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An assessment of lentic ceratopogonids, ephemeropterans, trichopterans and oribatid mites as indicators of past environmental change in Finland

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I studied a dataset of surface sediment samples from 80 lakes with zoological macroremain analysis to assess the potential of fossil ceratopogonids (Diptera: Ceratopogonidae), ephemeropterans (Insecta: Ephemeroptera), trichopterans (Insecta: Trichoptera) and oribatid mites (Acarina: Oribatida) as palaeolimnological indicators in Finland. Results showed that late-winter hypolimnetic oxygen and climatic variables were most important in influencing the occurrence and abundance of these taxa. Of the ceratopogonids, the *Bezzia* type was an indicator of elevated hypolimnetic oxygen conditions, warm climate and oligotrophy, while the *Dasyhelea* type indicated low hypolimnetic oxygen conditions, moderately cool climate and mild acidity. Ephemeropterans, trichopterans and oribatids indicated warm climatic conditions and oribatids were also indicative of elevated oxygen conditions and small oligotrophic lakes. Results of this study can be useful in palaeolimnological studies because the fauna examined provides a valuable supplementary data source for multiproxy studies.

Introduction

Palaeolimnology uses the physical, chemical and biological information preserved in lake sediments to reconstruct past environmental conditions. It provides a unique method to understand the long-term environmental dynamics in aquatic systems existing prior to human observation records and instrumental measurements. Having data on past environmental conditions is important in preservation, conservation and restoration efforts. Current climate warming is particularly acute in the polar regions, which are ecologically very sensitive (Magnuson *et al*. 2000). The vast number of lakes in the circumpolar region makes these palaeolimnological methods especially useful tools in reconstructing and interpreting past environmental conditions (Pienitz *et al*. 2004) and the sensitivity of high-latitude lakes makes them excellent harbingers of future environmental changes. Studying modern aquatic communities will allow researchers to establish baseline conditions against which future changes can be compared.

The palaeoecological archives in lake deposits include plant macrofossils, pollen, algae and some invertebrates. Fossil (or subfossil) organisms respond uniquely to the changing environment, reflecting past climate, nutrient conditions, oxygen content, pH, pollution or ecological interactions. Furthermore, fossil assemblages are representative of modern communities, since they gather the signal from different seasons and multiple habitats (Frey 1960, Nevalainen 2008). The use and importance of botanical and algal records in palaeolimnology is well established (Birks & Birks 2004, Battarbee 2000), but of the many invertebrate groups that are preserved as fossils (Frey 1964) only a few are fairly well studied. The most commonly used invertebrate remains in palaeolimnology are the cladocerans (Crustacea: Cladocera) (Rautio 2007) and chironomids (Insecta: Diptera: Chironomidae) (Walker 2001) that are generally abundant in lake sediments, taxonomically identifiable and responsive to particular environmental perturbations. Additionally, ostracods (Crustacea: Ostracoda) are an important group of fossils (Holmes 2001), but unfortunately they are typically preserved only in alkaline environments. Although the remains of many other invertebrates, such as protozoans, bryozoans, oribatid mites (Acarina: Oribatida), other insects and molluscs are found in lake sediments, they are still underexploited in palaeolimnology (Smol 2002). This is because they are often rare in sediments, selectively preserved, difficult or impossible to identify, or their autecology is not adequately studied. However, the use of these less frequently occurring zoological remains in palaeolimnological studies may provide an important source (proxy) of additional information on environmental changes. Fossil chironomid analysis is often used in studies concerning Holocene environmental dynamics, such as in temperature (reviewed in Brooks 2006) and lake productivity (reviewed in Brodersen & Quinlan 2006). The analytical methods include sieving through a 100-μm mesh and hand-picking the chironomid head capsules with fine forceps under a stereomicroscope. Therefore, it is also very easy to simultaneously separate other remains of similar size, such as other insects and oribatid mites. The only more frequently used insect group so far, in addition to chironomids, is the chaoborids (Diptera: Chaoboridae) that have been used as indicators of historical fish populations, but only in North America (reviewed in Sweetman & Smol 2006).

