.7	141	20.4	4.16	0.07	1506	1.4	0.30	1429	8.7
JA0003	Jezero Zeleno	1983	0.6	2.5	24	46.35139	13.79917	8.0	91	14.6	2.23	0.09	1039	0.8	0.30	1327	22.2
JA0001	Jezero pod Vršakom	1993	0.6	5	54	46.36000	13.80278	7.7	130	21.2	2.68	0.54	1237	1.4	0.55	1922	12.7
JA0002	Jezero Rjavo	2002	1.3	10	36	46.35556	13.80000	7.6	135	21.9	3.09	0.12	1483	1.3	0.43	1637	11.5
RE0010	Tauš Gemelele	1920	2.5	5.3	29	45.36618	22.84159	6.5	11	1.2	0.11	0.78	29	2.6	0.23	375	5.3
RE0008	Tauš Negru	2036	4.0	24.8	61	45.36014	22.82890	6.1	13	1.3	0.12	0.96	29	2.6	0.13	360	3.8
RE0017	Lacul Stîrbul	2082	1.0	8.7	35	45.36461	22.85460	6.5	13	1.4	0.13	1.05	40	2.4	0.18	431	2.6
R10011	Ezero Bliznaka	2243	9.1	27.5	217	42.20122	23.31497	6.8	29	4.1	0.38	1.09	209	3.0	0.32	244	7.1
R10009	Ezero Bubreka	2282	8.5	28	61	42.20556	23.30678	6.6	23	3.3	0.33	0.63	139	3.0	0.37	149	14.7
R10008	Ezero Okoto	2440	6.8	37.5	42	42.19964	23.30584	7.2	23	2.9	0.28	0.85	115	3.8	0.33	182	7.1
R10010	Ezero Sulzata	2535	0.7	4.5	11	42.19750	23.31028	7.0	32	2.6	0.36	1.81	94	4.5	2.07	189	17.6

- iii) A series of four partial CCAs with regions treated as covariables were performed for each of the environmental variable groups WC, LS, A, and G to partition the variation accounted for by each of these groups into a within-region and a between-region component.
- iv) A series of partial CCAs were performed to enable a full partitioning of the variation in the faunal assemblage data into independent components representing the unique and shared variation between each of the different environmental variables at the within-region and between-region scales (VANDVIK & BIRKS, 2002; ØKLAND, 2003).

We present (partial) CCA diagrams to visualize patterns in faunal assemblage composition within and among lake districts. The ordination diagrams were drawn in CANODRAW (TER BRAAK & ŠMLAUER, 2002).

Results

Chironomids dominated the fauna (68 % of all taxa and 61 % of all individuals). The most commonly encountered species were *Heterotrissocladius marcidus*, *Micropsectra radialis*, *Prodiamesa olivacea* and *Paratanytarsus austriacus* (Appendix). Other common invertebrates were the turbellarian *Crenobia alpina* and the mayfly *Siphonurus lacustris*. With the number of individuals of benthic invertebrates sampled ranging from 24 to 1525 per lake, and a total of 118 species recorded, sampling issues may potentially have a considerable effect on recorded species richness and diversity. Therefore, species accumulation and rarefaction curves were used to explore patterns of species richness among the lake districts. Chironomid species accumulation curves indicated that there was high species turnover among lakes within each region, but also that turnover varied among regions, being relatively high in Central Norway and relatively low in the Julian Alps and the Tatra mountain lake districts (Fig. 2a). Species richness was significantly different between regions when comparing a subset of 14 lakes from each (t-test, $p < 0.001$). The differences between the accumulation and rarefaction curves for total invertebrates as well as chironomids in the Italian Alps indicated that species had a heterogeneous and clumped distribution within this region (Fig. 2b). These patterns suggest that species respond to underlying environmental and/or spatial gradients within regions, and that patterns vary among regions. These issues were explored in more detail using ordinations.

The first step in the multivariate statistical analyses was to explore the relative explanatory power of different groups of potentially important explanatory factors for the total variability in the faunal assemblage data by means of variance partitioning. This analysis showed that four groups of potentially important explanatory variables differed considerably in explanatory power; lake water chemistry appeared to be the strongest driver of faunal assemblages in these data and accounted for almost 35% of the variability. Altitude (18%) and geography (10%) accounted for considerably lower fractions of the faunal assemblages (Table 2), whereas lake size or maximum lake depth did not account for any statistically significant patterns in the littoral faunal assemblages.

