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Fossil midge larvae (Diptera: Chironomidae) as quantitative indicators of late-winter hypolimnetic oxygen in southern Finland: a calibration model, case studies and potentialities

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We examined the relationship between fossil chironomid assemblages and environmental variables in 30 lakes in southern Finland with particular attention to hypolimnetic oxygen. Ordination techniques (DCA, CCAs) and Monte Carlo permutation tests were used to identify the most important parameters controlling the chironomid distributions. Based on the λ_1:λ_2 ratios of the variables, the greatest potential for quantitative inferences was with hypolimnetic oxygen ($\lambda_1:\lambda_2 = 0.767$). Therefore, inference models for past late-winter hypolimnetic oxygen were developed using weighted-averaging partial least squares (WA-PLS) techniques. The best model used one WA-PLS component, with a cross-validated coefficient of determination (r^2_{jack}) of 0.72 and a root-mean-squared error of prediction (RMSEP) of 2.351 mg l^{-1}. The model was tested on two short-core sediment sequences. The results indicated that quantitative estimations of hypolimnetic oxygen changes provide a useful tool for palaeolimnology and lake management in assessments of lake ecosystems, and in restoration projects in southern Finland.

Introduction

Understanding of past environments provides essential information for studies on current ecosystems and environmental problems (Smol 1992, Huntley 1996, Vincent and Pienitz 1996). Larvae of non-biting midges (Insecta: Diptera: Chironomidae) are especially well adapted to the needs of palaeolimnology, since they can be considered as stenotopic, ubiquitous, abundant, identifiable, species-rich, complementary and sensitive (Brooks *et al*. 2007). Fossil chironomids (sclerotized chitinous head capsules) have been used, for instance, in studies on the palaeoclimate (reviewed in Brooks 2006) and as indicators of lake productivity, eutrophication and hypolimnetic oxygen (reviewed in Brodersen and Quinlan 2006).

Oxygen is a necessary requirement for aquatic organisms having aerobic respiration, and seasonal and spatial changes in oxygen availability affect their life strategies, distribution, behaviour and interactions with other organisms (Davis 1975). Low dissolved oxygen (DO) conditions in the hypolimnion enhance internal phosphorus loading and may release toxic chemicals from the sediments (Auer *et al*. 1993, Sondergaard *et al*. 2001). The DO is influenced by the duration of ice cover, lake morphometry, lake productivity, catchment properties (soils) and temperature, and thus palaeolimnological indicators of oxygenation may provide valuable clues to water-column mixing, water depth, the trophic conditions of a lake and climate (Cohen 2003).

Chironomid metabolism is directly affected by dissolved oxygen and egg development slows considerably in low oxygen conditions (Pinder 1992). Oligotrophic lakes with well-oxygenated conditions are usually chironomid-species rich, but only a few of these species are also high in abundance, while eutrophic, poorly-oxygenated lakes are inhabited by only a few, but abundantly appearing chironomid species, such as *Chironomus plumosus*. No chironomids occur in permanently anoxic conditions (Bryce and Hobart 1972, Kansanen 1985). The hypolimnetic oxygen conditions particularly affect profundal chironomids, while littoral species are not as directly influenced, and thus during long periods of anoxia assemblages may become dominated by littoral taxa (Hofmann 1986, 1998, Kansanen 1986, Walker *et al*. 1993, Lindegaard 1995, Itkonen *et al*. 1999, Clerk *et al*. 2000).

In an assessment of the pollution history of lake Vanajavesi, southern Finland, Kansanen (1985) established a succession from an oligotrophic *Micropsectra–Monodiamesa* community to a eutrophic *Chironomus anthracinus* and finally a *Chironomus plumosus* community. Likewise, Salonen *et al*. (1993) showed that in Enäjärvi, a lake in southern Finland, sewage loading from the municipality of Nummela led to a dominance of profundal-living *Chironomus plumosus* as eutrophication and oxygen consumption in the lake increased. Granados and Toro (2000) interpreted from lake sediments in central Spain that the recent reduction of *Chironomus* had been caused by the warming climate, since the length of the ice-cover period is associated with oxygen depletion, which is a key factor especially regulating *Chironomus* abundance in the lake. Brodersen *et al*. (2008) showed that the link between temperature and respiration physiology is one of the most important biological mechanisms enabling the use of midges as temperature and climate indicators.

Oxygen consumption is most intense at the sediment–water interface, and a decline in oxygen concentration with depth is especially likely to occur when ice develops (Wetzel 2001). In low oxygen conditions some chironomids enter a summer diapause or aestivation (Armitage 1995). However, certain species from the tribe Chironomini (known as blood-worms, e.g. *Chironomus plumosus*) are even able to tolerate temporary anoxia due to the ability to accumulate glycogen and degrade it from anaerobic metabolism. Brodersen *et al*. (2004) proposed a classification for chironomid species based on their oxy-regulatory capacity using an experimental approach and showed that typical taxa of cold, oligotrophic lakes also favoured well-oxygenated conditions. In Ontario, Canada, Quinlan *et al*. (1998) presented chironomid-based inference models for past hypolimnetic anoxia, while Little and Smol (2001) and Quinlan and Smol (2001a) developed chironomid-based models for late summer hypolimnetic oxygen that gave valuable information on changes in the oxygen conditions of lakes in the area. Later, Quinlan and Smol (2002) interpreted long-term oxygen changes using chironomids in the same area, finding that in general, present oxygen levels were similar to natural, pre-industrial ones. Ilyashuk *et al*. (2005) applied the calibration data set of Quinlan and Smol (2001a) to infer Holocene oxygen changes in the Kola Peninsula, Russia. The results provided evidence that the model was able to reconstruct general trends in hypolimnetic oxygen content, although it was developed outside the geographical region of the study site. The authors speculated that after a lowering of the lake level ca. 7000 cal. yr BP, weakened thermal stratification of the lake led to improved hypolimnetic oxygen conditions.

To understand anthropogenic effects on aquatic ecosystems, it is of utmost importance to know the pre-disturbance conditions. Chironomid analysis provides an excellent tool for palaeolimnological interpretations, and when combined with other proxies it offers detailed information on the environmental history of lakes. In Finland, nearly 90% of the population lives in the southern parts of the country. This has led to marked culturally induced ecosystem changes in southern Finland, while many lakes in northern parts have remained pristine. Luoto (2007) demonstrated that chironomid distribution in northern Finland was predominantly controlled by temperature, but in southern Finland other environmental factors were also important.

This geographical difference is most likely human-induced, although no detailed explanation has thus far been provided. Therefore, we examined the distribution and abundance of chironomids in 30 shallow lakes in southern Finland to identify the factors underlying the patterns. We particularly focused on hypolimnetic oxygen, which together with nutrients appears to have had a key role in many previous chironomid-based reconstructions from southern Finland (Kansanen 1985, Salonen *et al*. 1993, Itkonen and Olander 1997, Itkonen *et al*. 1999, Meriläinen *et al*. 2000, 2001, 2003, Hynynen *et al*. 2004). We used late-winter hypolimnetic oxygen measurements, because the lowest oxygen levels usually occur during the late winter in Finland. We aim to develop a new quantitative tool for lake management evaluations and for palaeolimnological studies in southern Finland. Using multivariate ordination, regression and calibration techniques, the capability of a chironomid-based late-winter hypolimnetic oxygen inference model introduced in this paper is assessed and applied in two case studies. Additionally, the ease of applicability of the model in lake management evaluations is discussed.