The larval stages of insects are mainly used in palaeolimnological studies. Aquatic ceratopogonid (Insecta: Diptera: Ceratopogonidae, known as the biting midges or 'no-see-ums') larvae are carnivorous, while terrestrial larvae feed on plant material (Brooks *et al*. 2007). Ceratopogonids are widely distributed in standing waters, but are much less common than chironomids and chaoborids (Walker 2001). Walker and Mathewes (1989) showed that ceratopogonids were indicative of mild climatic conditions from low to mid elevations in the Canadian Cordillera. Ephemeropterans (Insecta: Ephemeroptera, mayflies) occur mostly in running water, but some are restricted to the littoral zones of lakes (Brooks *et al*. 2007). Larval trichopterans (Insecta: Trichoptera, caddisflies) are often found in anoxic sediments with abundant organic detritus (Elias 2001). They provide valuable information on the environment, since many of the species have narrow temperature, trophic and pH tolerances and are restricted to particular substrates (Elias 2001). Many trichopteran families are restricted to running waters (Cohen 2003). Oribatid mites are a diverse group, with more than 11 000 described species to date. Oribatid mites found in lake sediments are often limnetic, but wetland and terrestrial species also occur (Solhøy & Solhøy 2000). Aquatic oribatids are commonly associated with aquatic macrophytes (Cohen 2003).

Taphonomic processes regulate the preservation of aquatic insects and mites, and determine in what numbers and where the remains are found. Only some body parts, such as chitinized insect head capsules and mouth parts and oribatid exoskeletons, are preserved in the fossil material. However, low pH conditions and oxidation may accelerate the rate of chitin degradation. The identification of fossil insects other than chironomids is difficult, due to a lack of identification keys and most keys for modern insects require entire specimens (Elias 2001). Useful keys for larval ceratopogonids are not available; however two distinct larval types (*Bezzia* Kieffer and *Dasyhelea* Kieffer) are apparent (Walker 2001). The mandibles of ephemeropteran and trichopteran larvae are often found in lake sediments, but their identification is restricted to general levels. Fossil trichopterans may be more precisely identified based on the sclerites from the head capsule and thorax (Solem & Birks 2000, Elias 2001). However, these fragile parts are more easily destroyed and degraded and thus may provide inaccurate cues on trichopteran abundances. Due to the high diversity of oribatid mites, the identification of fossil specimens is confusing and they are often identified only as oribatids or as mites (Bennike & Böcher 1994, Engels *et al*. 2008). Thus, the full potential of oribatid analysis remains unused.

In the present study, I aim to assess the usability of ceratopogonids, ephemeropterans, trichopterans and oribatids as indicators of past environmental change based on a dataset of fossil specimens from surface sediment samples along a latitudinal gradient in Finland, covering 80 limnologically different lakes. My objective is to evaluate the potential of these animals as additional components in chironomid-based studies, serving as supplementary proxies. A method is introduced to utilize the entire supply of fossil remains and to save sediment material, since the animals studied are relatively scarce and large quantities of material (approx. 50–100 cm^3) are needed in quantitative analyses. Additionally, chironomid-based inference models may benefit from these larger samples and more thorough interpretations can be made of past environmental changes if other remains are incorporated in the calculations. The use of these taxa in palaeolimnological studies requires basic information on their distributional patterns and thus this paper endeavours to be a reference for fossil analysis. Using the same method as in zoological macroremain analysis, I present some environmental optima and tolerances for the taxa and try to seek the forcing factors behind their occurrence and abundance by applying statistical techniques.

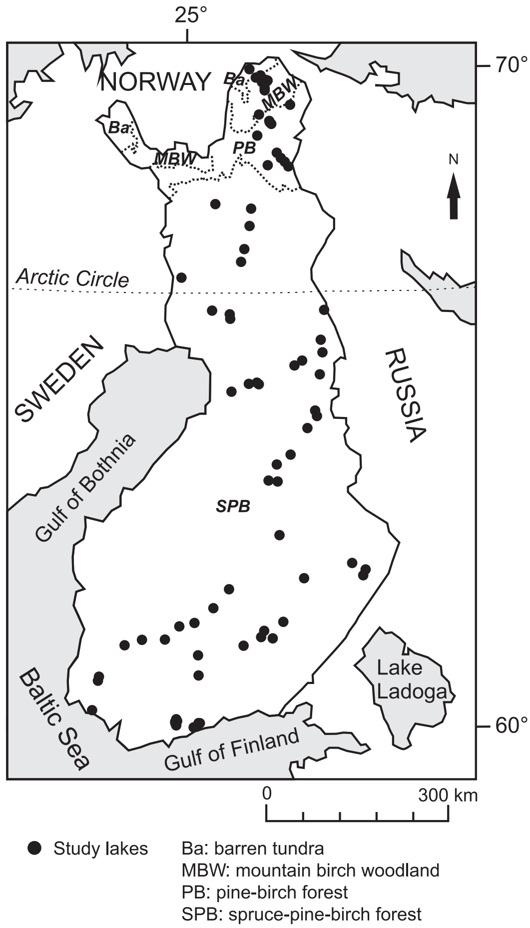

Fig. 1. Location of the 80 study sites in Finland.