Overall, 47.7% of the compositional variability was found at the among-regional scale, and more than half of this variability (24.9%), could also be accounted for by the measured explanatory variables and therefore reflects patterns that are structured by the environment (Fig. 3, Table 2). Lake-water chemistry appeared to be the over-riding environmental driver of faunal assemblage at this scale, but geographical location and altitude also contributed to the explained variation (Fig. 3). While all groups of variables can account for unique components of the variability there was also a shared fraction (a total of 6% of the variation) illus-

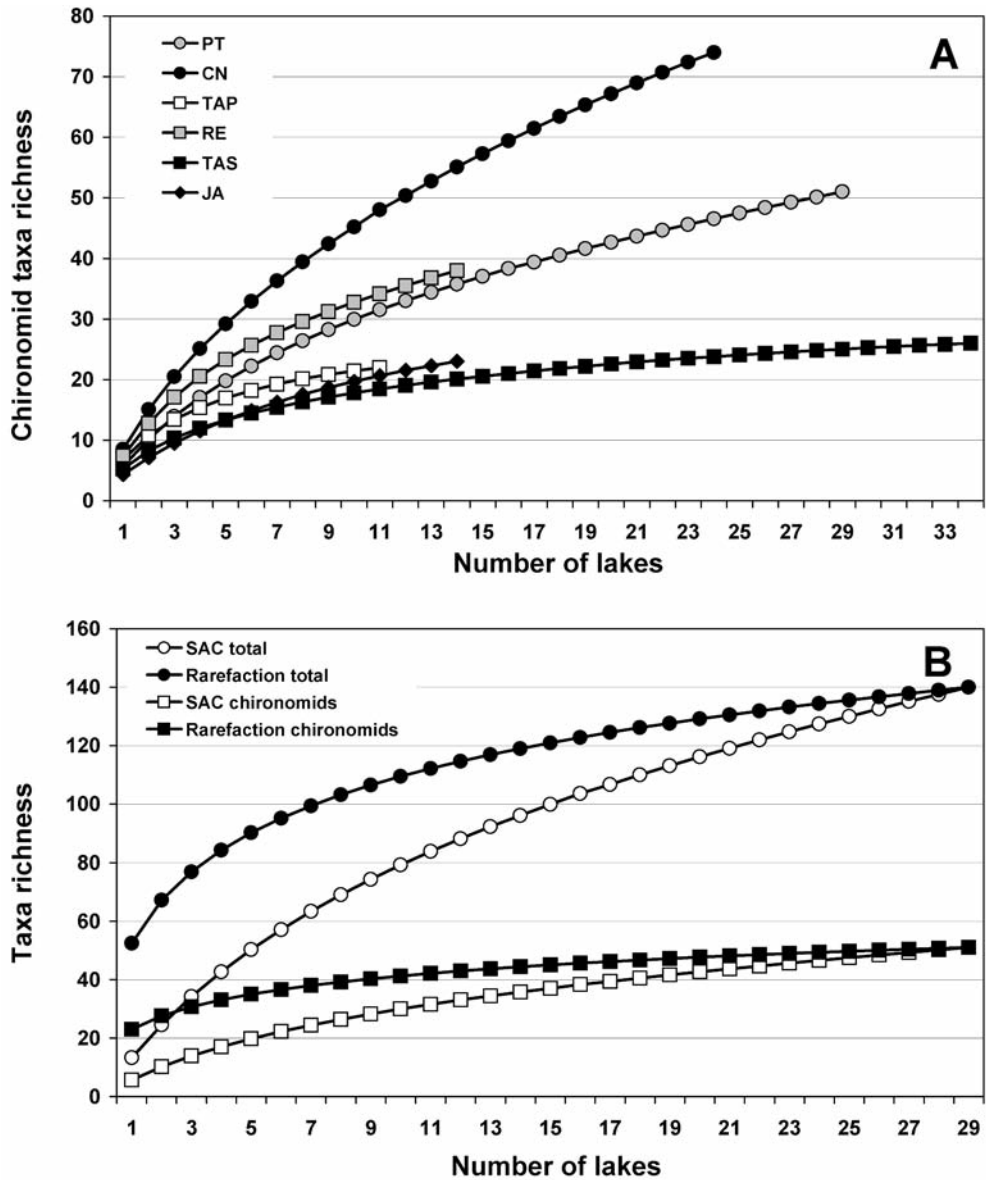


Fig. 2. A. Species accumulation curves for chironomids from the different lake districts. Symbols as in Fig. 1. B. Species accumulation curves and rarefaction curves for all invertebrate taxa and for chironomids only for the Italian Alps.