Material and methods

Study area and sites

The study area is located in southern Finland, ranging from 60°13´ to 63°05´N and from 22°00´ to 30°13´E (Fig. 1). The vegetation in the catchments of the 30 lakes in the data set consists of boreal coniferous forests, underlain by Precambrian granitic bedrock and typically having a thin soil layer. Some of the lakes are located in urban areas: lake 19 is a small pond in Vuosaari (a borough of Helsinki), lakes 25 and 27 are in the city centre of Mikkeli, lake 29 is located between the cities of Tuusula and Järvenpää, and lake 30 is located in the city of Naantali. The lakes are generally shallow and represent different environmental conditions (Table 1). The altitude of the lakes varies from 11 to 134 m above sea level (a.s.l.) and the range in mean T_{Jul} ranges from 15.9 to 17.0 °C (Table 1). The open-water season lasts ca. 6–7 months, usually from May to November depending on the year (Kuusisto 1986). In general, the study area is influenced by human activity, mainly by infrastructure, forestry and agriculture, although some sites have remained close to their pristine state.

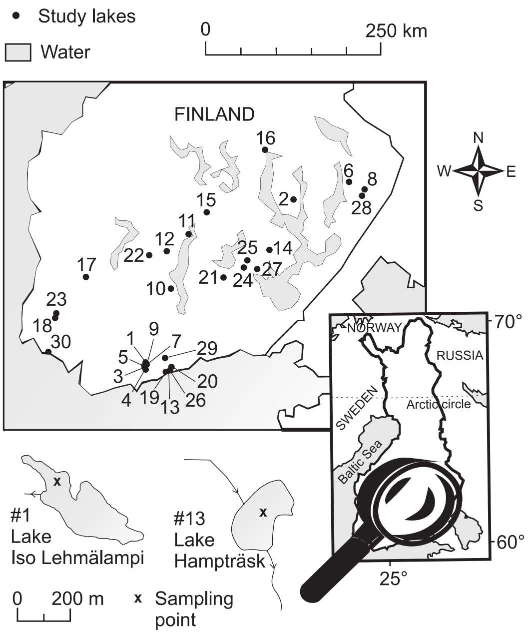

Fig. **1**. Location of the 30 study lakes in southern Finland and sampling points within the two lakes used for reconstruction.

The two lakes for case studies were chosen to represent both ends of the studied oxygen gradient. The environmental history of the lakes was previously well studied and the chironomid stratigraphies are also available (Luoto *et al*. 2008, Nevalainen *et al*. 2008). The first case study lake, Hampträsk (lake 13 in the calibration set, 60°17´N, 25°15´E), is located in a lowland area in the municipality of Sipoo and has suffered from enhanced nutrient input from the catchment due to historical and modern cultivation. The present summer total phosphorus (TP) is 58 μg l^{-1} and summer total nitrogen (TN) is 1123 μg l^{-1} (Nevalainen and Sarmaja-Korjonen 2008). The lake is known to have experienced oxygen depletion and winter fish kills during the harsh winter of 2002 (Ekholm 2007). The other case-study lake, Iso Lehmälampi (lake 1 in the calibration set, 60°20´N, 24°36´E), is situated in the municipality of Vihti and it lies in an upland area. The lake is naturally acidic (Korhola and Tikkanen 1991, Sarmaja-Korjonen and Alhonen 1999, Sarmaja-Korjonen 2001), but experienced a repeated major pH decrease in the 1980s leading to a value below 5.0 (Verta *et al*. 1990). Since then, the lake has recovered and the pH presently ranges between 5.1 and 5.8 (Nevalainen and Sarmaja-Korjonen 2008).

Field and laboratory methods

Surface sediment samples (topmost 0–1 cm), representing recent few years of sedimentation, were obtained with a Limnos-type gravity corer (Kansanen *et al*. 1991) between February and April 2005. The samples were placed in small plastic bags for storage in a coldroom at 4 °C. Limnological measurements (Table 1) were taken *in situ* during the collection of the sediment samples. Single measurements were performed with an Orion Model 1230 pH/mV/ORP/conductivity/dissolved oxygen/salinity/temperature meter before sediment sampling to avoid the resulting disturbance of the water column. The oxygen concentration was recorded from the hypolimnion, ca. 0.5 m from the bottom, and conductivity and pH from the epilimnion. The Orion dissolved oxygen meter calculated the oxygen concentration on the basis of the known relation-

Table 1. Location and characteristics of the 30 study lakes in southern Finland. The Mean T_{Jul} represents mean July air temperatures and the oxygen is measured from the hypolimnion during late winter.

Lake no.	Lat. (°N)	Long. (°E)	Elevation (m a.s.l)	Area (km^2)	Mean T_{Jul} (°C)	Oxygen (mg l^{-1})	Sampling depth (m)	pH	Conduct. (μS cm^{-1})
1	60.20	24.36	91.7	0.051	16.42	18.1	4.1	5.4	17
2	62.31	28.24	119.3	0.156	16.39	11.6	2.5	9.3	29
3	60.19	24.35	92.7	0.063	16.41	11.4	4.1	4.8	17
4	60.18	24.36	76.7	0.027	16.48	11.1	4.4	5.1	18
5	60.19	24.35	97.3	0.011	16.39	11.0	4.2	4.6	16
6	62.38	29.55	85.9	0.011	16.51	9.4	3.5	8.0	8
7	60.20	24.38	73.7	0.137	16.52	8.0	1.5	5.8	28
8	62.33	30.13	121.9	0.201	16.31	8.0	1.5	7.0	33
9	60.20	24.37	89.5	0.009	16.43	6.6	5.9	4.4	31
10	61.17	25.16	130.0	0.024	15.94	6.3	3.8	6.0	15
11	62.04	25.32	133.2	0.020	16.15	6.0	1.5	5.7	22
12	61.48	24.56	134.1	0.058	16.31	5.5	4.7	6.7	98
13	60.17	25.15	20.3	0.038	16.81	5.4	2.4	6.3	45
14	61.52	27.37	112.2	0.105	16.29	5.0	2.0	6.3	47
15	62.21	25.58	111.1	0.016	16.28	3.6	2.5	6.0	30
16	63.05	27.44	110.5	0.035	16.70	3.2	4.5	6.5	95
17	61.26	22.54	88.8	0.024	16.09	2.2	2.0	6.3	38
18	61.04	22.12	63.0	0.018	16.43	2.2	1.8	6.2	97
19	60.13	25.08	14.6	0.014	16.66	2.1	1.6	7.3	128
20	60.20	25.11	37.3	0.005	17.05	1.7	5.4	6.2	37
21	61.26	26.36	99.5	0.007	16.69	1.6	4.2	6.6	225
22	61.44	24.36	124.4	0.030	16.2	1.5	3.5	6.2	43
23	60.58	22.02	44.3	0.032	16.26	1.4	1.0	5.6	53
24	61.38	27.00	126.4	0.018	16.28	1.0	3.8	6.4	86
25	61.41	27.14	91.1	0.079	16.31	1.0	1.0	6.6	240
26	60.20	25.09	24.0	0.013	16.79	1.0	1.0	7.2	58
27	61.40	27.19	76.6	0.020	16.39	1.0	3.8	6.7	100
28	62.28	30.13	110.4	0.022	16.28	0.8	3.0	6.7	58
29	60.26	25.03	37.8	6.000	17.05	0.5	9.0	7.3	300
30	60.27	22.00	11.3	0.024	16.72	0.5	2.0	6.6	312
Mean			84.1	0.24	16.46	5.0	3.2	6.3	77
Median			91.1	0.02	16.40	3.4	3.3	6.3	44
Min.			11.3	0.01	15.94	0.5	1.0	4.4	8
Max.			134.1	6.00	17.05	18.1	9.0	9.3	312

ship between oxygen solubility, temperature and total atmospheric pressure. The oxygen meter has a resolution of 0.01 mg l^{-1} and an accuracy of ±0.5% of the measured value ±1 digit within an ambient temperature range of 5 to 30 °C. The Orion MSR™ (Minimum Stir Requirement) DO probe is a stable probe with very low oxygen consumption and zero current at zero oxygen concentration. The mean T_{Jul} was estimated using a geographical information system (GIS)-based method. The temperature data were provided by the Finnish Meteorological Institute and were based on the 1971–2000 climate normals, which take into account all Finnish meteorological data (S. Kultti pers. comm.).

