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Implications for the use of sedimentary invertebrate communities to infer past presence of fish

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ABSTRACT

Key-words: *Chaoborus, Chironomidae, Cladocera, community structure, paleolimnology, predation*

We investigated surface sediment assemblages of invertebrates from nine shallow lakes in southern Finland and assessed the relationship between invertebrate assemblages and fish status at local scale for the purpose of paleolimnological food-web studies. Invertebrate-based cluster analysis separated the fish-free lakes into their own group and the results also showed a strong and statistically significant relationship between fish status and faunal sedimentary assemblages. The present results from the local data set indicate good potential for developing quantitative invertebrate-based paleolimnological fish status models in the future. However, for the implementation of the models substantially more lakes with different fish status need to be examined that the effect of fish predation on invertebrate communities can be separated from other limnological forcing mechanisms.

RÉSUMÉ

Implications sur l'usage des communautés d'invertébrés sédimentaires pour inférer la présence passée de poisson

Mots-clés : *Chaoborus, Chironomidae, Cladocera, structure de communauté, paléolimnologie, prédation*

Nous avons étudié les communautés d'invertébrés du sédiment de surface de neuf lacs peu profonds du sud de la Finlande et établi la relation entre les assemblages d'invertébrés et le statut piscicole à l'échelle locale dans le but d'études paléolimnologiques des réseaux trophiques. L'analyse de classification basée sur les invertébrés a séparé les lacs sans poissons en un groupe isolé et les résultats ont aussi montré une forte et statistiquement significative relation entre le statut piscicole et les assemblages de faune sédimentée. Ces résultats d'un jeu de données locales indiquent un bon potentiel futur pour le développement de modèles quantitatifs du statut piscicole ancien basés sur la paléolimnologie des invertébrés. Toutefois, l'implémentation des modèles demande bien plus de lacs étudiés de différents statuts piscicoles de façon à ce que l'effet de la prédation sur les communautés d'invertébrés puisse être séparé des autres mécanismes limnologiques de forçage.

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INTRODUCTION

Freshwater lakes are currently highly stressed by human influence, for example pollution, draining and biomanipulation (Brönmark and Hansson, 2002). The human impact has intensified in modern times but in many cases it has prevailed for many decades or even centuries. Therefore, changes in various external factors, such as in temperature and nutrients influencing limnological and ecological status of lakes have gained much attention among paleolimnologists (*e.g*. Lotter *et al.*, 1997, 1998; Jeppesen *et al.*, 2001a; Smol *et al.*, 2005; Smol and Douglas, 2007). Reconstructions of past internal changes in lakes and their food-web structures have been performed using fossil remains of aquatic organisms in lake sediments, mostly remains of phytoplankton (diatoms and chrysophytes), zooplankton and zoobenthos (Cladocera, Chironomidae, Chaoboridae) (*e.g*. Sarmaja-Korjonen, 2002; Salonen *et al.*, 2006; Luoto *et al.*, 2008). Since fish body parts do not commonly preserve as fossils in lake sediment (Patterson and Smith, 2001) their past presence have been be tracked indirectly *via* fossil assemblages of their prey organisms that preserve in the sediments (*e.g*. Kitchell and Kitchell, 1980; Nykänen *et al.*, 2006; Manca *et al.*, 2007).

The ecological role of fish in lake ecosystems is invaluable, because they affect the abundance and diversity of their prey organisms, such as planktonic and benthic Cladocera and Diptera larvae (Kornijów *et al.*, 2005; Vašek *et al.*, 2006; Davidson *et al.*, 2007) through top-down control (Vanni *et al.*, 1997). Fish are also significant due to their participation in internal loading and recycling of nutrients that may affect planktonic organisms (Horppila *et al.*, 1998). The major structuring effect of fish predation on their prey is due to size-selectivity that leads to the dominance of small species and removal of large ones, thus changing community structures (Brooks and Dodson, 1965). However, fish do not necessarily always prey on largest species, but the most visible (*e.g*. highly pigmented) ones. This visibility selection of fish may also cause changes in their prey communities (Zaret, 1972; Zaret and Kerfoot, 1975).