trating the difficulties in separating the effects of different potentially important environmental variables in observational data. A CCA ordination diagram based on all subsets of explanatory variables showed that the overriding patterns in species turnover among lakes

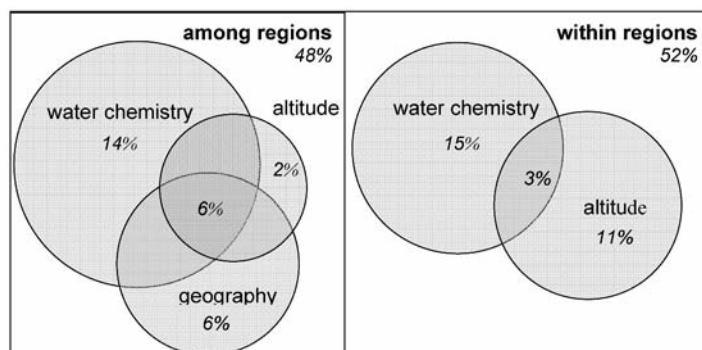


Fig. 3. Venn diagrams illustrating how the variation in the faunal assemblage can be decomposed into components accounted for by each of the three groups of significant environmental variables at the two spatial scales: among regions and within regions. The areas of the rectangles represent the total variation at each spatial scale; the circles represent the approximate variation accounted for by each of the groups of environmental variables at that scale. Overlaps between the different circles indicate joint variation components – variation that cannot be uniquely attributed to any one group due to collinearity in the environmental data. Based on data in Table 3.

could be found between the geographical regions of our study (Fig. 4a). These patterns appeared to be related to a primary gradient reflecting regional trophic differences with species like *Prodiamesa olivacea*, *Coryoneura scutellata* and *Pseudodiamesa branckii* being common in the ultraoligotrophic sites and acid sensitive species like *Siphonurus lacustris*, *Pisidium* spp. and *Lymnaea* spp. being more abundant in localities characterized by higher conductivity and nitrogen. A north – south gradient in species distribution is displayed by the

Table 2. Summary of the groups of explanatory variables and the variables retained in each group after forward selection. The total % explained is the variance accounted for when all significant variables in that group are included as explanatory variables in a CCA, the unique % explained is the variance accounted for after the effect of all other groups are removed in a partial CCA. These entries are expressed as % of total inertia. P-values are based on Monte Carlo permutation tests (see text).

Component	Variables included#	Total	% explained	
			p-value	Unique p-value
Water chemistry	<i>pH</i> , Cond, <i>Ca</i> , <i>Mg</i> , <i>Na</i> , <i>Alk</i> , SO ₄ , <i>Cl</i> , TN, <i>TP</i>	34.7	0.001	12.0 0.522
Lake size	<i>lake size</i> , <i>max. depth</i>			
Altitude	altitude, altitude*latitude, altitude*longitude	18.5	0.001	10.4 0.046
Geography	latitude, longitude	10.5	0.001	0.0*
Regions	6 regions (+/-)	47.7	0.001	22.8 0.013
Total explained	all significant variables above	64.3	0.001	

Variables excluded from each group after forward selection are written in italics,

* All the variability potentially explained by geography is also accounted for by the presence/absence variables representing regions.

Table 3. Results of all CA, CCA and partial CCA analyses performed to quantify the unique and shared variances of all groups of explanatory variables. Each column contains the results from a number of analyses performed using this particular group as an explanatory variable and includes different (combinations of) groups as covariables. Entries are in % of the total variance. P-values are based on 999 unrestricted Monte Carlo permutations. – = not available. For the individual variables included in each group, see Table 2.