Two short downcore sediment sequences (lake Hampträsk = 46 cm and lake Iso Lehmälampi = 24 cm) were cored through ice in February 2005, using a Limnos-type gravity corer (Kansanen *et al.* 1991). The water depth at the coring point in lake Hampträsk was 242 cm and in lake Iso Lehmälampi 412 cm. Both sediment sequences consisted of homogenous fine-detritus gyttja. The cores were sheared at 1-cm intervals in the field and the subsamples were placed in plastic bags for storage in a cold room.

The samples for chironomid analysis were prepared by applying standard methods (Brooks *et al.* 2007). The sediment was treated with heated 10% KOH for ca. 15 minutes and sieved through a 100-μm mesh. The residue was examined with a Bogorov counting chamber or a Petri dish under a stereomicroscope (ca. 25× magnification). Chironomid head capsules were extracted with fine forceps, mounted permanently in Euparal® on microscope slides and identified to the highest taxonomic resolution possible under a light microscope (400× magnification).

A minimum of 100 chironomid head capsules were identified from each sample, which exceeds the criteria for the minimum counting sum (40–50 head capsules) recommended for fossil chironomid analysis (e.g. Heiri and Lotter 2001, Larocque 2001, Quinlan and Smol 2001b). When the minimum counting sum is increased to about 100, the reliability of the results also significantly increases (Heiri and Lotter 2001). Identification was mainly based on the identification guides of Wiederholm (1983) and Brooks *et al.* (2007). Additionally, Heiri *et al.* (2004) was used in the identification of the Tanytarsini and Rieradevall and Brooks (2001) for the Tanypodinae larvae. The nomenclature follows that of Brooks *et al.* (2007).

Data analysis

Data analyses were performed using relative chironomid abundances. A detrended correspondence analysis (DCA) was used to explore patterns in the distribution of chironomid taxa in southern Finland and was run with detrending by segments. DCA is an indirect ordination method that summarizes the variation in species assemblages along the DCA axes (ter Braak 2003). A canonical correspondence analysis (CCA) was used to explore relationships between the chironomid assemblages and various environmental variables. CCA is a direct gradient technique that can be used to identify environmental variables that are related to the species assemblages (ter Braak 2003). When CCAs were run with only one environmental variable at a time, the statistical significance of each variable (surface area, mean T_{Jul}, sampling depth, pH, hypolimnetic oxygen and conductivity) was tested with a Monte Carlo permutation test (499 unrestricted permutations). Variables were considered significant if the permutation test value was significant at $P \leq 0.05$. 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 cumulative variance in the species data. Explanatory variables with high λ_1:λ_2 ratios have potential for quantitative inference models. The ordinations (DCA and CCAs) were performed using the program CANOCO, ver. 4.52 (ter Braak 2003).

A chironomid-based inference model for late-winter hypolimnetic oxygen was developed using weighted-averaging partial least squares (WA-PLS) methods (ter Braak and Juggins 1993) in the program C2, ver. 1.5.0 (Juggins 2007). Additionally, partial least squares (PLS), weighted averaging (WA) and modern analogue technique (MAT) models were compared with the WA-PLS model to explore the model type having best performance. The optimal number of WA-PLS components included in the transfer function was assessed using leave-one-out cross-validation. Additional components were considered useful if they gave a reduction in the prediction error of at least 5% (ter Braak & Juggins 1993, Birks 1998). The hypolimnetic oxygen reconstructions were evaluated using four different approaches (Birks *et al*. 1990, Birks 1998, Bigler *et al*. 2002, Velle *et al*. 2005): (1) by calculating the proportion of taxa from each fossil assemblage that was represented in the modern calibration set (lack-of-fit ≤ 95%), (2) by examining the squared residual distance (square residual length, SqRL) of the modern and fossil passive samples in a CCA with hypolimnetic oxygen as the sole constraining variable (lack-of-fit ≥ 10% of the extreme values in the modern calibration set), (3) by testing whether the samples have good modern analogues (MAT) (lack-of-fit ≥ 5% chord distance), and (4) by comparing the modern measured hypolimnetic oxygen values with the topmost inferred values.

Results and discussion

Chironomids

From the surface sediment samples of the 30 lakes, a total of 3461 chironomid head capsules were counted and 93 taxa were identified. The most common taxa, with the highest mean abundances, were *Psectrocladius (P.) sordidellus* type (7.2%), *Procladius* (7.0%), *Tanytarsus mendax* type (6.2%), *Zalutschia zalutschicola* type (5.9%), *Ablabesmyia monilis* type (5.5%) and *Chironomus anthracinus* type (4.6%). The highest maximum abundance (Table 2) was observed for *Psectrocladius (P.) sordidellus* type (58.7%), followed by *Zalutschia zalutschicola* type (43.9%), *Procladius* (38.6%), *Corynoneura lobata* type (29.7%), *Tanytarsus mendax* type (23.1%) and *Chironomus plumosus* type (20.8%). *Procladius* and *Ablabesmyia monilis* type occurred in 29 lakes, while none of the taxa were found in all the lakes. Overall, the taxa are typical of the fauna of lakes in Finland (Nyman *et al*. 2005, Paasivirta 2007).

Model development

Temperature is known to have a major effect on chironomid distributions, and many chironomid-based temperature inference models have been developed, such as those for northern Europe by Olander *et al*. (1999), Brooks and Birks (2001, 2004), Larocque *et al*. (2001), Seppä *et al*. (2002) and Luoto (2009). However, it has remained unclear whether chironomids respond to temperature directly through physiological temperature tolerances or indirectly through changes in the lake habitat (Brodersen *et al*. 2008). In warmer climatic conditions, limnological factors can have a dominant influence, such as lake trophic status (e.g. Brodersen & Lindegaard 1999, Brooks *et al*. 2001). Few studies have previously been performed on chironomids as palaeo-oxygen indicators (e.g. Brodin 1982, Walker *et al*. 1993), but several studies more recently carried out in Canada have led to the development of oxygen inference models (Quinlan and Smol 1998, 2001a, Little and Smol 2001).

Because the DCA in this study yielded gradient lengths of 2.0 (axis 1) and 1.9 (axis 2) standard deviation units (SD), numerical methods based on a unimodal response model were considered the most appropriate (Birks 1998). The environmental characteristics of the lakes varied as follows: hypolimnetic oxygen 0.5–18.1 mg l^{-1}, sampling depth 1–9 m, pH 4.4–9.3 and conductivity 8–312 μS cm^{-1} (Table 1). The CCAs showed that among the variables, hypolimnetic oxygen, conductivity, and mean T_{Jul} were significantly related to the chironomid data ($P \leq 0.05$; Table 3 and Fig. 2), and the best correlation was observed with late-winter hypolimnetic oxygen (λ_1:λ_2 = 0.767). According to ter Braak (2003), environmental variables with high λ_1:λ_2 ratios in constrained CCAs may be useful for inference models. In this study, therefore, a chironomid-based hypolimnetic oxygen inference model was developed from the data.

