# Chironomid-based classification of lakes in western Finnish Lapland

# Marjut T. Nyman\* and Atte A. Korhola

Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland; \*present address: Finnish Environment Institute, Research Department, P.O. Box 140, FI-00251 Helsinki, Finland (e-mail: marjut.nyman@ymparisto.fi)

Nyman, M. T. & Korhola, A. A. 2005: Chironomid-based classification of lakes in western Finnish Lapland. *Boreal Env. Res.* 10: 239–254.

For the implementation of the Water Framework Directive we need to develop an informative and cost-effective set of biological monitoring and assessment methods, especially for remote areas. Chironomids are known to be an abundant and speciesrich group that dominate the aquatic macroinvertebrate assemblages in the north and therefore should be an integral part of monitoring and assessment plans. In this paper, we aim to characterise lake types in subarctic Finnish Lapland using particular chironomid indicator taxa. Contemporary chironomid assemblages and 24 corresponding physical and chemical limnological variables were determined for 63 lakes. Among them, fifty shallow lakes ( $\leq 10$  m) were classified into biological lake groups using Two-Way Indicator Species Analysis (TWINSPAN). The environmental variables best discriminating between the groups were determined using canonical variates analysis (CVA). Classical lake typology was additionally applied to 13 deeper lakes. Among the shallow lakes, three lake groups were separated on the basis of their chironomid assemblages: (i) small and shallow organic-rich lakes, (ii) large and base-rich lakes, and (iii) cold and clear oligotrophic tundra lakes. The deep lakes were all, except one, oligotrophic. The degree of oligotrophy was related to temperature. The results indicate that the classification of shallow lakes using chironomid communities is a useful tool for developing a lake typology and in assessing and monitoring the remote subarctic lakes.

# Introduction

The European countries are obligated to assess and monitor the ecological status of their freshwaters as established by the EU Water Framework Directive (WFD, Directive 2000/60/EC). The assessment of ecological status of lakes and rivers should mainly be based on biological analyses. However, the development of an integrated, informative and cost-effective set of biological monitoring and assessment methods is still in progress (e.g. Heinonen *et al.* 2004) and the classification system has to be improved further in the course of the monitoring process.

The subarctic Fennoscandian lakes are important elements of the landscape and mostly unaffected by direct human disturbance. In these lakes, nutrients often fail to exceed the detection limits and the waters are very oligotrophic (Sorvari *et al.* 2000, Korhola *et al.* 2002). Temperature and length of the ice-cover period are thought to have strong effects on the biota in these ecosystems (e.g. Fjellheim *et al.* 2000). Lakes in Finnish Lapland are often recognised as pristine due to their remoteness. However, previous studies have demonstrated that this may not be the case; climate warming is already changing these systems (Sorvari *et al.* 2002, Smol *et al.* 2005). The absence of regular monitoring programmes in remote areas necessitates the development of a lake typology for the purpose of monitoring of waters of high or good ecological quality, as laid down by the WFD.

An integral part in the assessment of ecological status of freshwaters is the benthic macroinvertebrate fauna. Benthic macroinvertebrates constitute a useful proxy that integrates e.g. climatic, hydrological and geological variables. Additionally, they provide perspective in space and time and help to elucidate changes in variables within a lake and long-term changes in nature. The larvae of non-biting midges (Diptera: Chironomidae) often dominate benthic faunal communities in arctic waters, where they mainly graze on algae and detritus (Oliver 1968, Danks 1981). Despite the small size of the larvae (2-30 mm), the high density of chironomids, combined with a relatively short generation time, makes them a very important component in the aquatic food webs (Williams and Feltmate 1992, Tokeshi 1995). In particular, chironomids should be included in monitoring and assessment plans, because they are known to be an abundant and species-rich group that dominates aquatic macroinvertebrate assemblages in the north.

As early as 1922 Thienemann used chironomid larvae as water quality indicators in deep stratified lakes. The early history of the development of trophic classification systems using chironomids has been summarised in Brinkhurst (1974). Profundal chironomid assemblages respond to oxygen concentration, food quality and food quantity in a direct manner enabling the development of semi-quantitative trophic classification schemes based on midge composition (Sæther 1979, Wiederholm 1980). However, these lake classification systems are restricted to relatively deep, stratified lakes and are based on a few indicator species. In Finland, the traditional chironomid-based lake typology system cannot be applied in most cases since the mean depth of the Finnish lakes is only about 7 m (Atlas of Finland 1986), whereas the depth of summer stratification usually lies at approximately 10 m depending on the limnological and morphometric characteristics of the individual lake (Kansanen et al. 1984, Sorvari et al. 2000, Korhola et al. 2002). In thermally stratified lakes the chironomids that live in the profundal are only indirectly related to epilimnetic conditions through food availability. The heterogeneity of littoral habitats and seasonal differences in the abundance and distribution of littoral species in a given lake are greater than those seen in profundal species, resulting in shallow lakes fitting the existing classification schemes based on profundal species less well than the deep lakes. In addition, the littoral communities respond to different environmental pressures than profundal fauna, like changes in catchment vegetation, land use, acidification and water level fluctuations. Due to these reasons, and the fact that shallow lakes are abundant, the need for a classification system for shallow lakes is obvious.

The patchiness of freshwater habitats makes sampling of living chironomids laborious and time-consuming since many different methods must be employed and a plethora of biotopes sampled. A more efficient means of sampling the fauna is to take a deep-water surface sediment sample. This contains biotic remains (subfossils) of many aquatic organisms, including chironomids, which accumulate in the lake sediments. The deep-water surface sediment samples, which can be easily and rapidly sampled with a gravity corer (e.g. Renberg 1991), include a representative sample of the whole chironomid community living in a lake (Hofmann 1988, Brodersen and Lindegaard 1999, Little et al. 2000). There have been few attempts to try to classify shallow lakes using subfossil chironomids (e.g. Brodersen and Lindegaard 1999, Brodersen and Anderson 2002), partly due to taxonomic difficulties. The method should be developed further as a complementary and easy source of valuable biological information on lake types and status.

The main objective of this study is to elaborate the biological typology of subarctic shallow lakes using chironomid communities and to determine the environmental factors that best describe the groups. Additionally, we apply a classical lake-type scheme for the deep lakes. Our results can serve as baseline data for monitoring activities of these remote lakes.