Covariables \ Variables	Regions		Geography		Altitude		Chemistry		All	
	% explained	p(999)	% explained	p(999)	% explained	p(999)	% explained	p(999)	% explained	p(999)
None	47.7	0.001	10.5	0.002	18.5	0.001	34.7	0.001	65.5	
Regions	n.a.		n.a.		11.4	0.006	14.7	0.340		
Geography	41.6	0.001	n.a.		16.3	0.001	30.6	0.001		
Altitude	40.7	0.001	8.2	0.014	–		28.9	0.001		
Chemistry	27.8	0.001	5.6	0.033	12.7	0.007	–			
Chemistry & Altitude	–		5.6	0.050	–		–			
Chemistry & Geography	–		–		12.0	0.010	–			
Altitude & Geography	–		–		–		26.3	0.001		
All other variables	22.8	0.013	–		10.4	0.048	12.0	0.522		

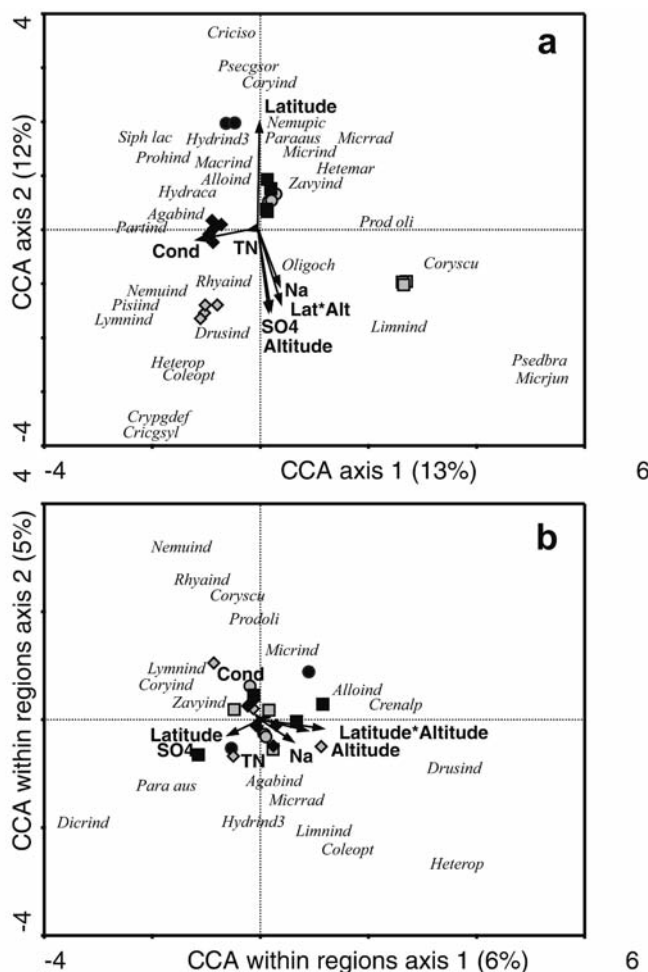


Fig. 4. (a) Ordination diagram visualizing overall trends in the faunal assemblages. The diagram is based on a canonical correspondence analysis with the significant subsets of all groups of explanatory variables included. (b) Ordination diagram zooming in on the within-regional patterns in faunal species assemblages. The diagram is based on a partial canonical correspondence analysis with regions as covariables and the significant subsets of all groups of explanatory variables. Symbols as in Fig. 1. Codes are explained in Appendix.

dominance of species like *Psectrocladius sordidellus*, *Nemurella* spp., *Paratanytarsus austriacus* and *Micropsectra radialis* at higher latitudes.

There were also strong patterns in species composition among lakes within the seven districts (Table 2), and 52.3% of the total variability in faunal assemblages was found at this scale. Although lake water chemistry was still the most important group of explanatory variables, the altitudinal gradient was relatively more important at this finer geographical scale. Because the broader regional patterns were of over-riding importance in the overall CCA analysis, a partial CCA, with regions included as covariables, was performed to zoom in on

the within-regional patterns. The results (Fig. 4b) show that altitude was the most important driver of the lake faunal assemblages at this scale, whereas variability in lake chemistry was mainly captured by the second pCCA axis.