For studies on past fish stocks, Jeppesen *et al*. (1996) created the first quantitative paleolimnological reconstruction model using the relationship between cladoceran remains and planktivorous fish. Prior to this quantitative method, cladoceran assemblages and morphology had been used in many studies to identify past changes in fish stocks and predation (Kerfoot, 1974, 1981; Salo *et al.*, 1989). More recently, Jeppesen *et al.* (2002, 2003) showed that size and abundance of ephippia of some planktonic cladoceran species are related to fish abundance and can therefore be used as indicators for planktivorous fish stocks. Also, the well-preserved mandibles of *Chaoborus* (Chaoboridae) larvae have been used to infer changes in past fish populations, since *Chaoborus* occurs in fish-free lakes or in lakes with refugia (hypolimnion) against fish predation (Uutala, 1990; Sweetman and Smol, 2006; Luoto and Nevalainen, 2009).

As stated above, in previous studies fish presence has been inferred using a single group of organisms, mostly Cladocera or *Chaoborus*. However, Sweetman and Smol (2006) suggested that the use of multiple proxies, *i.e*. several faunal groups together, may improve the past fish inferences. Therefore, in order to test the relationship between local invertebrate communities and fish status, we investigated fossil invertebrate assemblages from surface sediments of nine shallow and limnologically diverse lakes with different fish status in southern Finland. We included and enumerated all identifiable fossil invertebrate taxa (Cladocera, Diptera, Ephemeroptera, Trichoptera, and Oribatida) in the surface sediment samples and analyzed statistically their incidence in relations to different environmental variables. Our main aim was to distinguish the local relationship between invertebrate taxa and fish status and to assess the potentialities of fossil invertebrate assemblages as indicators for presence or absence of fish in future paleolimnological studies.

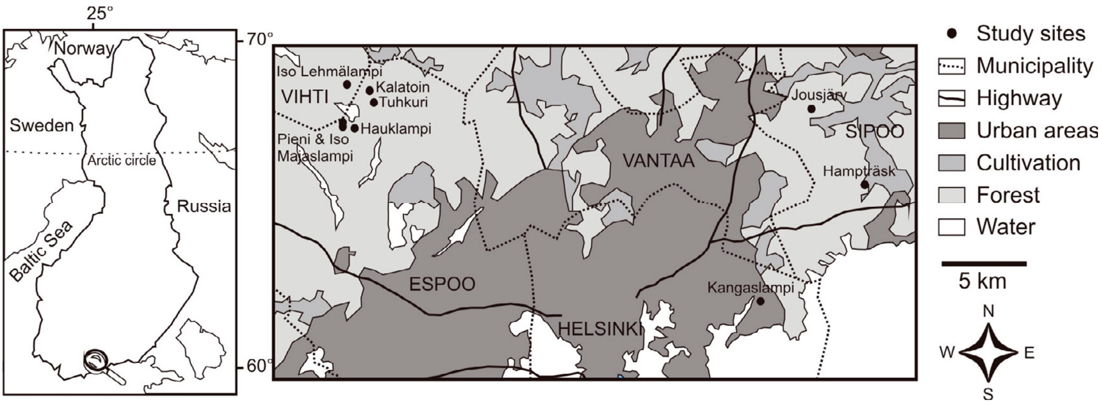

Figure 1
Distribution of the nine study lakes in southern Finland.

Figure 1
Situation des neufs lacs étudiés au sud de la Finlande.

Table I
Measured limnological variables (summer 2005) and fish status for the nine study lakes.

Tableau I
Variables limnologiques mesurées (été 2005) et statut piscicole des neuf lacs étudiés.