## Materials and methods

#### Sample collection and study area

This study is based on the re-analysis of 1 cm thick surface sediment samples taken with a Limnos-type gravity corer in July 1995 and 1998 from the deepest parts of 63 lakes in western Finnish Lapland (Olander et al. 1997, 1999). The chironomid remains were processed from the sediments under a stereoscope after KOH treatment, which deflocculates the organic material and makes it easier to pick out the chironomid larval head capsules to be mounted on microscope slides in Euparal. The head capsules were identified under a light microscope using 400× magnification. The identification followed Brundin (1948), Sæther (1975b, 1976), Oliver and Roussel (1983), Wiederholm (1983), Rieradevall and Brooks (2001) and protocols agreed to at several international meetings on the taxonomy of chironomid larval subfossils held since 1997. See Nyman et al. (2005) for further notes on taxonomy. After omitting unidentified chironomid head capsules and head capsules identified only to subfamily and tribal levels the total numbers for minimum, maximum and mean number of head capsules per sample were 61, 272 and 136, respectively.

The lakes along the 400 km long sampling transect are distributed across a major ecotonal gradient, from coniferous forest to barren tundra (Fig. 1). The bedrock consists of acidic and slowly weathering Precambrian plutonic and metamorphic rocks, except in the northernmost corner of the study area where slightly more readily weathering Paleozoic schists and gneiss predominate (Simonen 1980). Lakes are oligotrophic with total phosphorus concentrations under the detection limit (5  $\mu$ g l<sup>-1</sup>) in all lakes. The mean annual precipitation in the area ranges from 535 mm (south) to 414 mm (north), and the mean annual temperature ranges from +0.2 °C (south) to -2.6 °C (north) (Climatological Statistics in Finland 1991). The site-specific, altitude-corrected, mean July air temperature



**Fig. 1.** Study area in north-western Finnish Lapland along with the major land-cover features and isotherms for mean July air temperature (1961–1990).

ranges between +7.9 °C and +14.9 °C, yielding a relatively steep temperature gradient of 7 °C (all temperature data are based on the standard period of 1961–1990). The study area and the sites are described in more detail in Weckström and Korhola (2001) and Korhola *et al.* (2002).

#### **Environmental data**

For the 63 lakes, 24 physical, chemical and biological variables were determined representing regional variables (latitude, longitude and air temperature), catchment scale variables (vegetation-type, mire percentage and catchment roughness), and ecosystem scale variables. Water temperature (Wattemp) and lake depth (Depth) were measured in the field. The analyses of pH, conductivity (Cond), alkalinity (Alk), calcium (Ca), magnesium (Mg), sodium (Na), potassium (K) and total organic carbon (TOC) followed standard protocols used by the National Board of Waters

in Finland (Erkomaa et al. 1977). Latitude (Lat), longitude (Long), altitude (Alt), lake area (Area), lake perimeter (Perim), catchment area (Catch), catchment/lake ratio (Catch/Lake), catchment mire percentage (Mire), distance beyond treeline (DBT), vegetation type and catchment roughness (Rough) were determined from topographic maps (1:20 000). Vegetation type included three vegetation classes: coniferous forest (Conif), mountain birch woodland (Birch), and barren tundra vegetation (Barr). Catchment roughness, which is a function of contour lines per kilometre (for the exact calculation, see Korhola et al. 2002), was established to estimate the flushing rates of catchment waters. Shore development (Shore) was determined as the ratio of the length of the shoreline to the circumference of a circle of an area equal to that of a lake (Wetzel 2001: p. 34). This parameter can be used as a reflection of the amount of littoral biotopes in relation to the volume of the lake. For the determination of lake-specific mean July air temperature (Airtemp) and sediment loss-on-ignition (LOI), see Olander et al. (1999) and Bengtsson and Enell (1986), respectively. A more detailed description of the lake sampling protocol and water chemistry analyses is presented in Weckström and Korhola (2001) and Korhola et al. (2002). After the Kolmogorov-Smirnov test with Lilliefors' correction for normality using SPSS 10.0, the determinants having skewed distributions were log (x + 1) transformed, i.e. [Area], [Perim] and [Catch].

#### Data analysis

Rarefaction analysis using the program RARE-POLL (Birks and Line 1992) was performed to estimate taxon richness of the samples of varying size scaled down to same sample size. Rarefaction uses a random selection without replacement strategy, typically selecting a sample of the same size as the smallest count size of the entire population (the base count here was 61). The data for the taxon richness analysis consisted of 63 lakes and all 84 chironomid taxa. Untransformed species counts were used in the analysis.

Because our special interest was in the classification of shallow lakes on the basis of their chironomid communities, the multivariate data set of 63 lakes was split into two groups, one with 50 lakes of less than or equal to 10 m deep, and the other with 13 lakes with a depth range from 10.15 to 25 m (Table 1). Treating the shallow lakes separately enabled us to achieve

 
 Table 1. Summary of physical, chemical and biological characteristics for shallow lakes and deep lakes in northeastern Finnish Lapland.

	Shallow lakes ( $\leq$ 10 m) $n = 50$				Deep lakes (> 10 m) $n = 13$			
	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median
Latitude (°N)	67.8	69.3	68.6	68.7	66.9	69.3	68.8	69.1
Altitude (m)	197.5	1009.0	469.0	453.1	108.0	1024.4	648.2	588.2
Mire area (%)	0.0	64.2	11.6	1.5	0.0	11.0	1.9	0.0
Catch. area/Lake area ratio	3.1	156.4	23.8	9.8	4.9	134.6	28.6	12.3
Roughness index	0.0	22.7	8.0	7.8	4.6	30.6	13.3	10.7
Area (ha)	0.9	115.2	12.4	6.9	9.1	100.3	26.0	15.7
Airtemp. (°C)	7.9	13.8	11.4	11.3	7.9	14.9	10.3	10.4
LOI (%)	13	88	48	50	12	37	24	21
pH units	5.0	7.8	6.9	7.0	6.1	7.5	7.0	7.2
Alkalinity (mg l <sup>-1</sup> )	0.0	17.0	7.5	8.0	0.6	19.5	7.7	8.0
K (mg l <sup>-1</sup> )	0.1	0.9	0.4	0.4	0.1	0.8	0.3	0.3
Ca (mg $l^{-1}$ )	0.1	3.5	1.6	1.6	0.3	4.1	1.9	2.0
Na (mg $l^{-1}$ )	0.2	1.7	0.9	0.9	0.4	1.3	0.8	0.9
Mg (mg $l^{-1}$ )	0.1	1.3	0.4	0.4	0.1	1.9	0.5	0.4
TOC (mg $l^{-1}$ )	0.8	12.6	6.6	6.0	0.6	6.5	3.6	4.1
Rarefied taxon								
richness N (exp.)	9	31	18	17	11	25	19	19

more information about them, which would not have been the case were all the lakes treated together in the numerical analyses. The shallow lakes sampled were small (median area = 6.9 ha) and shallow (median  $Z_{max} = 4.3$  m) with simple bathymetries. The pH in the lakes varied between 5.0 and 7.8 and the lakes were characterised by low ionic strength (median conductivity = 23.8  $\mu$ S cm<sup>-1</sup>).