Discussion

In this paper, we present results from analyses on a unique dataset where detailed information on faunal assemblages of lakes across a broad geographic region was obtained in a standardized way, both with respect to the sampling and analytical protocols and the selection of sites within each lake district (i.e. number of lakes along an altitudinal gradient within the same watershed). This enabled us to disentangle patterns in the faunal assemblages at different scales (regional vs. local) and with respect to different environmental variables (climate, environment, lake size, etc.) We found considerable variability and strong patterns in the faunal assemblages at the among-regional scale, confirming our second working hypothesis. However, once these broad-scale patterns were controlled for, there were strong and consistent local-scale responses to altitude (i.e., local climate) and to local variability in lake-water chemistry. This confirms our first working hypothesis.

Studies of processes along gradients are important issues in monitoring long-term variation of environmental stressors. Climatic variations on a local scale, for example precipitation, exposure, temperature and length of ice cover influence the lake ecosystem both directly and indirectly through changed processes in the catchment (SCHINDLER et al., 1990; HENRIKSEN & HESSEN, 1997; TAIT & THALER, 2000). The benthic invertebrate community reacts to environmental changes by quantitative responses within the existing community and by qualitative changes through extinction and immigration. The latter will normally occur over a longer timescale depending on distance to nearest population, dispersal rate, lifecycle length and fecundity.

Lake fauna are more stable than stream fauna due to a more stable physical and chemical environment. In streams, migration through drift and upstream flight of insects are important dispersal mechanisms (MÜLLER, 1982; HERSHEY et al., 1993; FJELLHEIM & RADDUM, 1995). Stream fauna often display a monotonic decline in species richness with increased altitude (JACOBSEN, 2004). Exceptions to this are found in the transition zones between major ecotones like the treeline (GRACE et al., 2002; KUPFER & CAIRNS, 1996) or in localities heavily disturbed by man (LANG & REYMOND, 1993; TATE & HEINY, 1995). Lentic invertebrate assemblages within the same catchment should normally be more fragmented than lotic communities. Remote alpine lakes may, in a geographical sense, be regarded as "islands" where the benthic community diversity is in a dynamic equilibrium between immigration and extinction (MACARTHUR & WILSON, 1963; WELLS, 1983). In a zoogeographical sense, remote alpine lakes may be regarded as "stepping stones" for animal travel (see also BRANCELJ et al., 2009, for Cladocera). Even if the colonisation of such alpine ecosystems in some cases may be governed by chance, most of the colonising species are recruited from taxa pools in nearby water bodies. The differences in species composition are due both to biogeographical factors and to the fact that environmental gradients differ between alpine lake districts.

Our dataset demonstrates how collinearity in the environmental variables makes it difficult to attribute faunistic patterns to specific environmental factors. For example, the importance of altitude varies from south to north. The tree-line in our study area varies from approximately 2300 m a.s.l. in the southernmost Mediterranean latitudes to less than 1000 m a.s.l. in

coastal areas of West Norway (HOFGAARD, 1997; KÖRNER & PAULSEN, 2004). The importance of water chemistry on species distribution is obvious and seems to be a prominent factor within our dataset. The heterogeneous nature of the geo-lithology between the different lake-districts is important in this connection.

Usually, underestimating true species richness is caused by a failure to detect rare species. In our study, SAC for all lake districts except one did not reach an asymptote, indicating that the inventory was not complete. This illustrates a critical issue in sampling designs aiming to characterize whole-lake communities, namely that true species richness is unavoidably underestimated. Even taxa apparently well studied over long periods, when repeatedly inventoried, prove to be insufficiently studied, as illustrated by a detailed study of chironomid larval communities in alpine lakes in Retezat Mountains where 33 new chironomid species were added to the 117 species already inventoried there (COGĂLNICEANU et al., 2009). Using estimators of species richness is one way of dealing with such issues (COLWELL & CODDINGTON, 1994). The lack of latitudinal trends between the lake districts in estimated chironomid larvae richness or SAC can be explained by the importance of local and regional variables that overrule the latitudinal changes in climate. However, we note that there is also a potential problem related to differences in identification level within the different regions (BOGGERO et al., 2006).

The clumped and heterogeneous distribution of littoral invertebrates suggested by the differences between species accumulation and rarefaction curves stresses the importance of microhabitat diversity in maintaining high species diversity, even in lakes with apparently low habitat complexity.

