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# Boreal chironomid communities and their relations to environmental factors — the impact of lake depth, size and acidity

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The relationship between chironomid community composition and certain lake characteristics was investigated using canonical correspondence analysis (CCA) on literature-retrieved data sets from 38 localities in North America and 43 in northern Europe. Three separate analyses were performed, classifying the chironomids to subfamily, genus or species level. The results demonstrate that the occurrence and abundance of chironomids are a function of lake depth, size and acidity. The subfamily Diamesinae-Prodiamesinae was a good indicator of large deep lakes with higher pH values. Subfamily Orthocladiinae was an indicator of relatively small lakes with low pH and conductivity, while Tanytarsini occurred in lakes with relatively high pH value. Tanypodinae and in particular Chironomini appeared less influenced by the analyzed environmental factors than other chironomids. At the genus level, *Ablabesmyia* and *Zalutschia* and subgenus *Psectrocladius* and *Monopsectrocladius* dominated in small shallow lakes with low values of pH and conductivity, whereas *Prodiamesa*, *Cryptotendipes*, *Thienemaniella*, *Paratendipes*, *Stempellina* and *Cricotopus* dominated in large deep lakes with high pH. The most common chironomids, the genera *Procladius, Tanytarsus* and *Chironomus*, were less correlated with the environmental factors in the boreal lakes, although some *Chironomus* species appeared to be indicative of acid lakes.

## Introduction

Relationships between environmental factors and the structure and function of aquatic macroinvertebrate communities have received considerable attention (e.g. Thienemann 1925, Brundin 1956, Sæther 1975, Wiederholm 1981). Chironomid larvae have been considered to be the most promising biological indicator of water quality among freshwater macroinvertebrates because of their ubiquity and abundance in aquatic ecosystems. Early investigations were focused on species tolerance to hypolimnial anoxia and the importance of chironomids as indicators of lake trophy and water quality (Brundin 1956, Brinkhurst 1974, Sæther 1979). More recent developments in community ecology have lead to an increasing interest in chironomid species composition and assembly structure (e.g. Aagaard 1986, Tokeshi 1991, Goyke and Hershey 1992, Botts 1997), and the analysis of biological communities is regarded as an important part of the total evaluation of lakes (Wiederholm 1980, Claassen 1987). Chironomid assemblages have also been studied with respect to environmental gradients (e.g. Walker and MacDonald 1995, Olander *et al.* 1997). During the last decades, multivariate data analysis techniques, including canonical correlation and canonical correspondence analyses, have become a powerful tool in the analysis of the relationship between communities and environmental factors (Wright *et al.* 1984, Gittins 1985, ter Braak 1986). These tests have also been used successfully in studies of macroinvertebrates of lotic and lentic ecosystems (Ormerod and Edwards 1987, Johnson and Wiederholm 1989, Walker *et al.* 1991, Walker and MacDonald 1995, Fjelheim *et al.* 2000).

In the present study, canonical correspondence analysis (CCA, ter Braak 1988) has been used to investigate the relationship between chironomid communities and important characteristics of boreal lakes and ponds. The analyses were conducted using literature data from boreal lake localities in North America and northern Europe. Several environmental factors were considered for the investigation, but sufficient data sets were only found for four important variables; lake depth, size, acidity and conductivity. Acidification of lakes is one of the acute environmental problems in North Europe and North America (e.g. Mossberg and Nyberg 1979, Fjelheim *et al.* 2000), and is likely to influence the community structure of freshwater invertebrates and chironomids (e.g. Mossberg and Nyberg 1979, Raddum and Sæther 1981, Raddum *et al.* 1988, Meriläinen and Hynynen 1990, Brodin and Gransberg 1993). Chironomid taxa further differ in depth habitat use (Olander *et al.* 1997), and there is often a relationship between chironomid distribution and lake depth (e.g. Sæther 1979, Aagaard 1986, Walker and MacDonald 1995). Maximum lake depth was, therefore, also included in the analyses. Furthermore, according to the principles of island biogeography, larger ecosystems should have higher species diversity (MacArthur and Wilson 1963, Cody 1975). The benthos composition of lakes may thus be influenced by lake size (Timms 1979, Goyke and Hershey 1992), and this factor was therefore also taken into consideration in the analyses. The main objectives of the study were to elucidate the impact of these environmental variables on chironomid community composition and structure in boreal lakes, and to identify potential indicator groups of chironomid larvae for specific lake characteristics.

## Methods

### Data

The literature was reviewed for available data on chironomid communities and environmental factors of boreal lakes. Thirty-eight lakes situated in North America and forty-three lakes located in northern Europe were included in the study (Tables 1 and 2, respectively). Four environmental variables were implemented in the analyses; maximum depth, surface area, pH and conductivity, together with data on density of chironomid larvae (ind. $m^{-2}$). Methods of sampling generally included using an Ekman grab and washing through a 500 $\mu$m mesh net (e.g. Meriläinen and Hynynen 1990), except for Walker *et al.* (1985), who used a corer for sampling and a 355 $\mu$m mesh net for sorting. The mean of spring and summer density or otherwise the spring density of chironomids was obtained, and the mean density for the whole lake was calculated from littoral and profundal samples, or from samples taken at different depths of the lakes.

In the total data set from the boreal lakes, the chironomids had been classified to the genus level, whereas in part of the European data set they had also been identified and grouped to the species level (Meriläinen and Hynynen 1990). The North American data set mainly includes lakes from East Canada (Table 1), and the North European set lakes from southern Finland and Sweden (Table 2).