Taxa with > 3 occurrences and abundance > 1% in any lake were included in the inference model, following Weckström *et al*. (1997) and Korhola *et al*. (2002). After the species deletion, 63 of the total 93 taxa remained in the model. Only with DCA axes gradient lengths of less than 1.5 SD or greater than 4.0 SD, are either linear or unimodal methods, respectively, strongly recommended (ter Braak 2003). Thus, PLS, WA, WA-PLS and MAT models were compared to find out the model type having the best performance. The best model that had the highest r^2 and lowest RMSEP, mean and maximum biases was developed with WA-PLS techniques. Also the WA models had favourable performance statis-

Table 2. The most common chironomids from the surface sediments of 30 lakes in southern Finland and their codes in numerical analyses, occurrences, maximum and mean abundances, Hill's (1973) N2 diversity index and estimated optima and tolerances (weighted-averaging) for late-winter hypolimnetic oxygen (mg l^{-1}).

	Code	Occ.	Max.	Mean	N2	Opt.	Tol.
Einfeldia pagana type	Einf pag	10	7.0	1.2	7.4	1.9	1.7
Glyptotendipes pallens type	Glyp pal	12	12.3	1.4	6.1	2.1	1.9
Cricotopus cylindraceus type	Cric cyl	9	5.9	0.8	7.4	2.3	1.8
Polypedilum sordens type	Poly sor	9	3.8	0.5	6.6	2.4	2.4
Corynoneura lobata type	Cory lob	10	29.7	1.6	2.8	2.5	1.8
Parachironomus varus type	Parc var	9	3.4	0.4	6.5	2.5	1.8
Cricotopus undif.	Cricind	13	3.4	0.7	10.1	2.7	2.3
Paratanytarsus penicillatus type	Part pen	8	4.3	0.5	6.3	2.8	3.5
Sergentia coracina type	Serg cor	6	6.8	0.5	4.3	2.8	2.2
Endochironomus impar type	Endo imp	12	12.4	1.3	6.5	2.8	1.9
Paratanytarsus austriacus type	Part aus	9	3.6	0.5	7.4	2.9	2.9
Psectrocladius (M.) barbatipes type	Psec bar	10	6.0	0.8	6.3	2.9	2.2
Nanocladius rectinervis type	Nano rec	13	3.0	0.7	10.4	3.0	3.9
Corynoneura scutellata type	Cory scu	15	5.8	1.2	10.5	3.1	3.0
Limnophyes	Limnind	12	8.7	1.3	8.1	3.1	2.1
Endochironomus albipennis type	Endo alb	10	3.5	0.7	8.5	3.4	3.4
Natarsia puncata type	Nata pun	10	5.9	0.6	6.0	3.6	2.9
Tanytarsus glabrescens type	Tany gla	16	17.1	2.4	9.4	3.6	3.5
Chironomus plumosus type	Chir plu	23	20.8	2.9	8.5	3.7	4.2
Cricotopus (I.) Intersectus type	Cric int	21	7.7	1.6	13.4	4.0	3.7
Paratanytarsus undif.	Partind	16	9.4	2.0	10.5	4.4	3.8
Cladopelma viridulum	Clad vir	25	7.8	1.9	16.7	4.6	4.2
Polypedilum nubeculosum type	Poly nuc	21	7.1	1.7	14.9	4.6	4.6
Stempellinella	Stepind	12	3.3	0.5	9.4	4.8	3.6
Procladius	Procind	29	38.6	7.0	17.0	4.8	4.6
Zalutschia mucronata type	Zalu muc	10	9.2	0.7	4.7	4.9	3.2
Pagastiella orophila	Paga oro	16	5.9	1.1	11.1	4.9	4.8
Tanytarsus mendax type	Tany men	27	23.1	6.2	20.6	5.0	4.6
Cladotanytarsus mancus type	Clat man	22	17.7	3.4	11.6	5.1	4.4
Zalutschia zalutschicola type	Zalu zal	22	43.9	5.9	7.3	5.2	4.5
Chironomus anthracinus type	Chir ant	26	13.1	4.6	19.2	5.2	4.7
Microtendipes pedellus type	Mict ped	23	11.5	2.8	15.4	5.4	4.3
Corynocera ambigua	Cory amb	7	5.8	0.7	5.6	5.4	4.3
Tanytarsus undif.	Tanyind	26	10.5	3.1	18.9	5.5	4.9
Tanytarsus pallidicornis type	Tany pal	25	12.4	2.9	16.1	5.6	5.1
Ablabesmyia monilis type	Abla mon	29	15.6	5.5	19.5	5.6	4.9
Psectrocladius (P.) sordidellus type	Psec sor	28	58.7	7.2	10.0	5.8	4.6
Dicrotendipes nervosus type	Dicr ner	26	12.1	3.2	18.4	5.8	4.8
Psectrocladius (Allopsectrocladius) type	Psecall	16	25.0	2.2	5.0	5.9	4.4
Tanytarsus chinyensis type	Tany chi	14	7.3	1.1	8.8	6.0	4.4
Pseudochironomus prasinatus type	Pseu pra	12	4.8	0.7	9.6	6.0	5.6
Tanytarsus lactescens type	Tany lac	13	4.7	0.8	8.2	6.1	4.2
Lauterborniella agrayloides type	Laut agr	10	4.9	0.6	7.8	6.1	4.2
Psectrocladius (M.) calcaratus type	Psec cal	5	2.5	0.2	4.3	7.2	3.8
Heterotrissocladius marcidus type	Hete mar	9	8.2	0.9	6.3	7.8	4.1
Psectrocladius (M.) septentrionalis type	Psec sep	12	14.7	1.7	5.9	10.6	4.5
Heterotanytarsus apicalis type	Hett api	8	9.9	1.1	3.2	12.2	4.6

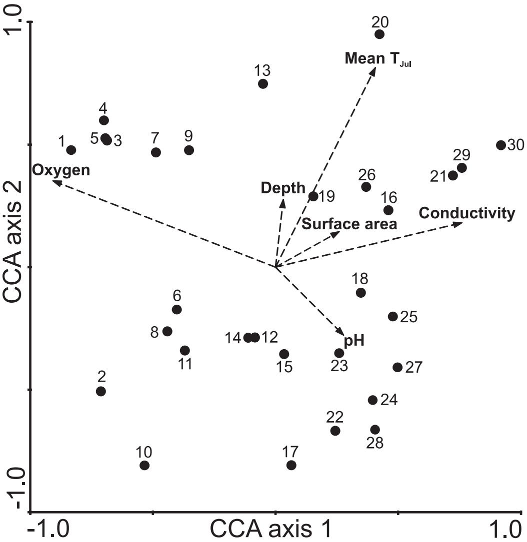

Fig. 2. CCA biplot of samples (lakes) and environmental variables, based on chironomid assemblages from the 30-lake set in southern Finland. The axes together explain 27.4% of the total variance.

tics. The PLS model suffered especially from decreased coefficient of determination (r^2_{jack}) and the MAT model was the most unsuitable one by all measures.

The best WA-PLS model was developed when only one WA-PLS component was used (leave-one-out cross-validation). A one-component WA-PLS model is the statistical equivalent model with WA with inverse deshrinking, having only a minor difference in their r^2 and RMSEP values. The root-mean-squared error of prediction (RMSEP) of the one-component WA-PLS model was 2.351 mg l^{-1} (an additional WA-PLS component increased the model RMSEP by 8.1%), the r^2_{jack} = 0.72, the mean bias 0.094 mg l^{-1} and the maximum bias 6.683 mg l^{-1} (Fig. 3a). The model appeared to predict late-winter hypolimnetic oxygen levels reasonably well and quite evenly within the observed oxygen gradient (Fig. 3a). The bias was illustrated as a fairly even distribution of residuals along the oxygen gradient (Fig. 3b), although one sample with anomalously high oxygen (lake 1) was found to be an outlier (*see* also Fig. 3a). The high value probably reflects supersaturation in the hypolimnion of this very acidic and almost ultraoligotrophic lake, but an error in the measurement can not be excluded. Nevertheless, all the samples were included in the model, because deleting the outlier reduced the performance statistics and did not change the outputs significantly. Additionally, there was a substantial plateau at a predicted value of ca. 4 mg l^{-1} from lakes with observed hypolimnetic oxygen of 0–8 mg l^{-1} (Fig. 3a). There is no particular relationship between these samples (lakes 3, 13, 14, 16, 17, 18, 19, 20 and 22) with reference to their environmental conditions (Table 1) or geographical distribution (Fig. 1). However, because there is relatively little change in the species assemblages at this portion of the gradient (Fig. 4), the taxon homogeneity may be the factor explaining the plateau of predicted values.