Material and methods

Study area and sites

The study area (60°13´–69°53´N, 22°00´–30°13´E) spans a 1080-km latitudinal transect from southern to northern Finland, covering 80 study lakes (Fig. 1). The lakes are generally small and shallow. Vegetation patterns change from southern boreal spruce (*Picea*)–pine (*Pinus*)–birch (*Betula*) forests to northern pine–birch forests, mountain birch (*Betula pubescens* ssp. *czeropanovii*) woodland and barren tundra (Fig. 1). Environmental and limnological characteristics vary considerably between the sites (Table 1). Mean annual temperature (T_{annual}) varies between –2.0 and 5.8 °C and mean annual precipitation between 400 and 660 mm.

Sediment sampling and data collection

Surface sediments were sampled with a Limnos-type gravity corer (Kansanen *et al*. 1991) during late winter and spring 2005. Subsamples for the zoological macroremains were prepared, apply-

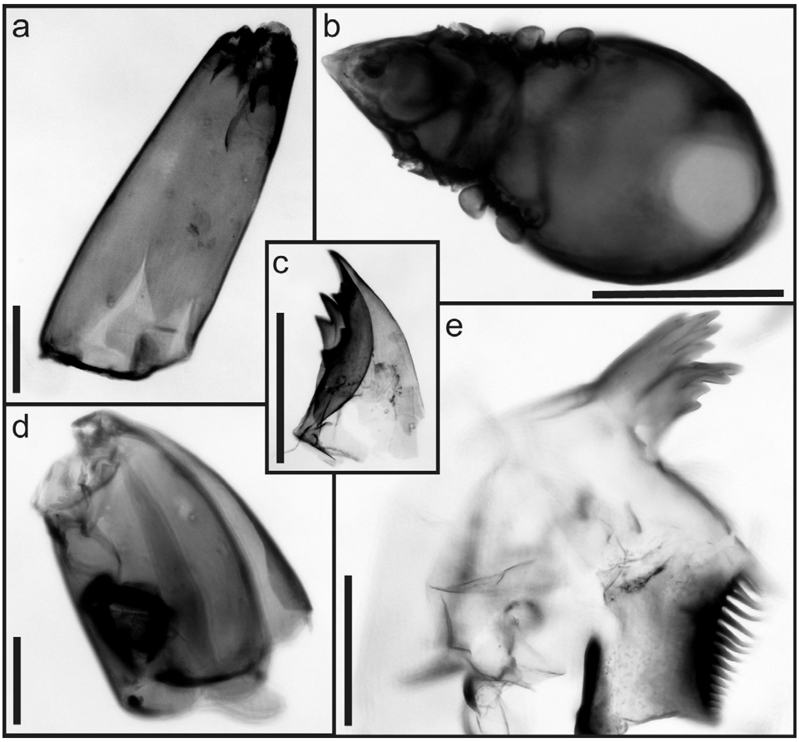

Fig. 2. Remains of the studied aquatic invertebrates from lake sediments in Finland. (**a**) head capsule of a *Bezzia*-type ceratopogonid, (**b**) exoskeleton of an oribatid mite, (**c**) mandible of a trichopteran, (**d**) head capsule of a *Dasyhelea*-type ceratopogonid, and (**e**) mandible of an ephemeropteran. The scale bar in the figures is 200 μm except in **c** where it is 100 μm.

ing the same procedure as used in standard methods for fossil chironomid analysis (Brooks *et al.* 2007). A minimum of 100 chironomid and chaoborid individuals were enumerated from each sample and the other zoological macroremains were retrieved simultaneously and added to the total sum from which the taxon-specific proportions were calculated. Results of the chironomid and chaoborid distributions were excluded from this study and are represented and discussed elsewhere (Luoto 2008). Identification was based on photographs and descriptions of fossil specimens [e.g. Solhøy (2001), Walker (2001, 2007), Rumes *et al.* (2005), Brooks *et al.* (2007)]. Ceratopogonids were identified based on the morphological features of their head capsules, ephemeropterans and trichopterans on the shape of their mandibles and oribatids on the morphological features of their cuticle (Fig. 2). Even though trichopteran remains other than the mandibles provide more detailed identification cues, these fragments are relatively fragile and can be easily damaged or degraded. Therefore, only mandibles were used in this study to better reflect the true occurrence of trichopterans, since the thickly chitinized mandibles are well preserved. For ephemeropterans and trichopterans, two mandibles were considered as one individual.