We used a semi-quantitative divisive classification technique, Two-Way Indicator Species Analysis, to classify the 50 shallow lakes less than 10 m deep. TWINSPAN classification is an informative and robust method especially for noisy data sets (Gauch and Whittaker 1981), as is usually the case with chironomid data with many taxa and many zero values. As pointed out by Kansanen et al. (1984), "the shallow water region constitutes a far less uniform environment" and "the fauna is more diverse and has many species with low abundances than the profundal zone". They suggested that only common taxa should be used in a chironomid-based classification (of shallow waters). Marchant (2002) stated, "only common taxa will produce sufficiently strong signals for the interpretation of environmental gradients" (but see also Cao et al. 2001). For the TWINSPAN the results of the chironomid analysis were introduced as percentages and all taxa with less than 2% abundance were removed in order to base the divisive classification upon more common taxa. Pseudospecies cut levels used were 2, 5, 7, 12 and 20. Otherwise, the program was asked to run a default analysis. Any pseudotaxon with frequency of occurrence three times more on one side of a division than the other is considered a good indicator. A pseudotaxon occurring twice as often on one side of a division as the other is called a preferential. We used the program TWINSPAN (Hill 1979, modified by Dr. Peter R. Minchin Feb. 1988-June 1997). The modified version uses the "strict" convergence criteria of Oksanen and Minchin (1997) for eigenanalysis. To decide how many groups to retain for further analysis, the program TWINDEND version 0.4 was used to calculate the within-group dispersion of all the TWINSPAN groups. The division was stopped when further division would have resulted in two groups in which one or both groups had a

mean dispersion of less than 50% of the total dispersion in the data. This approach resulted in three main lake groups that were used in further analysis (CVA). However, some subgroups are also discussed.

To see which linear combinations of environmental variables discriminate best between the TWINSPAN groups of shallow lakes, Canonical Variates Analysis (CVA) with Hill's scaling and focus on inter-species distances was performed using the program CANOCO v. 4.0. In CVA, the a priori lake groups are used as dummy response variables instead of the species data. To reduce size of the large original environmental data set, the obvious multi-collinear variables were identified one at time by studying the variances of their regression coefficients as indicated by the Variance Inflator Factors (VIF). Variables yielding higher VIFs than 20 were omitted (ter Braak and Smilauer 1998). To further reduce the large set of the (remaining) environmental variables (n = 17), a manual forward selection and associated Monte Carlo permutation tests (999 permutations) were performed. The significance levels (P < 0.05) of each forward-selected variable were Bonferroni-adjusted to correct multiple tests (Manly 1991). Rarefied taxon richness was included among the explanatory or 'predictor' variables in the CVA. This was reasonable, because in the rarefaction analysis the species data were introduced merely as counts (not abundances). The outcome of the rarefaction analysis is the expected number of species (or taxa) that has nothing to do with the percentages/abundances of the species and hence is independent of the assemblage structure.

If natural clusters exist in the data they should be obvious in the ordination (Legendre and Legendre 1998). To determine whether our TWINSPAN groups show well in ordination space we plotted the sites and environmental data in a CCA biplot. The sites (lakes) were classified according to their TWINSPAN grouping.

For the 13 lakes more than 10 m deep, the classical lake typology system using the key developed by Sæther (1979) was attempted. The quality and quantity of food as well as the availability of oxygen are generally considered to be the main factors defining the profundal chirono-

mid assemblages in deep stratifying lakes. The predominance of chironomids in the profundal zones of lakes and their response to trophic conditions make them useful in the classification of lakes. Sæther (1979) identified 15 different profundal chironomid communities typical of six oligotrophic ( $\alpha$ – $\zeta$ ), three mesotrophic ( $\eta$ – $\iota$ ) and six eutrophic ( $\kappa$ –o) lake types. These classes correlate well with trophic conditions expressed as mean concentrations of total phosphorous/mean lake depth or as total chlorophyll *a*/mean lake depth in many North American and European lakes (Sæther 1979, Wiederholm 1980).

## Results and discussion

In the study area, the altitude increases towards the north. As the 13 deep lakes are generally situated on steep terrains in the northernmost part of the research area, they are cooler and their catchments do not contain extensive mire areas. Lake waters of these deep lakes are consequently highly transparent with low TOC values (Table 1). In general, the water chemistry (e.g. base cations, pH) does not differ markedly between the two groups of relatively deep and shallow lakes, although some low-lying shallow basins surrounded by mires have polyhumic waters (TOC > 10 mg l<sup>-1</sup>) with pH below 6.

A total of 9598 chironomid head capsules were identified from the surface-sediment samples of the 63 lakes in NW Finnish Lapland. We found in all 84 taxa, four of which occurred only in some of the deeper lakes. These were Lasiodiamesa, Diplocladius, Orthocladius (E.) saxosus and Rheocricotopus. On the other hand, Georthocladius, Nanocladius balticus group, Smittia, Lauterborniella, Parachironomus vitiosus group and Stempellina, all with only one occurrence, were restricted to shallow lakes number 9, 13 or 29 within the mountain birch woodland. None of the taxa occurred in all lakes. Sergentia, Procladius, Psectrocladius (s. str.) and Tanytarsus lugens group were the most widespread taxa in the study lakes. Rarefied taxon richness values for the chironomid assemblages in the shallow lake data set ranged from 9 to 31, the mean value being 18, and from 11 to 25 (mean = 19) for the deeper sites.

## TWINSPAN classification of shallow lakes

#### Indicator taxa

The first level of the TWINSPAN division of the 50 shallow lakes resulted in two lake groups consisting of 42 and 8 lakes, the larger group being highly diverse, while the smaller group (Group3, Fig. 2) having clear dominance of Micropsectra. The other taxa preferring Group3 were Heterotrissocladius brundini, Heterotrissocladius grimshawi, Mesocricotopus, Parakiefferiella cf. fennica, Corynocera cf. oliveri, Micropsectra radialis type, Sergentia and Procladius (Fig. 3). Of the above mentioned species, H. brundini and H. grimshawi were found in high abundances in the 13 deeper lakes in the present survey. Mesocricotopus, P. cf. fennica and C. cf. oliveri were found in much smaller proportions in the 13 deep lakes than in Group3. In this dataset, high abundances of M. radialis type were observed in both shallow and deep lakes only if the derived lake-specific mean July air temperature was around 8 °C and the measured water temperature in July was around 10 °C. Raddum and Sæther (1981) and Brodin and Gransberg (1993) reported Sergentia in acid lakes. It is a common taxon in shallow tundra lakes in Canada (Walker and MacDonald 1995) and in lakes in northern Fennoscandia (Larocque et al. 2001). Sergentia (coracina) is a typical member of the T. lugens community in stratified lakes with good oxygen conditions (Brundin 1956). In this data set neither of these taxa showed any clear relationship with the lake depth.