The faunal assemblages in our data were dominated by species known to prefer ultraoligotrophic or oligotrophic conditions (SÆTHER, 1979). Although most of the fauna were detritus and/or algal feeders, several predatory species were abundant, like the chironomids *Cryptochironomus*, *Macropelopia*, *Procladius* and *Zavreliomyia*, the water beetles *Agabus* and *Hydroporus* and the triclad *Crenobia alpina*. It is expected that the invertebrate community will respond to changes in climate by a shift in trophic structure (DOUGLAS et al., 1994). Higher temperature and longer periods without ice-cover will directly result in altered species composition and increased growth of algae and macrophytes (SMOL & CUMMING, 2000; KORHOLA et al., 2002; SCHINDLER & SMOL, 2006), used either as food source or as substrate by benthic invertebrates related to these. An example was observed in the Norwegian Lake Øvre Neådalsvatn where littoral vegetation supports a dense population of the mayfly *Siphonurus lacustris*. The upper lake, L. Falbekktjørna does not support this species. *S. lacustris* also showed a sharp decrease towards high altitudes in the Julian Alps. In alpine lakes, we also have examples from benthic cores where changes in fauna composition are explained by climate change (WALKER & MATHEWES, 1989; ILYASHUK & ILYASHUK, 2001; ROSENBERG et al., 2004). In the Italian L. Paione Superiore (Table 1) a strong increase in the density of *Tanytarsus* can be interpreted as a long-term climatic trend (GUILIZZONI et al., 1996). A similar example is found in an Austrian lake, where the ultraoligotrophic *Pseudodiamesa branicki* was displaced by the oligotrophic *Micropsectra radialis* (RADDUM et al., 2004).

Although the Norwegian lakes are subjected to low acid deposition loads (WATHNE et al., 1997; CAMERON et al., 2002), the very soft nature of the surface water and the low ionic concentrations in these lakes may act as critical limits for the most sensitive invertebrates. Critical limit exceedance may also limit potential colonisers in other lakes of the studied areas. An

example is a total absence of freshwater snails in the soft water lakes of the present study. This group is favoured by high alkalinity and calcium content (ØKLAND & ØKLAND, 1986; LIEN et al., 1996), as in the Slovenian and the Bulgarian lakes, where species of the genus *Lymnaea* were found. In contrast to this, the presence of acidophilic species (*Heretotrissocladius marcidus* and *Procladius* sp.) in L. Paione Superiore indicates that anthropogenic pollution occurred during the last decade (GUILIZZONI et al., 1996). However, a core from Nižné Terianske pleso showed a stable community over time, despite the presence of increasing amounts of carbonaceous particles towards the top of the sediments indicating inputs of airborne pollutants (SPORKA et al., 2002).

The importance of nitrogen in these high altitude areas may have implications for flora and fauna. Besides acting as acidifying agents, nitrogen compounds also acts as fertilizers increasing the primary productivity. The effect of plants with modest requirements being displaced by species with higher demands for nitrogen (HENRIKSEN & HESSEN, 1997) may be considerable. This may also be amplified by increased temperature (SOMMARUGA-WÖGRATH et al., 1997). In our study, acid sensitive species like *Lymnaea* spp., *Pisidium* spp. and *Siphonurus* spp. seem to be favored by increasing nitrogen and elevated conductivity levels. Over the long term, the trophic status of the localities may be changed, which again may have major consequences for the benthic invertebrate communities.

The strong influence of the altitude x latitude interaction indicated that the response of the faunal assemblage to the altitudinal gradient varied with latitude. This is expected when lakes are sampled across such broad geographic gradients – as the climate and environmental conditions at any given altitude will differ considerably between the southernmost and the northernmost localities.

Environmental stress exposure close to the tolerance limits will normally be displayed as abnormal behavior or as sublethal mortality. During recovery, the time lag between acceptable environmental conditions and critical species abundance may be substantially longer than in the extinction phase due to immigration processes, sublethal mortality and the “Allee effect” (ALLEE, 1931). Examples from limed lakes and rivers show that the process of restoring sensitive fauna varies depending on type of habitat and species considered (RADDUM & FJELLHEIM, 2003). Lotic fauna restores more rapidly than lentic fauna (FJELLHEIM & RADDUM, 1993). Presence of nearby source populations enhances colonisation rates (RADDUM et al., 1997). Winged aquatic insects colonise more rapidly than less mobile animals, like crustaceans, snails and leeches (RADDUM & FJELLHEIM, 2003).