Table 3. Species environmental correlations, *P* values, cumulative variance of species data and λ_1:λ_2 ratios for the studied environmental variables based on the data set of 30 lakes in southern Finland.

	Species environment correlations	*P*	Cumulative % variance of species data	λ_1:λ_2
Oxygen	0.923	0.002	9.1	0.767
Conductivity	0.876	0.002	7.5	0.646
Mean T_{Jul}	0.817	0.002	6.7	0.616
Sampling depth	0.901	0.076	4.6	0.368
pH	0.841	0.150	4.2	0.332
Surface area	0.910	0.168	4.7	0.364

In the Canadian inference models for end-of-summer hypolimnetic oxygen, Quinlan and Smol (2001a) reported an r^2_{jack} of 0.56 and an RMSEP of 2.15 mg l^{-1}, while the best models of Little and Smol (2001) had an r^2_{jack} of 0.58. The better correlation in this study (r^2_{jack} = 0.72) is most likely due the fact that the largest gradient in the parameters that were measured is in DO, not in temperature. In the present dataset, the temperature gradient is only 1.1 °C, while in the other datasets for DO the temperature gradient is more than 5 °C. When the temperature gradient is larger, the significance of temperature is likely to increase. The present results already indicate that with such a short gradient, the temperature explains a high proportion of the variance. However, because the gradient in DO is as high as 17.6 mg l^{-1}, it has stronger influence on chironomids. Therefore, it may be presumed that the

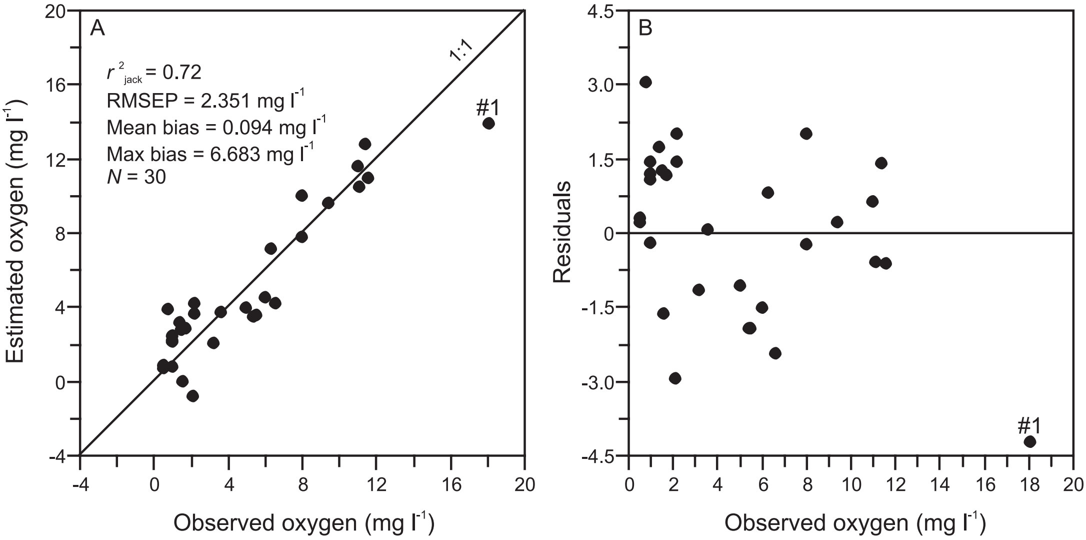

Fig. 3. (**a**) Relationship between chironomid-inferred and observed late-winter hypolimnetic oxygen, and (**b**) the residuals using a weighted-averaging partial least squares (WA-PLS) model. Sample #1 represents Iso Lehmälampi.

environmental factor that midges are responding to depends on scaling. As Brodersen *et al*. (2004, 2008) showed, temperature, metabolism and respiratory requirements are directly connected to each other and thus respiration physiology may be among the indirect causal responses and mechanisms making chironomids useful as climate indicators. It remains to be shown how large temperature changes we should expect before oxygen and climate in combination are the causal factors and how large climate changes should we expect before temperature eliminates the oxygen impact. The oxygen conditions can change under constant climate, but climate probably seldom changes without affecting oxygen conditions.

The comparison of the present inference model with the models of Quinlan and Smol (2001a) and Little and Smol (2001) is difficult and unsatisfactory, since they measure hypolimnetic oxygen levels during different seasons. Nevertheless, data on the minimal DO requirements of aquatic invertebrates is needed when studying low oxygen tolerances (Davis 1975), which in Finland usually occur during late winter. Winter oxygen depletion is especially common in shallow and productive ponds and lakes, where decomposition consumes a great deal of oxygen (Brönmark and Hansson 2005).

Response of taxa

The taxa having the strongest relationship with elevated late-winter hypolimnetic oxygen levels were *Heterotanytarsus apicalis* type, *Psectrocladius (M.) septentrionalis* type, *Heterotrissocladius marcidus* type and *Psectrocladius (M.) calcaratus* type (Table 2, Figs. 4 and 5). Additionally, *Lauterborniella agrayloides* type, *Tanytarsus lactescens* type, *Pseudochironomus prasinatus* type, *Tanytarsus chinyensis* type, *Psectrocladius (Allopsectrocladius)* type, *Dicrotendipes nervosus* type and *Psectrocladius (P.) sordidellus* type were more common in well-oxygenated lakes. The taxa associated with the lowest oxygen levels were *Einfeldia pagana* type, *Glyptotendipes pallens* type and *Cricotopus cylindraceus* type (Table 2, Figs. 4 and 5). In addition, *Polypedilum sordens* type, *Corynoneura lobata* type, *Parachironomus varus* type, *Cricotopus* undif., *Paratanytarsus penicillatus* type, *Sergentia coracina* type and *Endochironomus impar* type were identified as indicators of reduced late-winter hypolimnetic oxygen. Many of these taxa are large in body size, possess haemoglobin and/or live in tubes as sediment dwellers. These characteristics enable some species to withstand low hypolimnetic oxygen conditions (Int Panis *et al*. 1995). *Chironomus plumosus* type, a taxon