## Data analysis

Canonical correspondence analysis (CCA), a direct gradient technique available in the statistical program CANOCO version 3.12 (ter Braak, 1986, 1990), was used to assess the relationships between the distribution of chironomid taxa and the measured environmental variables. Environmental variables (except pH) were logarithmically transformed (base 10). Chironomid densities were also transformed to log (density + 1), to give a better approximation to normality of the values ranging from zero to many thousands. Because of sensitivity of the correspondence analysis to rare species, taxa constituting less than 2% of the total abundance were eliminated prior to the analysis (ter Braak 1988). Three separate analyses were performed using the four

**Table 1**. Environmental variables and mean chironomid densities for the North American lakes used in the analyses.

| No. | Lake | Data sources* | Localization | Maximum depth (m) | Area (km$^2$) | pH | Conductivity (µS cm$^{-1}$) | Density (ind. m$^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| 1 | Wood | 1 | British Colombia | 34 | 9.2 | 8.4 | 384 | 549 |
| 2 | Kalawalka | ,, | | 141 | 26 | 8.0 | 427 | 612 |
| 3 | Skaha | ,, | | 55.8 | 20.1 | 8.2 | 292 | 620 |
| 4 | Batchawana N | 2 | Ontario | 11.3 | 0.059 | 6.0 | 23 | 15 |
| 5 | Batchawana S | ,, | | 10.9 | 0.058 | 6.1 | 28 | 87 |
| 6 | Wishart | ,, | | 4.5 | 0.192 | 6.7 | 55 | 68 |
| 7 | Little Turkey | ,, | | 13 | 0.192 | 6.6 | 84 | 524 |
| 8 | Turkey | ,, | | 37 | 0.52 | 6.7 | 101 | 831 |
| 9 | Batchawana Bay | ,, | | 46 | 56 | 8.1 | 79 | 260 |
| 10 | PE1 | 3 | New Brunswick | 0.7 | 0.001 | 3.8 | 17 | 1600 |
| 11 | PE2 | ,, | | 1.5 | 0.005 | 3.8 | 17 | 900 |
| 12 | PE3 | ,, | | 2 | 0.005 | 3.8 | 17 | 2400 |
| 13 | PE4 | ,, | | 1.5 | 0.005 | 3.7 | 37 | 11000 |
| 14 | Kelly's Bog | ,, | | 2 | 0.005 | 4.2 | 10 | 1700 |
| 15 | Hebert Bog | ,, | Nova Scotia | 2.5 | 0.03 | 4.0 | 10 | 1800 |
| 16 | Joliccure-M Bog | ,, | New Brunswick | 1.5 | 0.005 | 4.0 | 10 | 5200 |
| 17 | Wood's Pond | ,, | | 2 | 0.01 | 4.0 | 10 | 4700 |
| 18 | L. Kennedy | ,, | | 2 | 0.02 | 4.8 | 8 | 1400 |
| 19 | Diligent Lake | ,, | Nova Scotia | 10 | 0.005 | 4.5 | 6 | 1200 |
| 20 | Chatham | ,, | New Brunswick | 1.5 | 0.07 | 4.1 | 10 | 1800 |
| 21 | Folly | ,, | | 3 | 0.19 | 4.9 | 38 | 700 |
| 22 | Despres | ,, | | 2 | 0.15 | 4.4 | 2 | 500 |
| 23 | Round | ,, | | 2 | 0.26 | 4.8 | 11 | 1700 |
| 24 | Fox Creek | ,, | | 1.7 | 0.10 | 5.6 | 29 | 2400 |
| 25 | South lake | ,, | | 1 | 0.14 | 6.2 | 16 | 5200 |
| 26 | Coal Branch | ,, | | 3 | 0.41 | 5.1 | 12 | 1100 |
| 27 | Johnston's lake | ,, | | 2 | 0.15 | 6.4 | 80 | 1600 |
| 28 | Blake Lake | ,, | | 6 | 0.17 | 6.4 | 18 | 2800 |
| 29 | Portey pond | ,, | | 1.5 | 0.04 | 6.1 | 70 | 2000 |
| 30 | Little fowler | ,, | | 1 | 0.03 | 6.8 | 18 | 1400 |
| 31 | Second Fowler | ,, | | 2 | 0.24 | 6.5 | 25 | 1700 |
| 32 | Smart's Pond | ,, | Nova Scotia | 1.5 | 0.02 | 6.2 | 41 | 7900 |
| 33 | Missiguash | ,, | | 1.2 | 0.03 | 6.5 | 128 | 3200 |
| 34 | Memramcook | ,, | New Brunswick | 1.2 | 0.30 | 7.0 | 150 | 1900 |
| 35 | Layton's Lake | ,, | Nova Scotia | 8 | 0.12 | 7.3 | 410 | 600 |
| 36 | Copp's Pond | ,, | | 20 | 0.04 | 6.5 | 40 | 1100 |
| 37 | Little Duck | ,, | | 9 | 0.04 | 6.7 | 41 | 600 |
| 38 | Pink Rock | ,, | New Brunswick | 20 | 0.02 | 4.6 | 35 | 1300 |

* 1: Sæther 1970, Sæther and Maclean 1972. 2: Dermott 1985, Jeffries *et al.* 1988. 3: Walker *et al.* 1985.

environmental variables as independent variables, and as dependent variables the density of chironomids grouped into: (1) 5 subfamilies or tribes including Tanypodinae, Diamesinae-Prodiamesinae, Orthocladiinae, Chironomini, and Tanytarsini, (2) 42 genera for the total set of 81 boreal lakes, and (3) 40 chironomid taxa grouped by the species level from the North European data set.