Table 1. Environmental data of the 80 lakes investigated in Finland. Hypolimnetic oxygen, pH and conductivity measurements are lacking from some of the lakes and the data analysis consisted only of the lakes with measured values (*N*).

	N	Min	Max	Mean
Mean T_{Jul} (°C)	80	11.3	17.1	14.9
Mean T_{annual} (°C)	80	–2.0	5.8	1.8
Elevation (m a.s.l.)	80	11.3	404.0	147.7
Depth (m)	80	0.5	7.0	2.7
pH	59	3.8	9.3	6.2
Oxygen (mg l^{-1})	31	0.5	11.8	5.5
Conductivity (μS cm^{-1})	58	8	312	58.1
Surface area (km^2)	80	0.003	0.988	0.104

Data on water chemistry (Table 1) were acquired during sediment sampling, using an Orion model 1230 pH/mV/ORP/conductivity/

dissolved oxygen/salinity/temperature meter. Measurements were taken from the hypolimnion for oxygen and from the epilimnion for conductivity and pH. Mean annual (T_{annual}) and mean July temperatures (T_{Jul}) were estimated, using a geographic information system (GIS)-based method. Temperature data used were provided by the Finnish Meteorological Institute and are based on climate norms for 1971–2000, which takes into account all Finnish meteorological data (S. Kultti pers. comm.).

Numerical techniques

All data analyses were performed using relative taxon abundances. Weighted averaging (WA) of the species-specific optima and tolerances for environmental variables were performed with the program C2, ver. 1.5.0 (Juggins 2007). Detrended correspondence analysis (DCA) was used to determine the methods used in further analyses. DCA is an ordination method that summarizes the variation in species assemblages along the DCA axes. The DCA was run with detrending by segments and without any transformation of taxon abundances. Canonical correspondence analysis (CCA) is a direct gradient technique that was used to identify the environmental variables that are strongly related to the species assemblages. The CCAs were also run without any transformation of taxon abundances. Manual forward selection of environmental variables was performed and a series of partial CCAs were run to determine whether environmental variables contributed significant additional influence on the faunal distributions (cf. Rühland & Smol 2002). When the CCAs were run with only one variable at a time, the statistical significance of each variable was tested with a Monte Carlo permutation test with 999 unrestricted permutations. The variables were considered significant if the permutation test value was $P \leq 0.05$. When only one environmental variable is used, the ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) indicates the relative significance of the specific variable in explaining the species data. Only λ_1 is canonical since only one independent constraint can be formed from the environmental variables. The DCA and CCAs were performed using the program CANOCO, ver. 4.52 (ter Braak 2003).

Results

Taxon composition and abundance

A total of 10 604 zoological individuals were enumerated from the samples, consisting mostly of chironomids (89.4%) and chaoborids (3.9%). Ephemeropterans occurred with an abundance of 2.5%, oribatids with 2.1%, *Bezzia*-type and *Dasyhelea*-type ceratopogonids both with 0.9% and trichopterans with 0.8%. Ephemeropterans occurred in 58 lakes, while oribatids were found in 50, *Bezzia*-type ceratopogonids in 45, trichopterans in 42 and *Dasyhelea*-type ceratopogonids in 27 lakes (Table 2). The taxa examined were missing from four lakes.