Further division of the 42 lakes resulted in two groups: one of 30 (Group1) and one of 12 lakes (Group2, Fig. 2). The indicator species for Group1 are *Monopsectrocladius*, genus near *Oliveridia* sp. (sensu Sæther 1980), *Psectrocladius s. str.* and *Dicrotendipes* (Fig. 3). Genus near *Oliveridia* sp. was found from depth 0.5–5 m in lake Rødlivann, Hordaland, Western Norway, a  $\gamma$ -oligotrophic lake (Sæther 1980). In our study, the taxon believed to belong to the same *Oliveridia* sp. as described in Sæther (1980), was mostly found in shallow (< 5 m deep) mesohumous lakes (calculated weighted average optima for TOC = 7.02 mg l<sup>-1</sup>) with moderately warm



**Fig. 2**. Dendrogram representing the classification of 50 shallow lakes using TWINSPAN (Two-Way Indicator Species Analysis). The indicator species relative abundance levels are expressed on an ordinal scale (1 = 2%–4.9%; 2 = 5%–6.9%; 3 = 7%–11.9%; 4 = 12%–19.9%,  $5 \ge 20\%$ ). Mn, number of misclassified negatives; mp, number of misclassified positives. For every group, mean dispersion as a percentage of total dispersion (Dt) is shown.

temperatures. The same distinct taxon is probably reported as *Oliverdia* in many lakes in subarctic Sweden (Larocque *et al.* 2001).

Langton (1980) found most species of Psectrocladius (s. str.) to be widely distributed in small, shallow bodies of stagnant water and in reservoirs and lakes. According to present results, Psectrocladius (s. str.) was also widespread in northwestern Fennoscandia (Fig. 3). In this study Monopsectrocladius seemed to be most abundant in the smallest pools and lakes with high organic content of the sediment and low pH (Figs. 3 and 4). This is in good accordance with Walker et al. (1985) and Mousavi (2002), who found these taxa from small shallow lakes with low pH. The taxa showing preference for Group1 included Allopsectrocladius/ Mesopsectrocladius, Paratanytarsus penicillatus type and *Microtendipes pedellus* group (Fig. 3).

The indicator taxa for Group2 consisting of 12 lakes were *Zalutschia zalutschicola* and *T. lugens* group (Fig. 2). *Z. zalutschicola* is a wellknown indicator species of polyhumic and shallow ponds, pools and lakes (Sæther 1976, 1979, Walker *et al.* 1985). *T. lugens* group, on the other hand, consists of at least four species in addition to *T. lugens* Kieffer (Pinder and Reiss 1986), and is generally indicative of cold conditions. Preferential taxa for Group2 are *Cricotopus*, *Tanytarsus chinyensis* group, *Cladotanytarsus mancus* group, *Heterotanytarsus* and *Zalutschia* cf. *tatrica* group. *Cricotopus* is commonly found to be associated with macrophytes (e.g. Brodersen *et al.* 2001). *Heterotanytarsus apicalis* is described as a northern oligotrophic species and an indicator of poly- and mesohumic waters (Sæther 1975a, 1979), which accords well with our results (Fig. 3).

Further division of the 30 lakes in Group1 resulted in three subgroups, Group1a, Group1b and Group1c (Figs. 2 and 3). Group1a comprises nine lakes, which can be referred to as *Psectrocladius* lakes. In addition to *Psectrocladius*, Group1b (n = 16) is characterised by *M. pedellus* group and *Tanytarsus pallidicornis* group. Group1c, comprising five lakes, accommodates the highest abundances (20%–63%) of *Paratanytarsus* species (Fig. 3). These lakes are among the most transparent lakes in this study (TOC = 2.2–4.9 mg l<sup>-1</sup>). *Paratanytarsus* seems



ർ







Fig. 4. Summary box-plot diagram of the distribution of some key environmental variables in the three main TWINSPAN groups. The box length is the interquartile range. Empty circles denote outliers (cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box). Stars denote extremes (cases with values more than 3 box lengths from the upper or lower edge of the box).

to prefer lakes situated above the treeline (correlation coefficient between taxon abundance and distance from the treeline = 0.364, P < 0.01). It is known from literature to thrive in oligotrophic ponds, pools and lakes (Reiss and Säwedal 1981, Klink 1983).

Many taxa indicative of warmth (e.g. *Ablabesmyia*, *T. pallidicornis* group, *Monopsectrocladius* and *C. mancus* group) were common in Group1 and Group2 but did not occur in Group3 (Fig. 3). *Corynocera ambigua* was abun-

dant in many lakes in Group1 and Group2 but had low occurrences in Group3. It also occurred in low abundances in five of the lakes with depths greater than 10 m.

The CCA analysis with sites and the TWIN-SPAN codes (Fig. 5) showed that the chironomid communities in north western Finnish Lapland change gradually without clear aggregates of ecological species assemblages. This was also true for the environmental variables, which, at this spatial scale, form gradually changing gra-



Fig. 5. Canonical correspondence analysis (CCA) biplot of 50 shallow lakes with their affiliation to TWIN-SPAN lake-groups, and 17 environmental variables after screening.

dients of variables. Inevitably, this may lead to some artificial boundaries between the lake groups. However, lakes in Group1 are located on the left hand side of the ordination diagram associated with increasing LOI values, whereas lakes in Group2 are found in the lower section of the diagram showing affinity towards higher base cation concentrations and larger lake areas. Group3 lakes are located in the right hand side of the diagram where LOI and temperature decrease and lake depth increases.

#### Lake typification

CVA revealed that the statistically significant environmental variables best discriminating the three major TWINSPAN lake groups are LOI, taxon richness, and Mg (Fig. 6). Due to the fact that the pH gradient was very short in our study, pH stood out only as a very weakly significant variable discriminating the lake groups. Many other environmental variables showed some association with the established lake groups, e.g. LOI and Airtemp decreased and depth increased from Groups 1 to 3, while taxon richness and Mg both had the highest values in Group2 (Figs. 4 and 6).