Taxon and site scores for each CCA were

**Table 2**. Environmental variables and mean chironomid densities for the North European lakes used in the analyses. Sources of data: Lake 39–73 (Meriläinen and Hynynen 1990); Lake 74 (Wiederholm and Eriksson 1977); Lake 75–81 (Mossberg and Nyberg 1978).

| No. | Lake code or name | Maximum depth (m) | Area (km$^2$) | pH | Conductivity ($\mu$S cm$^{-1}$) | Chironomid density (ind. m$^{-2}$) |
|---|---|---|---|---|---|---|
| 39 | 001 | 4 | 0.08 | 6.2 | 39 | 312 |
| 40 | 002 | 10 | 0.10 | 6.0 | 35 | 669 |
| 41 | 003 | 10 | 0.34 | 6.1 | 43 | 326 |
| 42 | 004 | 6 | 0.03 | 5.9 | 63 | 221 |
| 43 | 005 | 6 | 0.22 | 4.8 | 34 | 1297 |
| 44 | 006 | 6 | 0.24 | 6.0 | 41 | 1475 |
| 45 | 012 | 6 | 0.43 | 6.4 | 58 | 157 |
| 46 | 014 | 8 | 0.06 | 4.9 | 33 | 1600 |
| 47 | 016 | 14 | 0.42 | 5.9 | 33 | 214 |
| 48 | 017 | 6 | 0.06 | 5.7 | 35 | 3384 |
| 49 | 048 | 24 | 0.70 | 5.8 | 34 | 687 |
| 50 | 049 | 14 | 0.29 | 5.7 | 33 | 296 |
| 51 | 491 | 23 | 0.18 | 5.7 | 36 | 446 |
| 52 | 050 | 16 | 0.70 | 6.1 | 36 | 578 |
| 53 | 051 | 15 | 0.53 | 6.0 | 39 | 216 |
| 54 | 052 | 25 | 0.05 | 5.9 | 38 | 924 |
| 55 | 053 | 14 | 0.05 | 6.2 | 30 | 508 |
| 56 | 055 | 11 | 0.12 | 5.1 | 32 | 1418 |
| 57 | 067 | 15 | 0.30 | 5.5 | 28 | 911 |
| 58 | 088 | 9 | 0.78 | 5.1 | 21 | 1171 |
| 59 | 089 | 8 | 0.04 | 5.1 | 16 | 790 |
| 60 | 090 | 19 | 0.20 | 4.8 | 16 | 762 |
| 61 | 500 | 12 | 0.55 | 6.4 | 25 | 324 |
| 62 | 018 | 9 | 0.02 | 6.2 | 41 | 502 |
| 63 | 019 | 10 | 0.09 | 5.9 | 39 | 825 |
| 64 | 021 | 17 | 0.14 | 5.5 | 34 | 295 |
| 65 | 031 | 8 | 0.15 | 6.7 | 41 | 1451 |
| 66 | 071 | 15 | 0.45 | 6.0 | 37 | 911 |
| 67 | 039 | 5 | 0.30 | 6.5 | 70 | 1855 |
| 68 | 040 | 19 | 0.57 | 6.0 | 35 | 399 |
| 69 | 041 | 15 | 0.45 | 6.0 | 39 | 1389 |
| 70 | 431 | 20 | 0.71 | 6.3 | 35 | 640 |
| 71 | 044 | 18 | 0.23 | 5.9 | 30 | 1874 |
| 72 | 045 | 5 | 0.05 | 5.0 | 21 | 2394 |
| 73 | 451 | 12 | 0.08 | 6.2 | 20 | 1643 |
| 74 | Trestickeln | 20 | 90 | 4.3 | 48 | 560 |
| 75 | Trehorningen | 4.5 | 3.4 | 5.0 | 43 | 2100 |
| 76 | Svartsjön | 7 | 1.6 | 4.5 | 32 | 550 |
| 77 | Långsjön | 11 | 8 | 4.5 | 36 | 1160 |
| 78 | Trollkarlen | 11 | 3.1 | 4.2 | 37 | 1187 |
| 79 | Blanksjön | 15 | 11.5 | 4.9 | 30 | 743 |
| 80 | Iglafallssjön | 14 | 6.1 | 4.9 | 31 | 1419 |
| 81 | Vibollsjön | 7 | 10 | 4.7 | 31 | 434 |

plotted using triplot or biplot scores (ter Braak 1988). Statistical significance ($\alpha = 0.05$) of the CCA axes and the variables was tested using a full model Monte Carlo permutation test (199 unrestricted permutations).

## Results

The results of the CCA ordination based on chironomid taxa, environmental variables and their related sites are summarized in Figs. 1–3. For the first analysis, a triplot figure was produced for ordination of both taxa and sites (Fig. 1). For the two other analyses, ordination of lakes and related environmental variables are plotted for each analysis in the first biplots (Figs. 2A and 3A). In the second biplots (Figs. 2B and 3B), ordination of each taxon approximates its weighted-average position relative to other taxa, as well as its relationship to the displayed environmental variables. The lengths of the arrows representing the environmental variables indicate their relative importance in explaining the variation in the chironomid data, and their ordinations indicate their correlation with the ordination axes.

### Chironomids classified by subfamily or tribe level in the total set of boreal lakes

In the analysis of chironomids classified by the subfamily or tribe level, the eigenvalues for the first two CCA axes were 0.040 and 0.024, and the species-environment correlations for the same axes were 0.654 and 0.451, respectively. The first two CCA axes accounted for 23.3% of the variance in the weighted averages of the chironomid data (Table 3A). However, CCA axes 1 and 2 captured a high proportion (99%) of the variance in the chironomid-environmental relationship. The Monte Carlo test showed the full model to be significant for the first axis ($P$ = 0.005) and for all four canonical axes ($P$ = 0.005). The first axis accounted for approximately 62% of the variance explainable at the basis of the first and second axes. There was a high correlation between the horizontal CCA axis 1 and pH, surface area and conductivity.