The highest maximum abundances of the taxa studied in one lake were from the oribatids (16.2%) and ephemeropterans (15.8%). Taxa were most common in the spruce–pine–birch forest zone (adapted to the number of lakes examined), except for the *Dasyhelea*-type ceratopogonids, which were most common in pine–birch forests (Table 2). Trichopterans were the only taxon that occurred in the barren tundra. The lowest weighted averaging (WA) optimum for mean T_{Jul} and T_{annual} was with the *Dasyhelea*-type ceratopogonids (14.4 and 0.9 °C) and the highest with ephemeropterans (15.6 and 2.6 °C). The lowest elevation optimum was with ephemeropterans (121.1 m a.s.l.) and highest with the *Dasyhelea*-type ceratopogonids (161.7 m a.s.l.). Ephemeropterans had the highest optimum for water depth (3.0 m), while the lowest was with the *Dasyhelea*-type ceratopogonids (2.4 m). The highest pH optimum was with trichopterans (6.5) and the most acidic optimum was with the *Bezzia*-type ceratopogonids (6.1). Oribatids had the highest hypolimnetic oxygen optimum (6.8 mg l^{-1}) and the *Dasyhelea*-type ceratopogonids the lowest (3.3 mg l^{-1}). The highest conductivity optimum was with trichopterans (74.3 μS cm^{-1}) and the lowest with oribatids (53.0 μS cm^{-1}). Trichopterans also had the highest surface area optimum (0.134 km^2), while oribatids were restricted to small lakes.

Ordinations

DCA axes 1 and 2 showed gradient lengths of 2.4 and 2.7 standard deviation units, implying that methods based on the unimodal response model were most appropriate (Birks 1998) and therefore CCA was used in further analyses. The triplot for samples, taxa and environmental variables showed relatively even distributions along CCA axes 1 and 2 (Fig. 3). The CCA showed that latitude, mean air T_{Jul}, mean air T_{annual}, elevation and hypolimnetic oxygen were related significantly to the species data (Table 3). Lake surface area, depth, pH and conductivity showed no significant correlation. The highest λ_1:λ_2 ratio (indicating the relative significance of the specific variable in explaining the species data), species–environment correlation and cumulative percentage variance in the species data were with hypolimnetic oxygen (Table 3). When decomposing the variance between hypolimnetic oxygen and mean T_{Jul}, both variables suffered from the covariance (Table 3). The *Bezzia*-type and *Dasyhelea*-type ceratopogonids and the oribatids showed the strongest relationship with hypolimnetic oxygen and ephemeropterans were positively correlated with air temperature (Table 2 and Fig. 3). However, none of the correlations were particularly strong.

Discussion

Water chemistry

The distribution of ceratopogonid, ephemeropteran, trichopteran and oribatid remains in surface sediments of the 80 lakes examined shows some distinguishable patterns. Late winter hypolimnetic oxygen content showed the strongest relationship to the species data (Table 3). Taxa with the highest hypolimnetic oxygen optima

Table 2. Number of occurrences, effective number of occurrences (Hill's N2), maximum relative abundances of the total zoological macroremains, taxon-specific abundances in different forest zones and estimated optima (Opt.) and tolerances (weighted averaging) (Tol.) for environmental variables.

		Bezzia	*Dasyhelea*	Ephemeroptera	Trichoptera	Oribatida
Number of occurrences		45	27	57	41	50
Hill's N2 (1973)		31.3	16.8	32.6	31.2	25.9
Maximum abundance (%)		4.9	5.3	15.8	3.9	16.2
Barren tundra (%)		0	0	0	3.0	0
Mountain birch woodland (%)		22.2	21.1	7.0	9.2	19.3
Pine and birch forest (%)		22.2	51.2	25.9	33.3	18.4
Spruce–pine–birch forest (%)		55.6	27.7	67.1	54.5	62.3
Mean T_{Jul} (°C)	Opt.	15.3	14.4	15.6	15.2	15.4
	Tol.	1.4	1.3	1.1	1.4	1.3
Mean T_{annual} (°C)	Opt.	2.4	0.9	2.6	2.1	2.4
	Tol.	2.3	1.9	1.8	2.2	2.1
Elevation (m a.s.l.)	Opt.	131.7	161.7	121.1	141.3	132.7
	Tol.	65.4	44.3	55.3	71.9	59.1
Depth (m)	Opt.	2.9	2.4	3.0	2.9	2.7
	Tol.	1.7	1.5	1.6	1.5	1.6
pH (units)	Opt.	6.1	6.3	6.4	6.5	6.2
	Tol.	1.0	0.3	0.9	0.9	1.2
Oxygen (mg l^{-1})	Opt.	6.5	3.3	4.9	5.1	6.8
	Tol.	3.4	3.7	3.6	3.8	3.1
Conductivity (μS cm^{-1})	Opt.	54.7	65.1	69.2	74.3	53.0
	Tol.	52.1	55.4	73.5	81.0	49.8
Surface area (km^2)	Opt.	0.075	0.090	0.065	0.085	0.049
	Tol.	0.121	0.095	0.103	0.134	0.065