	Depth (m)	pH	Conductivity ($\mu s \cdot cm^{-1}$)	DO ($mg \cdot L^{-1}$)	Color ($Pt \cdot mg \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	Fish
1. Kalatoin (KAL)	5.9	4.5	26	8.9	100	24	526	No
2. Hauklampi (HAU)	4.4	5.0	19	10.5	25	<10	140	Yes
3. Iso Majaslampi (IML)	4.1	4.8	19	9.6	30	<10	201	Yes
4. Pieni Majaslampi (PML)	4.2	4.9	16	9.7	25	<10	191	Yes
5. Iso Lehmälampi (ILL)	4.1	5.1	17	8.9	30	25	382	Yes
6. Tuhkuri (TUH)	1.5	5.6	25	10.4	50	31	768	Yes
7. Jousjärv (JOU)	5.4	6.2	34	7.6	125	25	624	No
8. Hampträsk (HAM)	2.4	6.6	49	9.2	75	58	1123	Yes
9. Kangaslampi (KAN)	1.6	7.2	157	9.0	37.5	76	813	No

MATERIAL AND METHODS

> SITES

The nine study lakes are distributed in close proximity to each other in southern Finland, near the Helsinki district (Figure 1). They are all enclosed basins without any major inlets or outlets. The limnological variables: pH, conductivity, dissolved oxygen (DO), color, total phospohorous (TP) and total nitrogen (TN) of the lakes were highly variable ranging from acidic to circum neutral, from clear to brown-water, and from oligo- to eutrophic (Table I). The fish status of the lakes also varied, six of the lakes are currently inhabited by fish and three lakes are without permanent fish populations (Table I).

Lake Kalatoin is a fish-free, very acidic and dystrophic small (about 1 ha) lake. *Sphagnum* mosses and *Carex* spp. dominate the shores and the submerged vegetation consists of aquatic mosses and *Nuphar lutea*. The lake is surrounded by a small catchment with bog vegetation and several bedrock outcrops. Lakes Hauklampi (area 2.7 ha), Iso Majaslampi (area 6.3 ha), and Pieni Majaslampi (area about 1 ha) are located close to each other. They are acidic and oligotrophic lakes, with small and nutrient-poor catchments. Patches of mire, fractured bedrock outcrops, and *Pinus* forests cover the catchments, shores are inhabited by *Carex* spp. and *Sphagnum* mosses, and the aquatic macrophyte zone consists only of *Nymphaea alba*. Due to acidification (Kauppi *et al.*, 1990) the natural fish populations, consisting mainly of European perch (*Perca fluviatilis*), died out in the lakes in the 1980s. The lakes experienced a chemical recovery process during the 1990s. In 2002, perch were introduced into these lakes (35–120 per hectare), aiming to re-establish the populations (Nyberg *et al.*, 2010). Lake Iso Lehmälampi (area about 3 ha) is also an acidic and oligotrophic upland lake. The catchment is characterized by the presence of bedrock outcrops and paludified areas. The lake also experienced severe acidification in the 1980s and the succeeding recovery process in the 1990s. The lake became almost fish-free during the acidification (Verta *et al.*, 1990), but has since exhibited several introductions of whitefish (*Coregonus lavaretus*), roach (*Rutilus rutilus*), and perch (Nyberg *et al.*, 2010). *Sphagnum* mosses, *Carex* spp., and submerged *Nuphar lutea* and *Nymphaea alba* dominate the littoral and the shoreline. The rocky and paludified catchment is rather small and poor in nutrients. Lake Tuhkuri is an oligotrophic forest lake with surface area of 13.7 ha and it maintains a successful fish stock consisting mainly of perch. Several houses and summer houses are situated on its shores and the catchment is characterized by mixed forest (*Picea*, *Pinus*, *Betula*) and some bedrock outcrops. The aquatic vegetation consists of *Phragmites australis*, *Nuphar lutea*, and aquatic mosses. Jousjärv is a fish-free small (about 0.5 ha), dystrophic lake with paludified shores; *Sphagnum* mosses and *Carex* spp. cover the entire shoreline. Small hills with bedrock outcrops characterize the catchment. The paludified area surrounding the lake is ditched. Lake Hampträsk (area about 4 ha) is a shallow and meso-eutrophic with human influence on its surroundings and fish, mostly perch, inhabiting the basin. There are fields and houses near the lake and the paludified western shore is ditched. The aquatic vegetation consists mainly of *Phragmites australis* and *Nuphar lutea*. Lake Kangaslampi is a fish-free shallow, small (about 1 ha), eutrophic, and disturbed lake of natural origin with very high human impact. The lake is located in a suburb of Helsinki near the Baltic Sea within a densely inhabited area. The catchment is mostly built up, except for a small park. During the summer, algal blooms dominate the aquatic environment and thus oxygen depletion during the winter and summer is inevitable.