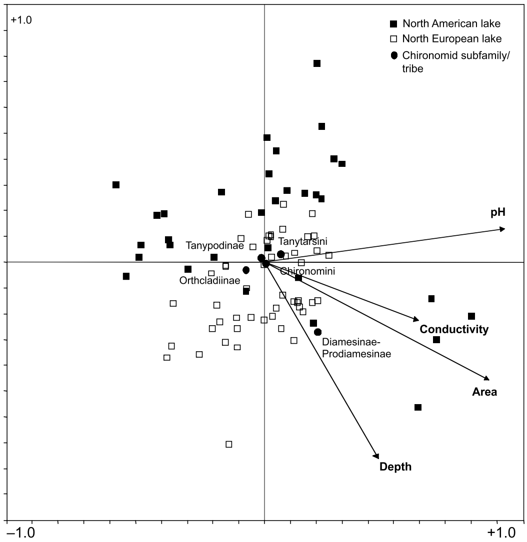


**Fig. 1**. Triplot ordination of sites and taxa scores by subfamily and tribe level, and the relationship with the environmental variables based on canonical correspondence analysis (CCA) for the total set of boreal lakes.

The maximum depth and partly also surface area, contributed markedly to the second axis (Table 4A).

Triplot of CCA ordination of taxa and site scores and the influences of environmental variables are plotted graphically in Fig. 1. The subfamilies Diamesinae-Prodiamesinae exhibited a strong positive correlation with the four environmental variables. Subfamily Tanytarsini showed a moderate positive correlation with pH, whereas the subfamily Orthocladiinae was negatively correlated with both pH, area and conductivity. Subfamilies Chironominae and Tanypodinae did not show any significant correlation with the environmental variables.

### Chironomid genera in the boreal lakes

In the analysis of the chironomid genera in the total set of boreal lakes, the eigenvalues for the first two CCA axes were 0.251 and 0.117, and the species–environment correlations for the same axes were 0.892 and 0.771, respectively. The first two CCA axes accounted for 13.6% of the variance in the weighted averages of the

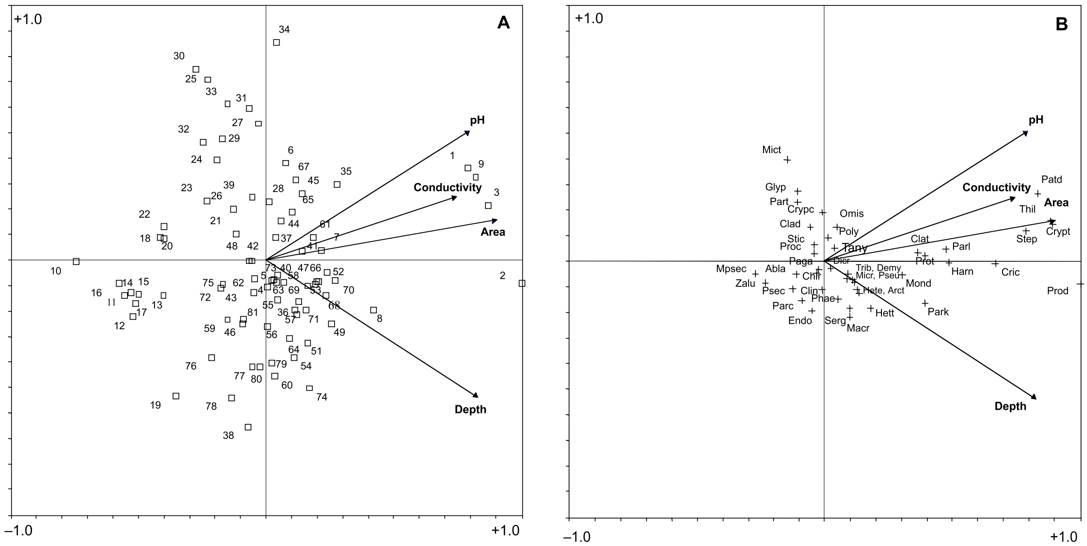


**Fig. 2**. Biplots ordination of sites (**A**) and genera (**B**) scores, and relationship with the environmental variables based on canonical correspondence analysis (CCA) for the total set of boreal lakes (Table 1 and 2). Abbreviations of chironomid taxa: Abla = *Ablabesmyia*; Arct = *Arctopelopia*; Clad = *Cladopelma*; Clat = *Cladotanytarsus*; Clin = *Clinotanypus*; Cryc = *Cricotopus*; Crypc = *Cryptochironomus*; Crypt = *Cryptotendipes*; Demy = *Demicryptochironomus*; Dicr = *Dicrotendipes*; Endo = *Endochironomus*; Glyp = *Glyptotendipes*; Harn = *Harnischia*; Hete = *Heterotrissocladius*; Hett = *Heterotanytarsus*; Macr = *Macropelopia*; Mict = *Microtendipes*; Mond = *Monodiamesa*; Mpsec = *Monopsectrocladius*; Omis = *Omisus*; Paga = *Pagastiella*; Parc = *Parachironomus*; Park = *Parakiefferiella*; Parl = *Paracladius*; Part = *Paratanytarsus*; Patd = *Paratendipes* ; Phae = *Phaenopsectra*; Poly = *Polypedilum*; Proc = *Procladius*; Prod = *Prodiamesa*; Prot = *Protanypus*; Psec = *Psectrocladius*; Pseu = *Pseudochironomus*; Serg = *Sergentia*; Step = *Stempellina*; Stic = *Stictochironomus*; Tany = *Tanytarsus*; Thil = *Thienemanniella*; Trib = *Tribelos*; Zalu = *Zalutschia.*