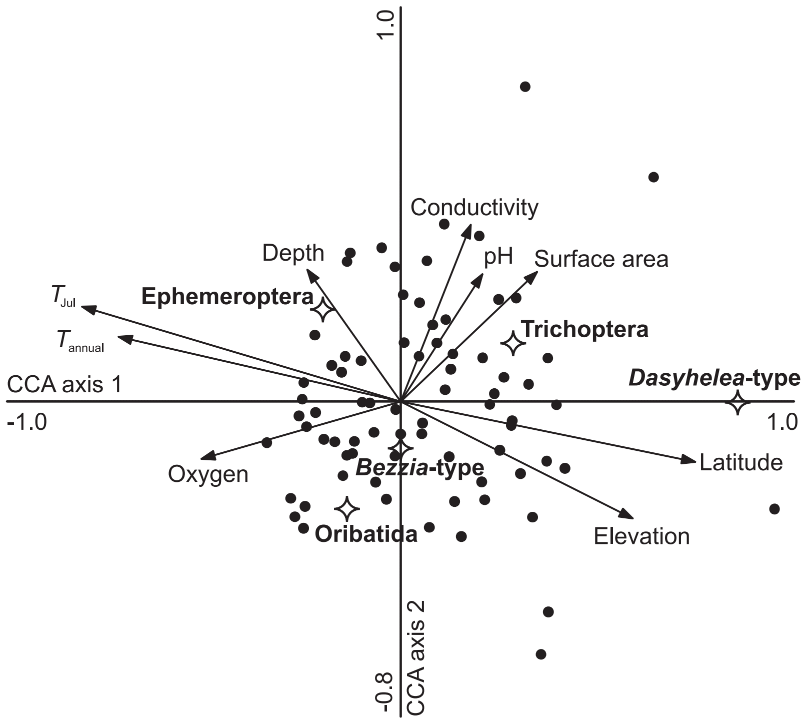

Fig. 3. CCA triplot of scores for sites, taxa and environmental variables based on the 80 lake dataset in Finland.

were the *Bezzia*-type ceratopogonids and the oribatids, while the lowest optimum was with the *Dasyhelea*-type ceratopogonids (Table 2). This is also clearly indicated in the CCA plot for species and environmental variables (Fig. 3) as opposite locations of the taxa along the axes. In southern Finland, deep-water oxygen content is also known to control the distribution of chironomids (T. Luoto & V.-P. Salonen unpubl. data). However, hypolimnetic oxygen was measured from only 31 of the 80 lakes (Table 1). Additional oxygen measurements from more lakes would therefore increase our understanding of its affects on the distribution and abundance of the taxa examined. The oxygen optimum for the *Dasyhelea*-type ceratopogonids was low (Table 2), suggesting that this taxon is a relatively strong indicator of reduced hypolimnetic oxygen

Table 3. Results of the partial CCAs: P values, λ_1:λ_2 ratios, species–environment correlations and cumulative percentage of variance of species data explained by the environmental variables are shown.

Variable	Covariable	P	λ_1:λ_2	Species-environment correlations	Cumulative % variance of species data
Oxygen	–	0.015	0.290	0.521	11.0
Oxygen	T_{Jul}	0.067	0.118	0.355	4.1
Mean T_{Jul}	–	0.001	0.211	0.494	7.4
Mean T_{Jul}	Oxygen	0.014	0.172	0.429	5.9
Latitude	–	0.001	0.179	0.460	6.4
Mean T_{annual}	–	0.001	0.167	0.442	5.9
Elevation	–	0.016	0.119	0.375	4.2
Surface area	–	0.142	0.061	0.285	2.2
pH	–	0.305	0.056	0.251	2.0
Conductivity	–	0.395	0.053	0.236	1.8
Depth	–	0.330	0.043	0.221	1.5

content. The oxygen optima for oribatids and the *Bezzia*-type ceratopogonids were higher than the dataset mean values (Tables 1 and 2), implying elevated hypolimnetic oxygen conditions. Fitting well with the present results, Bagge (1982a) speculated that the reason for low oribatid abundances in small forest lakes is a commonly occurring hypolimnetic oxygen deficiency.