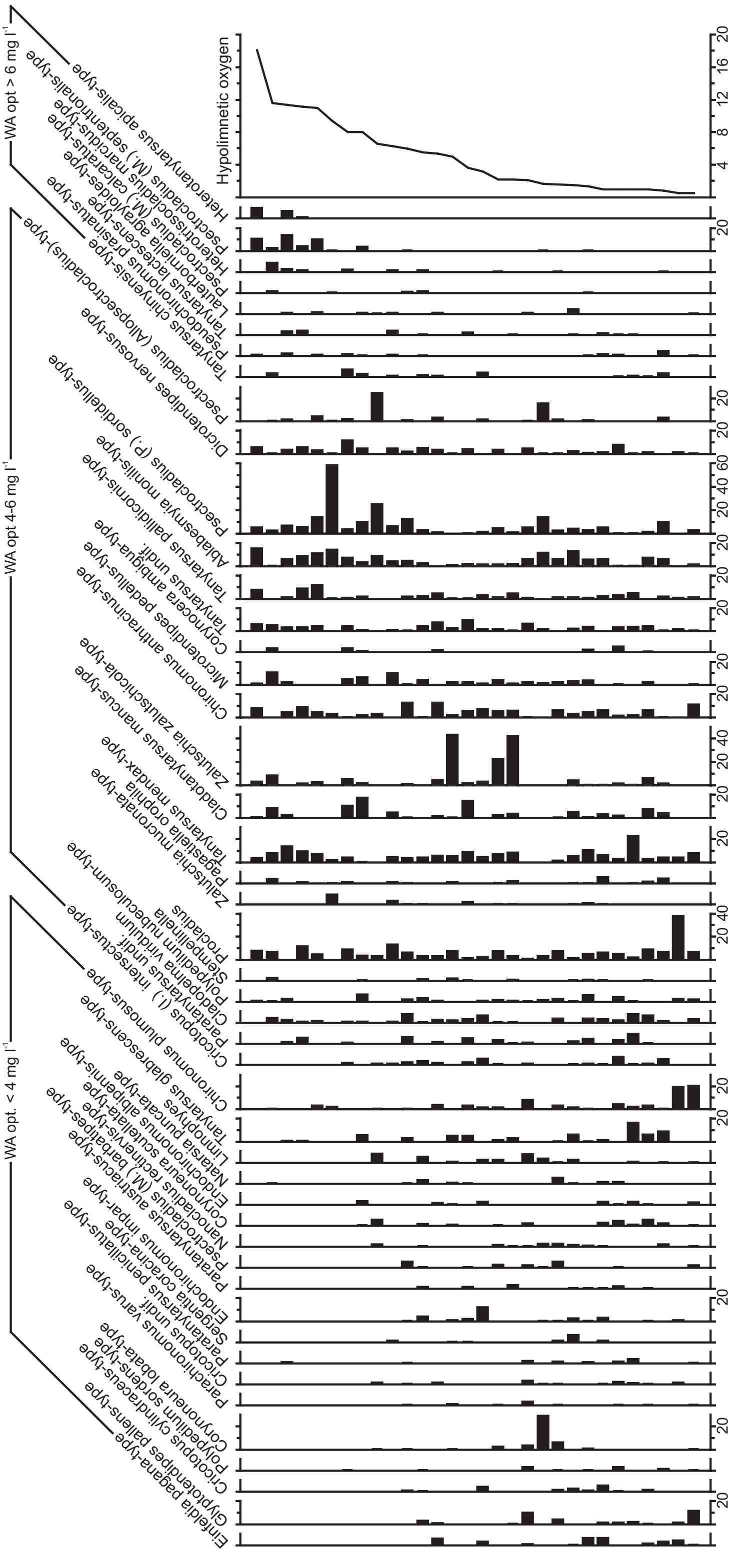

Fig. 4. Distribution of the most common chironomids in the 30 study lakes in southern Finland. The lakes are listed in order of their measured late-winter hypolimnetic oxygen content from the highest (top) to the lowest (bottom) and the taxa are ordered, based on their oxygen optimum from the lowest (left) to the highest (right).

well known to thrive in oxygen-deficient lakes (e.g. Wiederholm and Eriksson 1979, Kansanen 1985, Meriläinen *et al.* 2000), was also found to be indicative of low oxygen in this study (optimum 3.7 mg l^{-1}, tolerance 4.2 mg l^{-1}) (Table 2, Figs. 4 and 5).

The results of Little and Smol (2001), Quinlan and Smol (2001a) and Brodersen *et al.* (2004) confirm that *Heterotrissocladius marcidus* type, *Tanytarsus chinyensis* type, and *Psectrocladius (P.) sordidellus* type characterize high oxygen levels. However, some discrepancy exists between the present and previous data sets. Little and Smol (2001) reported *Sergentia* to be indicative of high oxygen conditions, but in this study, *Sergentia coracina* type was found to strongly indicate low oxygen levels (Table 2, Figs. 4 and 5). *Sergentia*, which is widely considered to be a mesotrophic taxon (e.g. Hynynen *et al.* 2004), possesses haemoglobin and can tolerate moderate oxygen depletion (Walker 1990), which points to it truly being an indicator of reduced oxygen conditions. It may also be that lake depths explain the discrepancy, because in the deep lakes in Canada *Sergentia* only survive at relatively high oxygen conditions, but in the shallow lakes in Finland it tolerates relatively poor conditions for shorter periods due to higher turbulence and epilimnetic productivity. However, the results of Quinlan and Smol (2001a) showed that *Sergentia* was an indicator of moderate oxygen depletion in Ontario, Canada, with highest abundances in hypolimnia with low 1-m-from-bottom oxygen concentrations, which is basically the same variable as being reconstructed in the present study. The comparison of taxa in these data sets is nevertheless complicated, because taxonomical differences exist between these geographically remotely located regions and the taxonomic resolutions in the studies are also different.

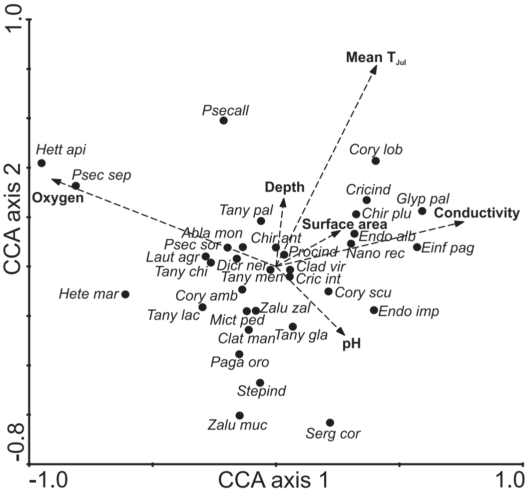

Fig. **5**. CCA biplot of species and environmental variables, based on the 30-lake set in southern Finland. The axes together explain 27.4% of the total variance.

Reconstructions

The performance of the chironomid-based late-winter hypolimnetic oxygen inference model was tested on two short-core sediment sequences from southern Finland. These lakes are limnologically different, representing meso-eutrophic (Hampträsk) and oligotrophic (Iso Lehmälampi) lake types. Detailed site descriptions, chronologies, sediment physical properties and microfossil assemblages of the lakes are presented in Luoto *et al.* (2008) and Nevalainen *et al.* (2008).

Reconstruction of the hypolimnetic oxygen levels in lake Hampträsk revealed that the 14th century was characterized by poor oxygen conditions (Fig. 6), possibly indicating that the lake was already nutrient rich at that time, as suggested by the presence of taxa associated with eutrophic lakes (e.g. *Glyptotendipes pallens* type and *Chironomus anthracinus* type). Oxygen levels increased during the 15th century. This coincided with an increasing chydorid (Chydoridae) ephippia content in the sediments of lake Hampträsk (Luoto *et al.* 2008), reflecting a shortened open-water period and harsh climatic conditions (Sarmaja-Korjonen 2003). The oxygen values decreased around 1500 AD, after which they increased again. This improvement in oxygen conditions occurred simultaneously with the onset of cooling during the Little Ice Age (LIA), as recorded in chironomid assemblages and the lowering of the organic content (loss-on-ignition, LOI) of the sediment in lake Hampträsk (Luoto *et al.* 2008). The LIA seems to be reflected in an increase in chironomid-inferred hypolimnetic oxygen levels, as they peaked twice, during the 16th and 17th centuries