Fig. 6. CVA biplot of three main TWINSPAN groups and forward selected environmental variables best discriminating Group1, Group2 and Group3. The lengths of arrows for environmental variables are 5x exaggerations.

Group1 consisted of small, shallow lakes with high LOI and intermediate alkalinity, temperature and taxon richness. The catchment roughness value was higher in Group1 than in Group2 indicating that the former lakes were situated on steeper terrain. Lakes in Group1 had lower TOC values than those in Group2 (Fig. 4).

Group2 consisted of large, warm lakes with large, flat catchments, high lakewater Mg and taxon richness and intermediate LOI values (Fig. 4). Group2 had relatively high mire percentage (mean = 17%). Organic carbon in oligotrophic lakes mostly originates from the terrestrial and wetland sources and littoral plant-zones (Wetzel 2001). It is quite evident that mires are responsible for the high organic carbon content of the adjacent lakes. The effect of catchment size (mean = 542 ha) was reflected in the high magnesium values of lakes in Group2; magnesium and calcium are weathering products derived from catchments.

Group3 consisted of lakes situated mostly on high altitude barren tundra, having cold, clear waters of low alkalinity values, with low LOI and taxon richness. The taxa preferring these lakes were typical cold stenotherms of oligotrophic lakes.

Lakes in Group1a had most organic sediments, low water alkalinity and low pH. They were the warmest lakes in Group1 but contained virtually no mires in their catchments. Group1b had lower LOI, higher TOC and alkalinity values than Group1a and the mire percentage was relatively high. *Paratanytarsus* lakes (Group1c) were clear water lakes with similar characteristics as those in Group3 except that they were shallower and had higher LOI and that the indicator taxa of Group3 were present in low abundance only. Group1c lakes had narrow ranges of LOI (mean = 41%), pH (median = 7.2) and TOC (mean = 3.8 mg l<sup>-1</sup>) and contained no mires in their catchments (Fig. 4).

Geographically, lakes in Group1 were distributed across a south-north transect spanning conifer, mountain birch woodland, and barren tundra. Group1c and Group3 were high altitude lakes mainly located on barren tundra. Lakes belonging to Group2 were not present in the barren tundra zone at all. Lakes in Groups 1a, 1b and Group2 were situated approximately at similar altitudes.

#### Typification of deep lakes

The lakes of a depth more than 10 m were mainly situated in the mountain birch woodland or in the barren tundra. However, lake 1 was exceptional among the deep sites in that it was the warmest of all of the study lakes located in the conifer forest zone. When interpreting the deep lake classification, one should bear in mind that our samples contained specimens derived also from littoral and sublittoral areas, but only profundal species listed in Sæther's key were used. In addition, many of the taxa used in Sæther's (1979) classification are found both in the profundal and littoral/sublittoral areas (e.g. T. lugens, M. radialis (as Lauterbornia coracina) and Sergentia coracina (as Phaenopsectra coracina)). These species may have slightly different trophic ranges in different habitats but in our study the classification was done by directly applying the Sæther's key. For example, if Pseudodiamesa was recorded from a lake, this particular lake was keyed out as  $\alpha$ -oligotrophic without considering the assemblage any further. Six out of the 13 deeper lakes in our data set were classified as being between  $\gamma$ - and  $\zeta$ -oligotrophic. The difficulty of distinguishing between lakes of the

type  $\gamma$  to  $\zeta$  is mainly due to the impossibility of separating subfossil specimens of Micropsectra groenlandica and Micropsectra notescens group, which separate  $\gamma$ -,  $\delta$ - and  $\alpha$ -oligotrophic lakes from the  $\zeta$ -oligotrophic lakes. Three lakes were  $\alpha$ -oligotrophic and three were  $\beta$ -oligotrophic (Fig. 7). Lake 1 was dominated by Sergentia and T. lugens group and keyed out to belong to the  $\lambda$ -eutrophic lake type. According to Paasivirta (2000), Sergentia is an indicator of moderately eutrophic conditions (in the true profundal zone), whereas the presence of T. lugens indicates only oligotrophic conditions. Both are cold-stenothermic taxa. The mesohumic conditions may cause oxygen deficiency if the hypolimnetic volume is small, as may be the case here. Even in oligotrophic lakes with a low hypolimnetic volume the profundal fauna may fail to reflect the actual epilimnetic water quality (see also Little et al. 2000). Especially if the lake is mesohumic/ polyhumic, the profundal fauna may indicate eutrophic conditions as the oxygen conditions weaken in the bottom (Heinonen et al. 2004).

## General discussion

According to the best of our knowledge, this is the first attempt to characterise lake groups among subarctic shallow lakes using chironomid communities. TWINSPAN analysis of chironomid assemblages successfully identified three major types of lake. The first level of division separated a group of cold lakes located on the barren tundra with low LOI and taxon richness from the larger group of warmer forest lakes with higher total organic carbon and LOI. The warm lakes were further divided into large, base-rich lakes with high taxon richness and the small organic-rich lakes. These main lake classes could be considered as characteristic lake types (among small lakes) when planning assessment and monitoring activities of waters in NW Finnish Lapland for the implementation of WFD. Chironomid communities typify lake groups, which are characterised by the environmental variables that reflect directly or indirectly the variables that will probably be the base of the Finnish lake typology in the statute that will be given by the Council of State.





When comparisons of contemporary macrozoobenthos are being made between lakes, it is recommended that such comparisons should be made between corresponding depth zones (Kansanen et al. 1984) or between similar mesohabitats (White and Irvine 1993, Tolonen et al. 2001). Sediment samples were used here as they are known to integrate remains of larvae from various habitats and depth zones (Anderson and Battarbee 1994). The need for taking several parallel samples from different habitats and seasons to find a representative collection of chironomids is overcome by analysing the top centimetre of sediment from the middle of the lake. The chitinous head capsules of the larval stage of chironomids are generally well preserved in lake sediments and can usually be identified to genus and in some cases to species. A study of shallow Danish lakes demonstrated that samples of living larvae showed a high degree of variation within the lake while surface sediment samples of subfossil chironomid remains seemed to be a persistent and reliable tool in the classification of shallow lakes (Brodersen and Lindegaard 1997). Since, in arctic lakes, the sedimentation rate may be very slow (e.g., 0.17 mm year-1 in lakes situated in NW Finnish Lapland; Sorvari et al. 2002), the uppermost centimetre of sediment integrates the last few years' chironomid production from the littoral and profundal zones. Since the reporting period for the WFD is six years, one sample within this period is sufficient to get an integrated picture of the possible changes in chironomid communities, which may be caused, for example, by changes in the lake catchments or by the climate change. Chironomids are also well suited for inferring reference conditions for a lake using paleolimnological techniques (e.g. Meriläinen et al. 2000, Ruse 2002).