High productivity is often reflected in water properties as elevated conductivity and low oxygen content. Conductivity was also negatively correlated with hypolimnetic oxygen in our dataset (Fig. 3). The oribatids and *Bezzia*-type ceratopogonids showed markedly low conductivity optima and their tolerances were also the lowest (Table 2). They can, therefore, be considered to indicate conditions of lower conductivity and thus possibly lower biological production and oligotrophy. pH optima were close to the mean of the dataset for all taxa (Tables 1 and 2). The highest optimum was with trichopterans which also showed the highest conductivity optimum. In contrast, the lowest pH optima were with the *Bezzia*-type ceratopogonids and with oribatids, which also showed the lowest conductivity optima (Table 2), reflecting the close relationship between the variables examined. This close relationship can also be seen from the CCA results, since the arrows for the variables are similarly orientated (Fig 3). However, conductivity and pH did not correlate significantly with the species assemblages (Table 3), but still some preferences within the taxa can be observed as discussed above. The only taxon with a low tolerance for pH was the *Dasyhelea*-type ceratopogonids and thus can be considered an indicator of pH to some extent, in this case an indicator of mildly acidic conditions (Table 2). Ephemeropterans had a pH optimum that was slightly higher than the mean value of the dataset (Tables 1 and 2), supporting the suggestion that they poorly tolerate acidic environments (Bagge & Salmela 1978).

Climate

Climatic factors are known to control the distribution of aquatic invertebrates in Finland and cladocerans and chironomids have been used in palaeotemperature reconstructions (Korhola 1999, Luoto 2008). The results of this study showed that mean T_{Jul}, mean T_{annual}, latitude and elevation were significantly correlated with the species data (Table 3). All these variables are directly or indirectly linked to climate. Ephemeropterans had the highest optima for mean T_{Jul} and T_{annual}, clearly higher than the mean temperatures of the dataset (Tables 1 and 2), and also had the lowest tolerances. Additionally, ephemeropterans had the lowest optimum for elevation and were absent at tundra sites and very rare in mountain birch woodland, occurring mostly in southern spruce–pine–birch forests (Fig. 1 and Table 2). Therefore, ephemeropterans are apparently indicative of warm climatic conditions in Finland. The only taxon in the dataset that appears to indicate cooler, although not cold, climatic conditions was the *Dasyhelea*-type ceratopogonids. Its optima for mean T_{Jul} and T_{annual} were clearly lower and the elevation optimum was higher than the dataset mean values, while its tolerances were also relatively low (Tables 1 and 2). Ceratopogonidae occurred mostly in the northern pine–birch forest zone, supporting the fact that the *Dasyhelea*-type ceratopogonids prefer cooler climates (Fig. 1 and Table 2). The other taxa had higher temperature optima and lower elevation optima than the dataset mean values (Tables 1 and 2). Due to their optima and narrow tolerances (Table 2), *Bezzia*-type ceratopogonids, trichopterans and oribatids can probably be considered indicative of moderately warm climatic conditions, since they also occurred mostly in the southern spruce–pine–birch forest zone (Fig. 1 and Table 2).

Morphometry

In addition to the above-mentioned limnological conditions and climatic factors, lake depth is an important factor behind the taxonomic compositions of certain invertebrate groups in Finland (Korhola *et al.* 2000, 2005, Nevalainen *et al.* 2008). Even though the present dataset consisted mostly of small lakes (Table 1), oribatids can be recognized as indicators of small lakes because they were restricted to lakes with very small surface areas (Table 2). Lake size optima for the other taxa were also lower than the dataset mean values. Kansanen (1985) showed that living specimens of *Bezzia*-type ceratopogonids were abundant in the littoral zone of a large lake complex in southern Finland, but were less frequent in the sublittoral and rare in the profundal zones. Therefore, small lakes with relatively large littoral areas were also probably more commonly inhabited by *Bezzia*-type ceratopogonids in this study. The results of Paasivirta (1982) from several lakes in southern Finland showed that watermite species were almost always found in littoral habitats, although a few species occurred at a 4-m depth in one of the lakes. In the present study, ephemeropterans had a relatively low optimum for lake size. Bagge (1982b) showed that ephemeropterans occurred only in the littoral zone and preferred small lakes in southern Finland, indicating that this taxon is possibly an indicator of shallow waters. Additionally, Tolonen *et al*. (2001) showed that ephemeropterans and trichopterans were characteristic of the shallow littoral zone in a large lake system in eastern Finland.