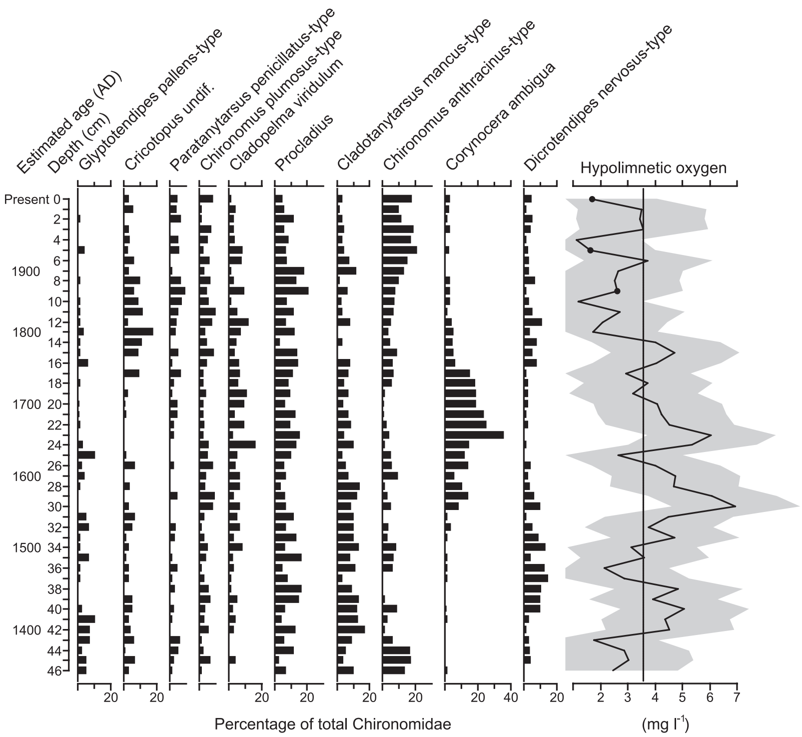

Fig. **6**. Relative abundances of the 10 most common chironomids and reconstructed late-winter hypolimnetic oxygen for the past 700 years from Hampträsk, southern Finland. The dashed line represents the mean inferred value (3.6 mg l^{-1}) and the grey area indicates the root-mean-squared error of prediction (RMSEP = 2.351 mg l^{-1}). Samples with 'good' fit to hypolimnetic oxygen are indicated by dots in the reconstruction curve. The age estimations are based on radiocarbon dates and on an applied time-depth model (Luoto *et al.* 2008).

(Fig. 6). Tiljander *et al*. (2003) noted from annually laminated lake sediments from southern Finland that during two periods, ca. 1580–1630 and 1650–1710 AD, a wetter and colder climate prevailed. The study of Luoto *et al*. (2008) also suggested that the Little Ice Age was not uniformly cold, as cold-indicating chironomids peaked at separate depths and chydorid ephippia had two maxima, which was consistent with the results of Tiljander *et al*. (2003).

The dominating chironomids during the LIA were *Tanytarsus lugens* type, *Micropsectra insignilobus* type and *Corynocera ambigua* (Luoto *et al*. 2008), which indicate cold climatic conditions (Luoto 2009). However, *T. lugens* type and *M. insignilobus* type are missing from the present calibration set for DO and thus they do not contribute to the oxygen reconstruction. This is because they have northern distributions (Luoto 2009), and they occur only in very low abundance in the DO dataset (southern Finland). However, if these taxa would contribute to the oxygen reconstruction they would probably increase the reconstructed values, since they are known to prefer deep and cold lakes with good hypolimnetic oxygen conditions. The cold climate episode of ca. 1700 AD is also presented in history books, as around 25% of the local population of Sipoo died in a famine (Rantanen and Kuvaja 1994). After the Little Ice Age, especially from the 19th century onwards, the oxygen conditions deteriorated (Fig. 6), most likely as a consequence of climate warming and induced nutrient enrichment in the lake (Luoto *et al*. 2008), as cultivation in the catchment increased.

In lake Iso Lehmälampi, the reconstruction revealed that good hypolimnetic oxygen conditions (> 11 mg l^{-1}) prevailed in late Holocene (Fig. 7). According to Nevalainen *et al*. (2008), the water level in lake Iso Lehmälampi lowered from ca. 400 AD onwards and reached its minimum just before the Medieval Warm Period (MWP), ca. 800–1000 AD. From ca. 1100 AD the inferred hypolimnetic oxygen levels increased, possibly due to an elevation of the water level and consequent change in late-winter oxygen conditions as a result of the enlarged volume of the lake (Fig. 7). However, this interpretation is in contrast to the results of Ilyashuk *et al*. (2005) who speculated that

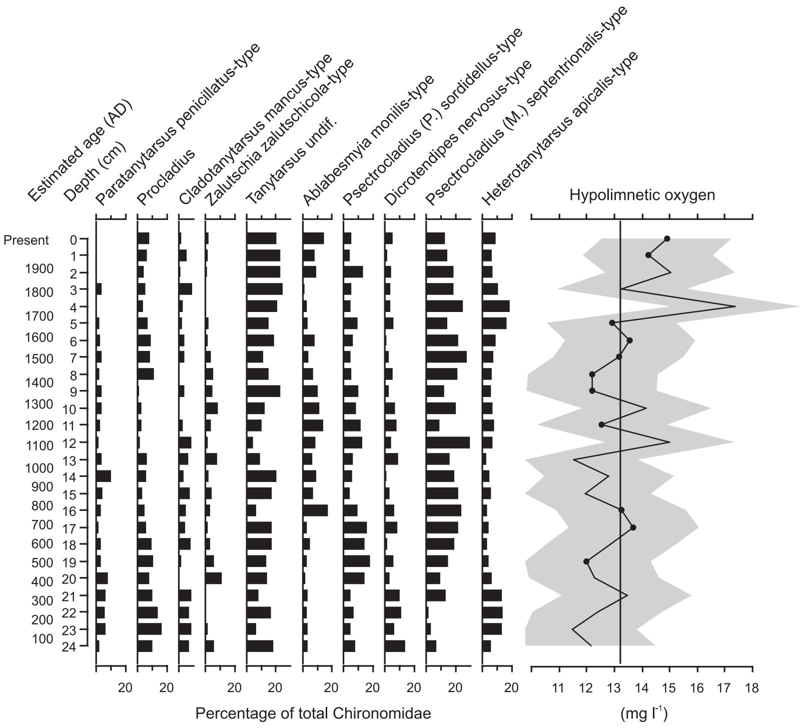

Fig. **7**. Relative abundances of the 10 most common chironomids and reconstructed late-winter hypolimnetic oxygen for the past 2000 years from lake Iso Lehmälampi, southern Finland. The dashed line represents the mean inferred value (13.2 mg l^{-1}) and the grey area indicates the root-mean-squared error of prediction (RMSEP = 2.351 mg l^{-1}). Samples with 'good' fit to hypolimnetic oxygen are indicated by dots in the reconstruction curve. The age estimations are based on radiocarbon dates and on an applied time-depth model (Nevalainen *et al.* 2008).

lowering of the lake level weakened the thermal stratification and led to improved hypolimnetic oxygen conditions in a lake in the Kola Peninsula, Russia. In lake Iso Lehmälampi, the oxygen levels experienced a new major increase around 1700 AD (Fig. 7), occurring simultaneously with the coldest period of the LIA in southern Finland indicated by Luoto *et al*. (2008). The elevated oxygen conditions were represented by increased abundance of *Heterotanytarsus apicalis* type and *Psectrocladius (M.) septentrionalis* type, which are taxa having the highest hypolimnetic oxygen optima in the present dataset (Table 2 and Fig. 4). After a short reduction ca. 1800 AD that was probably caused by the warming climate, the inferred hypolimnetic oxygen levels increased during the 20th century and have remained high until the present. This could reflect a reduction in the biological production of the lake caused by anthropogenic acidification (Verta *et al*. 1990). Although the lake has always been acidic and oligotrophic (Korhola and Tikkanen 1991), the additional reduction in biological production could have reflected as improved winter oxygen conditions because oxygen consumption under the ice decreased.