> SAMPLING AND SAMPLE ANALYSES

Surface sediments (topmost 1–2 cm) from the nine study lakes were sampled with a Limnos gravity corer through ice in February and March 2005. Limnological measurements were taken from the epilimnion during summer in 2005 with an Orion Model 1230 pH/mV/ORP/conductivity/dissolved oxygen/salinity/temperature meter (Thermo Fisher Scientific, Waltham, MA, USA). In the laboratory the sediment samples were prepared for fossil Cladocera analyses according to methods described in Szeroczyńska and Sarmaja-Korjonen (2007) and for fossil chironomid and zoological macroremain analysis according to methods described in Brooks *et al.* (2007) and Luoto (2009). For Cladocera analysis the sediment samples were heated and stirred in 10% KOH on a hot plate for approximately 20 minutes. After the heating, samples were sieved through a 44-μm mesh and mounted in glycerine jelly on preparation slides. A minimum of 200 carapaces of the Chydoridae and all the other identifiable cladoceran remains were identified and counted under a light microscope and the most abundant body part was chosen for each species to represent its individuals. The proportional abundances for all cladoceran species were calculated from the sum of total individuals. For zoological macroremain analysis (*i.e*. Diptera, Ephemeroptera, Trichoptera, Oribatida) the sediment samples were treated with warm 10% KOH for 10–20 minutes and sieved through a 100-μm mesh. The residue was examined under a stereomicroscope and remains were handpicked with fine forceps for exact identification and enumeration. The remains were mounted on Euparal, the identification was performed under a light microscope and a minimum of 100 chironomid headcapsules and other identifiable zoological macroremains were counted. The proportional abundances of all invertebrates were calculated from the total number of counted individuals so that the Cladocera and Diptera were considered separately in the abundance calculation, but proportions of other invertebrate groups (Ephemeroptera, Trichoptera, Oribatida) were calculated from the total sum of Diptera and other invertebrates. The proportional abundances of these separate faunal groups were used in the statistical analyses.

> DATA ANALYSES

Two-way indicator species analysis (TWINSPAN) was used as a divisive technique to classify the nine lakes according to their invertebrate assemblages with pseudospecies cut levels set to 0, 2, 5, 10 and 20%. Relative species abundances were used with square-root transformation of species data and downweighting of rare species to stabilize the variance. The TWINSPAN was performed using the program WinTWINS, version 2.3 (Hill and Šmilauer, 2005).

Detrended correspondence analysis (DCA) was applied to choose between linear- or unimodal-based methods in further numerical analyses by estimating the lengths of compositional gradients (DCA axes 1 and 2). The DCA was run with detrending by segments and using square-root transformation of species data and downweighting of rare species. No transformations were performed for environmental data. Of the environmental variables, fish presence was entered as nominal variables, using binary codes (value 0 when absent and 1 when present). DCA is an indirect ordination method that summarizes the variation in species assemblages along the DCA axes (ter Braak, 2003). Redundancy analysis (RDA) was chosen (lengths of DCA gradients < 2) to explore relationships between invertebrate assemblages and environmental variables. RDA is a linear technique that can be used to identify environmental variables that are strongly related to the species assemblages. The RDAs were performed using correlation matrix, square-root transformation of species data, and downweighting of rare species and run with only one environmental variable at a time to test the statistical significance of the variables. The significance of each variable was tested with a Monte Carlo permutation test (999 unrestricted permutations) and 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 cumulative variance in the species data. Explanatory variables that have high λ_1:λ_2 ratios can be used in quantitative inference models. For RDA ordination the analysis was run with the most significant environmental variables (fish, DO, color, TP). The DCAs and RDAs were performed using the program CANOCO, version 4.52 (ter Braak, 2003).