chironomid data (Table 3B). The canonical axes 3 ($\lambda_3 = 0.053$) and 4 ($\lambda_4 = 0.028$) explained an additional 1.9% and 1.1% of variance, respectively. However, CCA axes 1 and 2 captured a large proportion (81.9%) of the variance in the chironomid-environmental relationship. Both first and all canonical axes were significant ($P < 0.005$). The first axis accounted for approximately 68% of the variance explainable on the basis of the first and second axes. High correlation existed between the horizontal CCA axis 1 and the four environmental variables of area, maximum depth, pH and conductivity. The pH and maximum depth also contributed markedly to the second axis (Table 4B).

Biplots of chironomid genera and site scores and the influences of the four environmental variables for the boreal lakes are plotted in Fig. 2. Genera *Zalutschia, Ablabesmyia, Parachironomus*, *Endochironomus*, and subgenus *Psectrocladius* and *Monopsectrocladius* showed negative correlation with pH, area and conductivity. Genera *Microtendipes, Glyptotendipes, Paratanytarsus, Cryptochironomus* and *Cladopelma* further showed negative correlation with maximum depth. Genera *Prodiamesa, Cryptotendipes, Thienemanniella, Stempellina, Paratendipes* and *Cricotopus* did on the other hand show a strong positive correlation with all four environmental variables.

## Chironomid species in the North European lakes

In the analysis of chironomid species from the North European lakes, the eigenvalues for the first two CCA axes were 0.138 and 0.095, and the species–environment correlations for the same axes were 0.881 and 0.878, respectively. The first two CCA axes accounted for 10.3% of the variance in the weighted averages of the

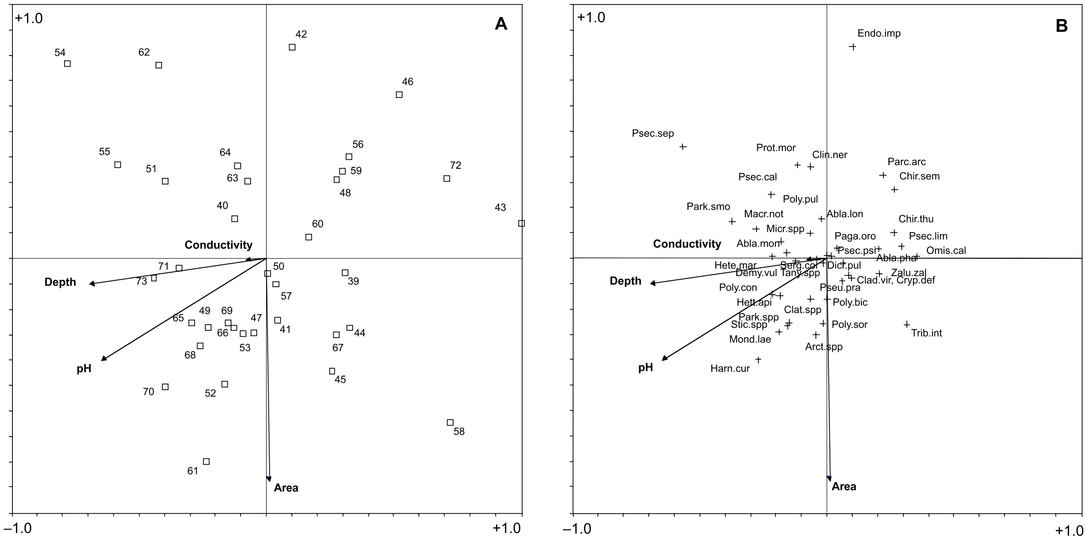


**Fig. 3**. Biplots ordination of sites (**A**) and species (**B**) scores, and relationship with the environmental variables based on canonical correspondence analysis (CCA) for the North European data set (Table 2, ref. 1). Abbreviation of chironomid taxa: Abla.lon = *A. longistyla*; Abla.mon = *A. monilis*; Abla.pha = *A. phatta*; Arct.spp = *Arctopelopia* spp.; Chir.sem = *Chironomus semireductus* gr.; Chir.thu = *Chironomus thummi*; Clad.vir = *Cladopelma viridula*; Clat.spp = *Cladotanytarsus* spp.; Clin.ner = *Clinotanypus nervosus*; Cryp.def = *Cryptochironomus deffectus* gr.; Demy.vul = *Demicryptochironomus vulneratus*; Dicr.pul = *Dicrotendipes pulsus*; Endo.imp = *Endochironomus impar*; Harn.cur = *Harnischia curtilamellata*; Hete.mar = *Heterotrissocladius marcidus*; Hett.api = *Heterotanytarsus apicalis*; Macr.not *Macropelopia notata*; Micr.spp = *Micropsectra* spp.; Mond.bat = *Monodiamesa bathyphila*; Omis.cal = *Omisus caledonicus*; Paga.oro = *Pagastiella orophila*; Parc.arc = *Parachironomus arcuatus*; Park.smo = *Parakiefferiella smolandica*; *Parakiefferiella* spp.; Poly.bic = *Polypedilum bicrenatum* gr.; Poly.con = *P. convictum* gr.; Poly.pul = *P. pullum*; Poly.sor = *P. sordens* gr.; Proc.spp = *Procladius* spp.; Prot.mor = *Protanypus morio*; Psec.cal = *Psectrocladius calcaratus*; Psec.lim = *P. limbatellus* gr.; Psec.psi = *P. psilopterus* gr.; Psec.sep = *P. septentrionalis* gr.; Pseu.pra = *Pseudochironomus prasinatus*; Serg.cor = *Sergentia coracina*; Stic.spp = *Stictochironomus* spp.; Tany.spp = *Tanytarsus* spp.; Trib.int = *Tribelos intextus*; Zalu.zal = *Zalutschia zalutschicola.*