On the local scale, the simplicity of the faunal assemblages above the tree line and the close geographical situation of lakes within the same region suggest that there should be low faunistic variance within regions. The benthic communities in alpine lakes are generally simpler and less diverse than those at lower altitudes. The tree line normally represents a major ecotonal break in diversity. A multiproxy study by HEEGAARD et al. (2006) showed that the taxonomic composition of three groups of aquatic organisms was the subject of a major change just below the tree line along an alpine gradient in the Swiss Alps. Due to the geographical situation of the localities of the present study it should be expected that the faunistic composition should be simple and dominated by a few taxa. Most of the species colonising these lakes are recruited from nearby lakes. It should therefore be expected that the variance within regions is low compared to that between regions. Climate-driven processes operate both on a large geographical scale (HURRELL, 1995) as well as on minor scales. Our data indicate that collinearity was more pronounced between regions than within. This implies

that the study of lakes within regions gives an important dimension to the study of climate-driven processes on a broader geographical scale.

Conclusions

1. The fauna of all lake districts was mainly composed of oligotrophic/ultraoligotrophic species, predominantly chironomids which made up more than 60 % of all individuals.
2. Species accumulation curves indicate that there were strong association and distribution patterns in chironomid larval communities both within and between regions as indicated by the differences in slope and shape. Ordination analyses showed that all groups of explanatory variables contributed to the patterns in faunal assemblages, but whereas lake water chemistry could account for an appreciable 35% of the variability, altitude (19%) and geography (11%) accounted for considerably less. Lake size or maximum depth did not significantly affect the littoral faunal assemblages.
3. The strongest patterns in species turnover were found between the geographical regions. More than 2/3 of the variation in faunal assemblages at this scale could be accounted for by the measured environmental variables. The strongest patterns were related to lake-water chemistry, notably conductivity and nitrogen, but broad-scale latitudinal patterns and altitude also contributed to the overall variability in faunal assemblages. There were no apparent latitudinal trends in chironomid species richness, suggesting that despite strong responses in terms of species composition, diversity as such is not affected by the latitudinal trend in climate.
4. At the within-region scale, the altitudinal gradient had a strong influence on the faunal assemblages, but lake-water chemistry also contributed to the among-lake variability. The effects of these two groups of variables were relatively independent of each other at this scale.
5. Since the trophic structure of the benthic community may be explained by both altitudinal and latitudinal factors, more detailed information on the ecology of alpine lake species may give important information on climate change issues.

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Appendix 1: continued

	CN	CN	PT	PT	RE	RE	RE	RI	RI	RI	TA	TA	TA	TA	TA	TA	TA	JA	JA	JA	JA	JA	JA				
Code	0016	0017	0026	0027	0028	0008	0010	0017	0008	0009	0010	0011	0007	0009	0010	0011	0017	0022	0001	0002	0003	0004	0005	0006	0007		
Stenophylax vibex (Curtis, 1834)																											
Hydracarina																											
Hydracarina	2	9	4	13	111			7	2	5	8		2	3	3			1				3	2	5			
Amphipoda																											
Niphargus sp.																						3	3	1	1		
Gastropoda																											
Lymnaea sp.								6		8												2	2	6	30	5	
Heteroptera																											
Heteroptera indet.								2		269												2	12				
Megaloptera																											
Sialis sp.										3	2																
Oligochaeta																											
Oligochaeta indet.	44	28	152	151	428	381	67	71	77	126	84	26	10	184	73	46	12	10	102	16	55	32	43				
Tricladida																											
Crenobia alpina (Dana, 1766)		1		47				19		34			2	20	55	61	73										
Bivalvia																											
Pisidium sp.								5	1	1	6											12	10	5	14	20	
Coleoptera																											
Agabus sp.	1			4	3					4	1											3	2	7	1	2	5
Coleoptera indet.				2				1	18	2																	
Hydroporus sp.				1	40																	7	4				