Both reconstructions seemed to give reasonable estimates for late-Holocene late-winter hypolimnetic oxygen conditions. The mean inferred value for lake Hampträsk was 3.6 mg l^{-1} and for lake Iso Lehmälampi 13.2 mg l^{-1} (dashed lines in Figs. 6 and 7), implying a correct reconstruction trend when compared with their known limnological conditions. The meso-eutrophic status of lake Hampträsk is illustrated as clearly lower oxygen levels than in oligotrophic lake Iso Lehmälampi, reflecting the relationship between oxygen and nutrient conditions. It should be noted, however, that it is difficult to separate the effects of DO and biological productivity (Sæther 1979). High productivity is often reflected in water properties as elevated conductivity, which in this study was negatively correlated with hypolimnetic oxygen (Figs. 2 and 5). Another important remark is that the inferences for lake Iso Lehmälampi may be less accurate, because the calibration model underestimates the hypolimnetic oxygen content of lake Iso Lehmälampi, representing lake 1 in the dataset (Fig. 3a) having also high residuals (Fig. 3b). This is most likely due to the anomalously high measured oxygen content, indicating supersaturation in the hypolimnion. However, the estimated value for lake Iso Lehmälampi may also be more accurate than the measured anomalous value.

The taxa in the fossil samples were relatively poorly represented in the training set and only seven of the samples showed 'good' fit to hypolimnetic oxygen in lake Hampträsk. The main reason for this is that the studied time period is mostly affected by the cold LIA and thus cold associated chironomids that are not included in the calibration dataset (warm lakes) were common (e.g. *Tanytarsus lugens* type, *Micropsectra insignilobus* type and *Constempellina brevicosta*) (Luoto *et al*. 2008). Additionally, the MAT results showed that only 12 of the fossil samples had a good modern analogue in lake Hampträsk. However, the CCA results (SqRL < 10%) showed 'good' fit to all of the samples in lake Hampträsk, but also in lake Iso Lehmälampi. In lake Iso Lehmälampi, the taxa in the fossil samples were poorly represented in 12 of the samples. The MAT results showed 'poor' fit to hypolimnetic oxygen in four of the samples. Based on these evaluations if the model infers hypolimnetic oxygen adequately, it seems that the reconstruction of lake Iso Lehmälampi is generally more accurate than that of lake Hampträsk. When considering all the goodness-of-fit assessments, 12 of the samples (0–2, 5–9, 11, 16, 17 and 19 cm) in lake Iso Lehmälampi had 'good' fit to hypolimnetic oxygen (Fig. 7), but in lake Hampträsk only three of the samples (0, 5 and 9 cm) had 'good' fit (Fig. 6). However, also the 'poor' fit samples may provide accurate estimations and the 'good' fit samples may provide erroneous estimations (Bigler *et al*. 2002). Both reconstructions showed underestimation in the topmost samples when compared to the modern measured values. In lake Hampträsk, the underestimation was 3.7 mg l^{-1} and in lake Iso Lehmälampi 3.2 mg l^{-1}. Nevertheless, the lower estimations appears to be logical, because lake Hampträsk is known to have experienced oxygen depletion during late winter (Ekholm 2007) and the measured value in lake Iso Lehmälampi is anomalously high.

Both reconstructions indicated that during cold climate events, especially in the LIA, late-winter hypolimnetic oxygen conditions improved. This could indicate the effect of decreased biological production in the lakes during cold climate periods, which led to reduced oxygen consumption (secondary production and decaying) and consequently enhanced oxygen conditions. The low productivity in the lakes and thus well-oxygenated conditions therefore have an overwhelming effect countering the lengthened ice-cover period (cold climate), which is known to cause oxygen depletion when wind exposure and turbulence are inhibited. This is also illustrated in the biostratigraphy of lake Hampträsk as during cold climate episodes when chydorid ephippia, which indicate a lengthened open-water season (Sarmaja-Korjonen 2003), increase at ca. 1400 AD and later during the LIA (Luoto *et al*. 2008). The chironomids also inferred an increase in oxygen levels (Fig. 6). In an agreement with the present results, Quinlan and Smol (2002) reported that most of the lakes they examined in Ontario, Canada, have recorded some decline in the hypolimnetic oxygen content as a possible consequence of recent climatic warming. However, in the both reconstructions of the present study the samples showed 'poor' fit to hypolimnetic oxygen during the LIA. This may be because the magnitude of temperature change overrode the effect of hypolimnetic oxygen on chironomid assemblages. This is characterized by the fact that taxa that are seldom observed even from the most oxidized shallow lakes in southern Finland, but are common in cold northern lakes, dominated during the LIA in lake Hampträsk (Luoto *et al*. 2008).

The reconstructions demonstrate that late-winter hypolimnetic oxygen can be estimated using the chironomid-based inference model developed in this study and that the changes were greater than the model RMSEP of 2.351 mg l^{-1}. The application of the model is most satisfactory when its results can be compared with other proxies that give estimates for the duration of the open-water season and nutrient status, which are important environmental factors regulating DO availability in the hypolimnion.

Implications for lake management

Lake sediment research is evidently important for modern lake management and restoration projects (Valpola 2006). Information from a comprehensive palaeolimnological study can be used to consider the goal and tools for a possible remediation process (Valpola and Salonen 2006). Oxygen depletion, which is often associated with eutrophication, is a serious lake management problem and can be considered as the greatest single threat to global freshwater resources (UNEP 1999, Smol 2002). Prolonged hypolimnetic oxygen depletion causes the elimination of fish and other biota from the deep water, and the release of orthophosphate from the sediments causes internal loading of phosphorus and thus increased eutrophication.

Chironomids have been shown to be an informative and cost-effective monitoring and assessment tool for the implementation of the Water Framework Directive of the European Union (Nyman and Korhola 2005). The performance statistics of the present chironomid-based late-winter hypolimnetic oxygen inference model and its application in two case study lakes indicate that it is able to provide reliable palaeo-oxygen estimates. Because lakes that receive anthropogenic sources of nutrients record decreases in DO (Quinlan and Smol 2002), the estimation of hypolimnetic oxygen changes provides a useful tool when assessing anthropogenic effects. The recent climate change is also a major concern in lake management. The combined use of chironomid-based oxygen and temperature inference models may help in interpreting chironomid responses to changes, as discussed by Quinlan *et al*. (1998). However, the use of chironomids to infer two parameters in the same lake increases the ambiguity, because it may not be certain which of the factors impacted the chironomid communities most.

Conclusions

This study revealed that late-winter hypolimnetic oxygen is strongly related to chironomid distributions in 30 lakes in southern Finland, and the development of a chironomid-based hypolimnetic oxygen inference model is therefore justified. Numerical analyses indicated that the developed model had favourable performance statistics and it was applied to two short-core sediment sequences. The inferences provided logical results, as both reconstructions adjusted well to the limnological changes known from their Late-Holocene history (e.g. eutrophication and acidification) and oxygen levels were at their highest during cold climate periods, e.g. the LIA. Besides productivity (and temperature), the reconstruction of lake Iso Lehmälampi also indicated that water depth may be an important regulator of late-winter hypolimnetic oxygen conditions.

The model can provide valuable information on past hypolimnetic oxygen conditions and may serve as a tool for lake management when setting guidelines for preserving or restoring water quality. Additionally, the model can be useful in other multi-proxy palaeolimnological studies as it provides a rare proxy for winter limnological conditions.

In the future, the oxygen inference model could be further developed with additional lakes in the data set. Calculation of the Anoxia Factor (AF), which would require substantially more time and resources, could improve the reliability of measurements as the duration of oxygen stress would be included (Little and Smol 2001), and a standard method for hypolimnetic DO concentration calculations (of stratified lakes) would be an asset (*see* e.g. Bella 1970, Cornett and Rigler 1980, Quinlan *et al*. 2005 for details).

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