chironomid data (Table 3C). The canonical axes 3 ($\lambda_3$ = 0.085) and 4 ($\lambda_4$ = 0.058) explained an additional 3.8% and 2.6% of variance. Canonical axes 1 and 2 captured a relatively large proportion (61.9%) and axis 3 an additional 22% of the variance in the chironomid–environmental relationship. Monte Carlo test showed the full model to be significant for both first and all four canonical axes ($P$ = 0.005). The first axis accounted for approximately 59% of the variance explainable at the basis of the first and second axes. High correlation existed between the horizontal CCA axis 1 and the measured maximum depth and pH, whereas surface area was strongly correlated with the second axis (Table 4C).

Biplots of species (or species groups) and site scores and the influences of environmental variables are plotted in Fig. 3. The species *Endochironomus impar* (Walker), *Parachironomus arcuatus* (Goetghebuer), *Chironomus semireductus* gr., *C. thummi* gr. (Kieffer), *Omisus caledonicus* (Edwards), *Psectrocladius limbatellus* gr. (Holmgren) and *Ablabesmyia phatta* (Egger), were negatively correlated with pH, whereas *Harnischia curtilamellata* (Malloch), *Monodiamesa bathyphila* (K.), *Stictochironomus* spp., *Polypedilum convictum* gr. (Walker) and *Parakiefferiella* spp. in contrast were positively correlated. *Omisus caledonicus, Tribelos intextus* (Walker), *P. limbatellus* gr., *C. semireductus* gr., *C. thummi, Parachironomus arcuatus, E. impar*, *A. phatta* and *Z. zalutschicola* Lipina, were negatively correlated with maximum depth, whereas *Psectrocladius septentrionalis* gr. Chernovski, *Parakiefferiella smolandica* (Brundin), *Macropelopia notata* (Meigen), *Harnischia curtilamellata*, *P. convictum* gr. and *Heterotrissocladius marcidus* (Walker) were positively correlated. Furthermore, *E. impar, P. septentrionalis* gr., *Protanypus morio* (Zetterstedt), *Clinotanypus nervosus* (Meigen), *Parachironomus arcuatus*, *Psectrocladius calcaratus* (Edwards) and *C. semireductus* gr. showed negative correlation with lake area, whereas *H. curtilamellata, Arctopelopia* spp., *M. bathyphila, Stictochironomus* spp., *P. sordens* gr. (van der Wulp) and *Parakiefferiella* spp. showed a positive correlation. Conductivity did in contrast have no significant influence on the chironomid species composition of the North European lakes (Table 4C and Fig. 3B).

## Discussion

The study demonstrates that the composition and abundance of chironomid communities are influenced by lake characteristics such as size, depth and pH. Among the five subfamilies and tribes, Diamesinae and Prodiamesinae showed a strong positive correlation with the four environmental variables, particularly maximum depth and surface area, and tended to dominate in relatively deep and large lakes with high values of pH and conductivity. The subfamily Orthocladiinae did on the other hand show a moderate negative correlation with the four environmental variables, and particularly pH. The Orthocladiinae are mostly reported from acid lakes (e.g. Mossberg and Nyberg 1979), but several species are also reported to be common in the profundal zone of large lakes (e.g. *Heterotrissocladius* spp.; Sæther 1979, Aagaard 1986, Walker and MacDonald 1995). Subfamily Tanytarsini was positively correlated with pH. Tanytarsini is reported as typical for oligotrophic and oligohumic lakes (Mossberg and Nyberg 1979, Dermott 1985). Tanypodinae and especially Chironomini had only a weak correlation with the environmental variables, and seemed less influenced by different environmental factors. This is in agreement with other reports that *Chironomus* and *Procladius* (the main proportion of subfamily Chironomini and Tanypodinae, respectively), are commonly found both in acidic and non acidic lakes (e.g. Brundin 1956, Mossberg and Nyberg 1979, Wiederholm 1983, Walker *et al.* 1985). In an experimental study, Chironomini and Tanypodinae were also reported as the most resistant groups to pH depression (Allard and Moreau 1985).

As shown in the biplots of sites and environmental variables, most of the North American

**Table 3**. Statistics of the canonical correspondence analyses (CCA) including eigenvalues, correlations and percentage of variation explained by the first two canonical axes.