Even though there are evident faunal patterns resulting from the alteration of lake surface areas, the taxon-specific optima for lake depth were all quite similar (Table 2). Nevertheless, ephemeropterans had the highest depth optima and *Dasyhelea*-type ceratopogonids the lowest (Table 2). However, it does appear that within the taxa examined, the influence of surface area is more important than that of depth.

General remarks

Results from this study provide some clear evidence of the indicator value of the sedimentary remains of ceratopogonids, ephemeropterans, trichopterans and oribatids (Table 4). However, since the number of the specimens examined remained low due to the scarcity of the taxa, substantially more research is still needed to clearly pinpoint the indicator value of these taxa. Additional surface sediment samples and increased counting sums together with supplementary limnological measurements could further support the indicator potential of these taxa. Other observations of habitat characteristics would also be beneficial, such as vegetation type. For example, Tolonen *et al*. (2003) showed that the abundances of ephemeropterans and trichopterans were significantly affected by macrophytes, because ephemeropterans were positively associated with vegetation density and trichopterans were most abundant at intermediate densities. Vegetation patterns can also be important factors behind oribatid and ceratopogonid abundances (Solhøy 2001, Brooks *et al*. 2007). Taphonomic effects, such as selective offshore transport in larger lakes, may also influence the presence or absence of different taxa in combined chironomid and macroremain-based reconstructions, with low nonchironomid counting sums.

One of the main limitations of the zoological macroremain analysis is the difficulty in fossil taxonomy, since many important body parts that are used in identification of intact specimens are lacking in fossils, which inevitability leads to the use of lower taxonomy. There are currently 80 ceratopogonid, 54 ephemeropteran and over 200 trichopteran and watermite species in Finland (Olsen *et al*. 1999) that live in lentic, lotic and terrestrial environments, and thus probably the most important future goal in development of the use of remains is an improvement in fossil taxonomy (if possible). Oribatid and trichopteran analyses, although requiring abundant sample material, are potentially very useful

Table 4. Synthesis of the indicator value of the taxa examined, based on the dataset of 80 lakes in Finland.

	Bezzia	*Dasyhelea*	Ephemeroptera	Trichoptera	Oribatida
Hypolimnetic oxygen	elevated	reduced	–	–	elevated
Climate	warm	cool	warm	warm	warm
Lake size	–	–	small	–	small
Nutrient conditions	oligotrophy	–	–	–	oligotrophy
pH	–	mild acidity	–	–	–

palaeolimnological methods, due to advances in preparation and identification techniques (Solem & Birks 2000, Solhøy & Solhøy 2000, Elias 2001, Solhøy 2001). Additionally, there are great uncertainties in trying to apply modern species ecology to fossil assemblages where lower taxonomic resolution must be used, due to the different taxonomy and the subsequent clumping of taxon-specific ecological data. If the taxonomic resolution could be increased, most likely the taxon correlations with some environmental variables would improve. Nevertheless, even with the current low taxonomic resolution the value in understanding the environmental requirements of the taxa examined in palaeolimnology is high, because they occur constantly or are sometimes abundant in downcore studies (T. Luoto unpubl. data). The taxa examined were missing from the surface sediments of this study in only four of the lakes. Additionally, the use of the zoological macroremain analysis instead of contemporary ecological data in optimum and tolerance assessments prevents any errors from possibly occurring due to the use of different methods.

Conclusions

Late-winter hypolimnetic oxygen and climatic variables were the most important factors influencing the occurrence and abundance of lentic ceratopogonids, ephemeropterans, trichopterans and oribatids in lakes in Finland. *Bezzia*-type ceratopogonids are indicators of elevated hypolimnetic oxygen conditions, warm climates and oligotrophy, while *Dasyhelea*-type ceratopogonids are indicators of low hypolimnetic oxygen conditions, cool climates and mildly acidic lakes. Ephemeropterans, trichopterans and oribatids indicated warm climatic conditions and oribatids were also indicative of small oligotrophic lakes and elevated oxygen conditions. The results and interpretations of this assessment may be useful in downcore palaeolimnological studies and in evaluations of lake ecosystems for the purpose of lake management and restoration projects, because the fauna examined provides a valuable supplementary proxy. This study also demonstrates the potential use of the studied zoological macroremains as an additional component in chironomid-based studies. However, substantially more research is still needed to fully exploit the fossil communities of freshwaters in palaeoecology.

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