Among the measured environmental variables, Mg, a surrogate of lake alkalinity and base cation status, and taxon richness were found to be important factors in discriminating between the lake groups. Lakes with higher base cation content and, consequently, higher alkalinity, are known to have higher diversity than base-poor, acid lakes (e.g. Friday 1987, Otto and Svensson 1983). In some previous studies, alkalinity and related factors, such as the base cation status, were similarly found to be important discriminators of chironomid communities, yet in these studies the ranges of alkalinity and base cation concentration were larger than in our study (Pinder and Morley 1995, Ruse 2002). However, our results demonstrate that these factors may be important in shorter ranges, too. The lakes of Group2 are large and have higher Mg and taxon richness than other groups. The link between alkalinity and chironomids may be explained by the macrophyte occurrence. Vestergaard and Sand-Jensen (2000) showed that alkalinity and macrophyte richness were in close positive correlation. There is also a known relationship between the macrophyte occurrence and littoral chironomid communities (Hershey 1985, Brodersen et al. 2001). At least Equisetum, Phragmites, Carex and Nitella types of lakes can be found in the area studied (Rintanen 1982). According to island biogeographical theory (Mac Arthur and Wilson 1963), large lakes have higher diversity. The effects of area and alkalinity are linked in lake ecosystems, since large lakes, in addition to having more available habitats, tend to receive more solutes.

Independent of the taxon richness and Mg, LOI was also an important environmental variable in accounting for differences between the lake groups along the first CVA axis (Fig. 6). LOI measures the organic content of the sediment and thereby reflects the available food for chironomids on and in the sediments. On the other hand, low LOI can indicate erosional input of minerogenic matter from the catchment and confound the picture of the relationship between production and LOI. However, LOI is an important correlate of conditions affecting benthic biota and, in combination with data on algal production and aquatic macrophytes, it could provide additional valuable information on lake types and influences on chironomid ecology.

The criterion of a good indicator species was difficult to meet in some cases because the study lakes form an environmental continuum rather than discrete groups. According to Legendre and Legendre 1998 "good indicator species should be mostly found in one group only and be present at most of the sites belonging to that group". Although many indicator taxa occur in more than one lake group they are present in most of the sites of their own group in greater quantities than in other groups. Some ambiguous divisions, especially at the subgroup level, may be the consequence of the classification method. TWIN-SPAN uses ordination for an overall view of the data and the cut points along CA axis 1 may not be at the right place so that sites that have a similar species composition may be separated (*see* Belbin and McDonald 1993). The taxonomic

Belbin and McDonald 1993). The taxonomic resolution may not be high enough in some taxa to effectively separate the groups. A few very common taxa, like *Procladius, Tanytarsus*, and *Psectrocladius*, may contain several species that have different environmental requirements and that may serve as useful indicator species. Their identification with higher taxonomic resolution would provide more useful lake groups (*see* also Kansanen *et al.* 1984).

The great habitat variability in littoral areas is reduced in the relatively stable profundal areas resulting in limited species numbers. Many profundal taxa are relatively easy to identify in comparison to littoral taxa. The classification of deep lakes using the lake typology system follows quite closely the temperature rank of the lakes with the coldest lakes being ultraoligotrophic (Fig. 7). Thus, the trophic situation of lakes at the oligotrophic end of the trophic system seems to be partly related to temperature. The fauna, taxon richness and environmental characteristics of these lakes resemble those of Group3 in shallow lakes. Only a few taxa (Lasiodiamesa, Diplocladius, Euorthocladius saxosus and Rheocricotopus), each with one occurrence, were restricted to deep lakes. However, these are rheophilic taxa and their presence may be the result of cold stream water discharge from snow packs into the particular lake in which these taxa occur.

Our results indicate that the methods using chironomid communities in shallow lakes is a useful tool for developing a lake typology. Chironomid analysis could provide baseline data for assessing and monitoring the ecological state of remote subarctic lakes in the future.

Acknowledgements: We thank Jan Weckström and Petri Shemeikka for collection of the initial field data. We are grateful to Steve Brooks for the valuable comments on the manuscript and correction of the language. Constructive criticism provided by Jarmo Meriläinen, Heidi Vuoristo and an anomymous reviewer is appreciated. Financial support of the Academy of Finland (contract: 50557) is greatly appreciated.

#### Nyman & Korhola • BOREAL ENV. RES. Vol. 10

## References

- Anderson N.J. & Battarbee R.W. 1994. Aquatic community persistence and variability: a palaeolimnological perspective. In: Giller A.G., Hildrew A.G. & Raffaeli D.G. (eds.), *Aquatic ecology: scale, pattern and process*, Blackwell Scientific Publications, Oxford, UK, pp. 233–259.
- *Atlas of Finland* 1986. Waters, Appendix 132. Helsinki: National Board of Survey and Geographical Society of Finland.
- Belbin L. & McDonald C. 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science* 4: 341–348.
- Bengtsson L. & Enell M. 1986. Chemical analyses. In: Berglund B.E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology*, John Wiley, Chichester, pp. 423–452.
- Birks H.J.B. & Line J.M. 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene* 2: 1–10.
- Brinkhurst R.O. 1974. The benthos of lakes, 1st ed., Blackburn Press, Caldwell, New Jersey, USA.
- Brodersen K.P. & Anderson N.J. 2002. Distribution of chironomids (Diptera) in low arctic West Greenland lakes: trophic conditions, temperature and environmental reconstruction. *Freshwater biology* 47: 1137–1157.
- Brodersen K.P. & Lindegaard C. 1997. Significance of subfossile chironomid remains in classification of shallow lakes. *Hydrobiologia* 342/343: 125–132.
- Brodersen K.P. & Lindegaard C. 1999. Classification, assessment and trophic reconstruction of Danish lakes using chironomids. *Freshwater Biology* 42: 143–157.
- Brodersen K.P., Odgaard B.V., Vestergaard O. & Anderson N.J. 2001. Chironomid stratigraphy in the shallow and eutrophic Lake Sobygaard, Denmark: chironomid-macrophyte co-occurrence. *Freshwater Biology* 46: 253– 267.
- Brodin Y.-W. & Gransberg M. 1993. Responses of insects, especially Chironomidae (Diptera), and mites to 130 years of acidification in a Scottish lake. *Hydrobiologia* 250: 201–212.
- Brundin L. 1948. Über die Metamorphose der Sectio Tanytarsariae connectens (Dipt. Chironomidae). Arkiv für Zoologi 41 A: 1–22.
- Brundin L. 1956. Die bodenfaunistischen Seetypen und ihre Anwendbarkeit auf die Südhalbkugel. Zugleich eine Theorie der produktionsbiologischen Bedeutung der glazialen Erosion. Report of the Institute of Freshwater Research, Drottningholm 37: 186–235.
- Cao Y., Larsen D.P. & Thorne R.St.-J. 2001. Rare species in multivariate analysis for bioassessment: some considerations. J. N. Am. Benthol. Soc. 20: 144–153.
- Climatological Statistics in Finland 1991. Supplement to the Meteorological yearbook of Finland, 90, Part I – 1990. Finnish Meteorological Institute.
- Danks H.V. 1981. Arctic arthropods. A review of systematics and ecology with particular reference to the North American fauna, Entomological Society of Canada, Ottawa, Canada.