| | Axis 1 | Axis 2 |
|---|---|---|
| **A**: Total data set–Subfamily/tribe level | | |
| Eigenvalue | 0.040 | 0.024 |
| Species–environment correlation | 0.654 | 0.451 |
| Cumulative percentage variance of species data | 14.5 | 23.3 |
| Cumulative percentage variance of species–environment relation | 61.7 | 99.0 |
| **B**: Total data set–genus level | | |
| Eigenvalue | 0.251 | 0.117 |
| Species–environment correlation | 0.892 | 0.771 |
| Cumulative percentage variance of species data | 9.3 | 13.6 |
| Cumulative percentage variance of species–environment relation | 55.9 | 81.9 |
| **C**: North European data set–species level | | |
| Eigenvalue | 0.138 | 0.095 |
| Species–environment correlation | 0.881 | 0.878 |
| Cumulative percentage variance of species data | 6.1 | 10.3 |
| Cumulative percentage variance of species–environment relation | 36.7 | 61.9 |

lakes were small, shallow and acidic or close to neutral (Fig. 2A). There were, however, three lakes with high pH in the North American data set (Wood, Kalawalka, and Skaha; pH > 8). The North European lakes had a wider range of variation in the environmental variables, including pH (Fig. 3A). In spite of this, a close similarity existed in the composition of chironomid fauna between the North American and North European data set. The Nearctic chironomid fauna is suggested to be relatively similar in composition to the Palearctic (e.g. Ashe *et al.* 1987). Of 21 taxa encountered in Canada by Walker *et al.* (1991), nineteen taxa were also found in North Fennoscandia (Olander *et al.* 1997). Similarly, in our study comparing chironomids from Canada and Fennoscandia, 31 genera out of the total 40 genera present were found in both the North American and North European lakes.

*Zalutschia*, *Ablabesmyia, Psectrocladius* and *Monopsectrocladius* were situated in the direction of low pH, generally being found in highly acidic lakes. These four genera had negative correlations also with maximum depth, surface area and conductivity. However, all these genera favored the lower end of the pH gradient and dominated in small, shallow, acidic boreal lakes. This is in agreement with Walker *et al.* (1985), who stated that *Chironomus*, *Psectrocladius*, *Monopsectrocladius*, and *Zalutschia* are characteristics of bog lakes and peat polls with low pH and conductivity. Reports from the literature further indicate that both *Psectrocladius* and *Zalutschia* are numerous in acid and humic lakes (Brundin 1949, Mossberg and Nyberg 1979, Walker *et al.* 1985). *Psectrocladius* is the most typical chironomid of humic acidified lakes (Henrikson *et al.* 1982, Dermott 1985), and *Monopsectrocladius* is an abundant group in other acid lakes (Dogherty and Morgan 1991). The species *Psectrocladius fennicus* Storå and *P. limbatellus* gr. are particularly numerous in acidic lakes (Meriläinen and Hynynen 1990, Brodin and Gransberg 1993). Genus *Zalutschia*, and especially *Z. zalutschicola*, is often considered as an indicator of dystrophic conditions, and is commonly found in stratified humic and acid lakes (Brundin 1956, Sæther 1975, 1979, Mossberg and Nyberg 1979, Walker *et al.* 1985, Johnson and Wiederholm 1989). The genus *Ablabesmyia* is known from different types of lakes (Brundin 1949). While *Ablabesmyia monilis* (L.) is considered as an acid sensitive species (Brodin and Gransberg 1993), *Ablabesmyia longistyla* Fittkau has been reported to be numerous in acidic lakes (Meriläinen and Hynynen 1990).

The genera *Cladopelma, Glyptotendipes, Pagastiella* Brund. (Dogherty and Morgan 1991), *Stictochironomus* sp., *S. rosenshoeldi* (Zetterstedt) and *Procladius* (Raddum and Sæther 1981, Meriläinen and Hynynen 1990) have particularly been reported from acid lakes. Accordingly, in the present analysis these taxa were located almost at the lower end of the pH influence. Furthermore, genera *Parachironomus* and *Endochironomus* were found to prefer the lowest pH, whereas *Microtendipes, Glyptotendipes* and *Paratanytarsus* preferred the shallower lakes. *Dicrotendipes* sp., *D. pulsus* (Walker) (Dogherty and Morgan 1991), *Microtendipes* (Griffiths 1992), *Pseudochironomus prasinatus* (Stæger) (Raddum and Sæther 1981) and *Phaenopsectra* (Henrikson *et al.* 1982), are also reported abundant in acid lakes, but according to the results of the present CCA, these taxa were

**Table 4**. Weighted correlation matrix among CCA species and environmental ordination axes for; — **A**: the total set of boreal lakes and chironomid subfamily/tribes, — **B:** boreal lakes and chironomid genera, — **C**: North European lakes and chironomid species.

| | Maximum depth | Surface area | Conductivity | pH |
|---|---|---|---|---|
| **A** | | | | |
| SPEC.AX1 | 0.288 | 0.567 | 0.388 | 0.607 |
| SPEC.AX2 | –0.342 | –0.205 | –0.102 | 0.059 |
| ENVI.AX1 | 0.440 | 0.867 | 0.593 | 0.928 |
| ENVI.AX2 | –0.759 | –0.456 | –0.226 | 0.130 |
| **B** | | | | |
| SPEC.AX1 | 0.741 | 0.804 | 0.664 | 0.710 |
| SPEC.AX2 | –0.416 | 0.122 | 0.191 | 0.392 |
| ENVI.AX1 | 0.830 | 0.901 | 0.744 | 0.796 |
| ENVI.AX2 | 0.540 | 0.158 | 0.248 | 0.509 |
| **C** | | | | |
| SPEC.AX1 | –0.612 | 0.010 | –0.069 | –0.571 |
| SPEC.AX2 | –0.089 | –0.768 | –0.006 | –0.352 |
| ENVI.AX1 | –0.694 | –0.011 | –0.079 | –0.648 |
| ENVI.AX2 | –0.101 | –0.875 | –0.007 | –0.401 |

apparently less influenced by pH. Furthermore, *Sergentia* which is known as a common taxa in the profundal zone (Sæther 1979, Brodin and Gransberg 1993), was more correlated with depth than *Phaenopsectra*.

The genera *Procladius, Tanytarsus* and *Chironomus* are important chironomid groups reportedly dominating in most boreal lakes (e.g. Brundin 1949, Sæther 1975, Mossberg and Nyberg 1979, Walker *et al.* 1985). Neither *Procladius* nor *Tanytarsus* showed any strong correlations with either pH or the other environmental variables. Similarly, there was weak or no correlations between the genus *Chironomus* and the environmental variables. This observation is consistent with literature findings that *Chironomus* can be found in both shallow acid humic lakes and deep lakes with low or normal pH (Brundin 1949, Wiederholm and Eriksson 1977, Mossberg and Nyberg 1979, Sæther 1979, Raddum and Sæther 1981, Dermott 1985). At the species level, in contrast, there were relatively strong negative correlations between pH and both *Chironomus thummi* gr. and *C. semireductus* gr. It thus seems that some *Chironomus* species may be indicators of acid lakes. Owing to the large proportion of larvae belonging to *Chironomus, Procladius* and *Tanytarsus* (e.g. Walker *et al.* 1985, Griffiths 1992), a more detailed analysis of these genera and their relationship to environmental factors should suggestively be carried out.

With respect to the species composition of the North European lakes, the species *Harnischia curtilamellata*, *Monodiamesa bathyphila*, *Stictochironomus* spp., *Polypedilum convictum* gr. and *Parakiefferiella* spp. appeared to be the best indicators of high pH. *Psectrocladius septentrionalis* gr., *Parakiefferiella smolandica*, *Harnischia curtilamellata*, *Psectrocladius calcaratus*, *Macropelopia* spp. Thienemann, *Polypedilum convictum* gr., *Heterotanytarsus apicalis* (K.) and *Heterotrissocladius marcidus* were further typical representatives of the deeper lakes. Among those, *Parakiefferiella* and *Heterotrissocladius* are known primarily from large and deep lakes (Walker and MacDonald 1995). *Z. zalutschicola, Psectrocladius limbatellus* gr., *Omisus caledonicus*, *Tribelos intextus* and *Chironomus semireductus* gr. were the typical species present in the shallow North European lakes. *Zalutschia* has similarly been reported abundant from other shallow lakes (Walker *et al.*1985, Walker and MacDonald 1995). *Endochironomus impar, Psectrocladius septentrionalis* gr. and *Protanypus morio* were further typically present in the small lakes, whereas *Harnischia curtilamellata*, *Arctopelopia* spp., *P. sordens* gr., *Monodiamesa bathyphila* and *Stictochironomus* spp. mostly were found in larger lakes. Large lakes were, however, underrepresented in the analysed lake set, and chironomid species such as *Heterotrissocladius subpilosus* (K.) and *H. määri* Brund. were absent from the data even though they are known to occur commonly in the deep profundal areas of large boreal lakes (Sæther 1979, Aagaard 1986, Meriläinen *et al.* 2000).

Of the four studied environmental variables, the chironomid community was generally less influenced by conductivity than the other variables (Table 4). Some authors have found no significant relationships between the species composition of chironomids and physical and chemical factors (Hilsenhoff and Narf 1968, Welch 1952), and Dermott (1985) found only weak correlations between macroinvertebrate abundance and pH and alkalinity. However, in many other studies certain correlations have been shown to exist between chironomids and environmental characteristics (e.g. Brundin 1949, Sæther 1979, Wiederholm 1981, Aagaard 1986, Johnson and Wiederholm 1989, Johnson *et al.* 1990, Meriläinen and Hynynen 1990). The present study demonstrates that in ecological studies of chironomids, the overall influences of specific environmental variables can be determined by analyses of data using canonical ordination methods. Unfortunately, only a limited number of environmental variables could be included in the analyses due to restrictions in the available data sets. Furthermore, small lakes with a high pH range dominated the lake set that was available for the analyses, whereas sufficient data only were obtainable from a few large lakes. These aspects may constrain the generality of the conclusions, and more studies of chironomid communities and environmental factors in boreal lakes would therefore be beneficial for further multivariate analyses. Standardization of sampling methods, employing a wide range of variation in lake characteristics, identification of chirononomid larvae to the possible lowest taxonomic level, and taking into account seasonal and spatial variation (Gerstmeier 1989, Johnson *et al*. 1993) would also highly improve such analyses. Both regional and broader biogeographical studies should further be recommended for such investigations.

In conclusion, several of the chironomid taxa from the boreal lakes showed significant relationships with the environmental factors. Lake size, depth and acidity influenced the chironomid community of boreal lakes nearly in the same direction for the North American and European lakes. At the subfamily and tribe level, relatively strong relations existed between some chironomid taxa and the investigated environmental variables, although Tanypodinae and especially Chironomini seemed to be less influenced by the environmental conditions. At the generic level, *Ablabesmyia*, *Zalutschia*, *Psectrocladius*, and *Monopsectrocladius* were characteristic for small shallow acid lakes, whereas *Prodiamesa, Cryptotendipes, Thienemanniella, Stempellina,* and *Paratendipes* were typical of large, deep lakes with high pH. Furthermore, *Microtendipes, Glyptotendipes* and *Paratanytarsus* were representatives of shallow lakes. The most abundant chironomid groups, *Procladius, Tanytarsus* and *Chironomus*, were less correlated with the environmental factors, although some *Chironomus* species seemed to be indicators of acid lakes. The analyses suggest that some of the studied chironomid taxa may serve as adequate indicators of the environmental conditions. Similarly, empirical models implementing environmental variables may show to be good predictors of the dominant taxa of chironomid communities in boreal lakes.

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