- Erkomaa K., Mäkinen J. & Sandman O. 1977. Vesiviranomaisen ja julkisen valvonnan alaisten vesitutkimuslaitosten fysikaaliset ja kemialliset analyysimenetelmät. *Vesihallitus, Tiedotus* 121.
- Fjellheim A., Boggero A., Halvorsen G.A., Nocentini A.M., Rieradevall M., Raddum G. & Schnell Ø.A. 2000. Distribution of benthic invertebrates in relation to environmental factors. A study of European remote alpine lake ecosystems. *Verh. Internat. Verein. Limnol.* 27: 484–488.
- Friday L.E. 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. *Freshwater Biology* 18: 87–104.
- Gauch H.G. & Whittaker R.H. 1981. Hierarchical classification of community data. J. Ecol. 69: 537–557.
- Heinonen P., Pietiläinen O.-P., Airaksinen O., Haapala A., Hammar T., Holopainen A.-L., Hämäläinen H., Issakainen J., Kanninen A., Karttunen K., Leka J., Lepistö L., Luotonen H., Manninen P., Mononen P., Mäkinen H., Niinioja R., Pilke A., Rissanen J., Sandman O., Servomaa K., Sojakka P., Tolonen K.T., Ustinov A., Vallinkoski V.-M., Valta-Hulkkonen K. & Vuoristo H. 2004. Monitoring and assessment of the ecological status of lakes — a pilot procedure developed and tested in the Life Vuoksi project. *The Finnish Environment* 719. Finnish Environment Institute. Edita, Helsinki.
- Hershey A.E. 1985. Littoral chironomid communities in an arctic Alaskan lake. *Holarctic Ecol.* 8: 39–48.
- Hill M.O. 1979. TWINSPAN a FORTRAN Program for Arranging multivariate data in an ordered two-way table by classification of the individuals and attributes, Ecology and Systematics, Cornell University, Ithaca, New York 14850, USA.
- Hofmann W. 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Paleo*geogr. Paleoclimat. Paleoecol. 62: 501–509.
- Kansanen P.H., Aho J. & Paasivirta L. 1984. Testing the benthic lake type concept based on chironomid associations in some Finnish lakes using multivariate statistical methods. *Ann. Zool. Fennici* 21: 55–76.
- Klink A.G. 1983. Key to the Dutch larvae of Paratanytarsus Thienemann & Bause with note on the ecology and the phylogenetic relations, Medeklinker, 3, Orgaan van Hydrobiologisch Adviesburo.
- Korhola A., Weckström J. & Blom T. 2002. Relationships between lake and land-cover features along latitudinal vegetation ecotones in arctic Fennoscandia. Arch. Hydrobiol. Suppl. 139: 203–235.
- Langton P.H. 1980. The genus *Psectrocladius* Kieffer (Diptera: Chironomidae) in Britain. *Entomologist's Gazette* 31: 75–88.
- Larocque I., Hall R.I. & Grahn E. 2001. Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). J. Paleolimnol. 26: 307–322.
- Legendre P. & Legendre L. 1998. Numerical ecology, 2nd English ed., Elsevier Science BV, Amsterdam, Netherlands.
- Little J.A., Hall R.I., Quinlan R. & Smol J.P. 2000. Past trophic status and hypolimnetic anoxia during eutrophi-

cation and remediation of Gravenhurst Bay, Ontario: comparison of diatoms, chironomids and historical records. *Can. J. Fish Aquat. Sci.* 57: 333–341.

- Mac Arthur R.H. & Wilson E.O. 1963. The theory of Island Biogeography, Princeton University Press, Princeton, UK.
- Manly B.F.J. 1991. Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed., Chapman & Hall/ CRC, London, UK.
- Marchant R. 2002. Do rare species have any place in multivariate analysis for bioassessment? J. N. Am. Benthol. Soc. 21: 311–313.
- Meriläinen J.J, Hynynen J., Teppo A., Palomäki A., Granberg K. & Reinikainen P. 2000. Importance of diffuse nutrient loading and lake level changes to the eutrophication of an originally oligotrophic boreal lake: a palaeolimnological diatom and chironomid analysis. J. Paleolimnol. 24: 251–270.
- Mousavi S.K. 2002. Boreal chironomid communities and their relations to environmental factors — the impact of lake depth, size, and acidity. *Boreal Env. Res.* 7: 63–75.
- Nyman M., Korhola A. & Brooks S.J. 2005. The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. *Global Ecol. Biogeogr.* 14: 137–153.
- Oksanen J. & Minchin P.R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. J. Veg. Sci. 8: 447–454.
- Olander H., Korhola A. & Blom T. 1997. Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in subarctic Fennoscandia: developing a tool for palaeotemperature reconstructions. J. Paleolimnol. 18: 45–59.
- Olander H., Birks H.J.B., Korhola A. & Blom T. 1999. An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene* 9: 279–294.
- Oliver D.R. 1968. Adaptations of Arctic Chironomidae. Ann. Zool. Fennici 5: 111–118.
- Oliver D.R. & Roussel M.E. 1983. The insects and arachnids of Canada, Part II: The genera of larval midges of Canada, Diptera: Chironomidae, Agriculture Canada Publ. 1745, Ottawa.
- Otto C. & Svensson B.S. 1983. Properties of acid brown water streams in South Sweden. Arch Hydrobiol. 99: 15–36.
- Paasivirta L. 2000. Propsilocerus species in Finland, with a chironomid index for lake sediments. In: Hoffrichter O. (ed.), Late 20th century research on Chironomidae: an anthology from the 13th International Symposium on Chironomidae, Shaker Verlag, Aachen, pp. 599–603.
- Pinder L.C.V. & Morley D.J. 1995. Chironomidae as indicators of water quality — with a comparison of the chironomid faunas of a series of contrasting Cumbrian tarns In: Harrington R. & Stork N.E. (eds.), *Insects in a changing environment*, Academic press, London, UK, pp. 272–293.
- Pinder L.C.V. & Reiss F. 1986. The pupae of Chironominae (Diptera: Chironomidae) of the Holarctic region — keys and diagnoses. *Ent. Scand. Suppl.* 28: 299–456.

- Raddum G.G. & Sæther O.A. 1981. Chironomid communities in Norwegian lakes with different degrees of acidification. Verh. Internat. Verein. Limnol. 21: 399–405.
- Reiss F. & Säwedal L. 1981. Keys to males and pupae of the Palaearctic (excl. Japan) *Paratanytarsus* Thienemann & Bause, 1913, n. comb., with descriptions of three new species (Diptera: Chironomidae). *Ent. Scand. Suppl.* 15: 73–104.
- Renberg I. 1991. The HON-Kajak sediment corer. J. Paleolimnol. 6: 167–170.
- Rieradevall M. & Brooks S.J. 2001. An identification guide to subfossil Tanypodinae larvae (Insecta: Diptera: Chironomidae) based on cephalic setation. J. Paleolimnol. 25: 81–99.
- Rintanen T. 1982. Botanical lake types in Finnish Lapland. Ann. Bot. Fennici 19: 247–274.
- Ruse L. 2002. Chironomid pupal exuviae as indicators of lake status. Arch. Hydrobiol. 153: 367–390.
- Sæther O.A. 1975a. Two new species of *Heterotanytarsus* Spärck, with keys to nearctic and palaearctic males and pupae of the genus (Diptera: Chironomidae). J. Fish. Res. Board Can. 32: 259–270.
- Sæther, O.A. 1975b. Nearctic and Palaearctic Heterotrissocladius (Diptera: Chironomidae). Bull. Fish. Res. Board Can. 193: 1–67.
- Sæther O.A. 1976. Revision of Hydrobaenus, Trissocladius, Zalutschia, Paratrissocladius, and some related genera (Diptera: Chironomidae). Bull. Fish. Res. Board Can. 195: 1–287.
- Sæther O.A. 1979. Chironomids communities as water quality indicators. *Holarctic Ecol.* 2: 65–74.
- Sæther O.A. 1980. New name for Oliveria Saether, 1976 (Diptera: Chironomidae) nec Oliveria Sutherland, 1965 (\*Cnidaria: Anthozoa), with a first record for the European continent. *Ent. Scand.* 11: 399–400.
- Simonen A. 1980. The Finnish Prekambrian. In: Alalammi P. (ed.), Atlas of Finland; Geology, Folio 123–126, National Board of Survey and Geographical Society of Finland, Helsinki, pp. 1–4.
- Smol J.P., Wolfe A.P., Birks H.J.B., Douglas M.S.V., Jones V.J., Korhola A., Pieniz R., Rühland K., Sorvari S., Antoniades D., Brooks S.J., Fallu M.-A., Hughes M., Keatley B.E., Laing T.E., Michelutti N., Nazarova L., Nyman M., Paterson A.M., Parren B., Quinlan R., Rautio M., Saulnier-Talbot E., Siitonen S., Solovieva N. & Weckström J. 2005. Climate-Driven Regime Shifts in Arctic Lake Ecosystems. *Proc. Nat. Acad. Sci.* 102: 4397–4402.
- Sorvari S., Korhola A. & Thompson R. 2002. Lake diatom response to recent Arctic warming in Finnish Lapland.

Glob. Change Biol. 8: 171–181.

- Sorvari S., Rautio M. & Korhola A. 2000. Seasonal dynamics of the subarctic Lake Saanajärvi in Finnish Lapland. *Verh. Internat. Verein. Limnol.* 27: 507–512.
- ter Braak C.J.F. & Smilauer P. 1998. CANOCO reference manual and user's quide to Canoco for Windows: software for canonical community ordination (Version 4). Microcomputer Power, Ithaca, NY, USA.
- Thienemann A. 1922. Die beiden Chironomus-arten der Thiefenfauna der norddeutschen Seen. Ein Hydrobiologisches Problem. Arch. Hydrobiol. 13: 609–646.
- Tokeshi M. 1995. Species interactions and community structure. In: Armitage P.D., Cranston P.S. & Pinder L.C.V (eds.), *The Chironomidae: Biology and ecology of nonbiting midges*, Chapman & Hall, London, UK, pp. 297–335.
- Tolonen K.T., Hämäläinen H., Holopainen I.J. & Karjalainen J. 2001. Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. Arch. Hydrobiol. 152: 39–67.
- Vestergaard O. & Sand-Jensen K. 2002. Aquatic macrophyte richness in Danish lakes in relation to alkalinity, transparency, and lake area. *Can. J. Fish. Aquat. Sci.* 57: 2022–2031.
- Walker I.R. & MacDonald G.M. 1995. Distributions of Chironomidae (Insect: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arctic Alpine Res.* 27: 258–263.
- Walker I.R., Fernando C.H. & Paterson C.G. 1985. Associations of Chironomidae (Diptera) of shallow, acid, humic lakes and bog pools in Atlantic Canada, and a comparison with an earlier paleoecological investigation. *Hydrobiologia* 120: 11–22.
- Weckström J. & Korhola A. 2001. Patterns in the distribution, composition and diversity of diatom assemblages in relation to ecoclimatic factors in Arctic Lapland. J. *Biogeogr.* 28: 31–45.
- Wetzel R.G. 2001. Limnology, 3rd ed., Academic Press, London, UK.
- White J. & Irvine K. 2003. Littoral meso-habitats in lakes: differences in their macroinvertebrate assemblages and their potential inclusion in assessing ecological quality. *Aquat. Conserv.* 13: 331–351.
- Wiederholm R. (ed.) 1983. Chironomidae of the Holarctic Region, Keys and Diagnosis. Part 1: Larvae. *Ent. Scand. Suppl.* 19. Lund, Sweden.
- Wiederholm T. 1980. Use of benthos in lake monitoring. J. Water Poll. Contr. Fed. 52: 537–547.
- Williams D.D. & Feltmate B.W. 1992. Aquatic insects, 1st ed., CAB International, Wallingford, UK.

Received 21 January 2005, accepted 31 May 2005