RESULTS

A total of 98 taxa, mostly Cladocera (39) and Chironomidae (54), were identified from the surface sediment samples of the nine lakes (Table II). Taxa occurring in all the lakes included *Bosmina* (*Eubosmina*) (Bosminidae), *Alona affinis*, *Alona guttata* var. *tuberculata*, *Alonella excisa*, *Alonella nana,* and *Chydorus sphaericus* s.l. (Chydoridae) of the Cladocera and *Ablabesmyia monilis*-type, *Procladius*, *Psectrocladius* (*Allopsectrocladius*), and *Psectrocladius sordidellus*-type of the Chironomidae. Other widely occurring taxa (in eight lakes) were cladoceran *Acroperus harpae* and chironomids *Chironomus anthracinus*-type and *Dicrotendipes pulsus*-type. In addition to Cladocera and Chironomidae, dipteran taxa *Chaoborus flavicans* (in four lakes) and *Bezzia*-type (Ceratopogonidae) (in seven lakes) were found in the samples (Table II). The remains of Ephemeroptera (in five lakes), Oribatida (in five lakes) and Trichoptera (in Hampträsk) were also found (Table II).

The TWINSPAN classified the lakes according to their fauna into two separate groups; lakes with fish (Hampträsk, Tuhkuri, Hauklampi, Iso Majaslampi, Pieni Majaslampi, and Iso Lehmälampi) and those without fish (Kalatoin, Jousjärvi, Kangaslampi) (Figure 2). The analysis also pointed the indicator taxa of particular lake groups or lakes. Indicator species for fish-free lakes were cladocerans *Alona guttata* var. *tuberculata*, *Alonella excisa*, *Alonella nana*, *Chydorus sphaericus* s.l., and chironomids *Psectrocladius sordidellus*-type, *Psectrocladius* (*Allopsectrocladius*), and *Corynoneura lobata*-type. Chaoborid *Chaoborus flavicans*, Ephemeroptera, and Oribatida were also included as indicative taxa of fish-free lakes.

The DCA axes showed gradient lengths < 2 ($\lambda_1 = 1.693$, $\lambda_2 = 1.204$) and therefore the RDA was chosen to study the species-environment linkages. The limnological variables included

Table II
Relative abundance of the invertebrate taxa in the surface sediments of the nine lakes. The abbreviations of the lakes are described in Table I. The codes for the individual taxa are used in Figures 2 and 3.

Tableau II
Abondance relative des taxons d'invertébrés dans les sédiments de surface des neuf lacs. Les abréviations des lacs sont dans le tableau I. Le code de chaque taxon est utilisé dans les figures 2 et 3.

	Code	KAL	HAU	IML	PML	ILL	TUH	JOU	HAM	KAN
CLADOCERA										
Leptodora kindti	*Lepto kin*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Sida crystallina	*Sida cry*	0.3	0.0	0.3	0.0	0.0	2.2	0.7	0.0	0.0
Diaphanosoma brachyurum	*Diap bra*	0.3	0.0	0.0	0.3	0.0	0.0	1.1	0.0	0.0
Holopedium gibberum	*Holo gib*	0.3	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Daphnia **spp.**	*Daphind*	0.0	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.0
Cariodaphnia **spp.**	*Ceriind*	1.6	0.3	0.0	1.3	0.2	0.3	0.4	0.0	0.4
Simocephalus **spp.**	*Simoind*	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Bosmina (Eubosmina)	*Bosmeub*	23.5	29.7	24.1	26.3	49.0	61.1	9.5	50.4	12.3
Bosmina longirostris	*Bosm lon*	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Ophryoxus gracilis	*Ophr gra*	0.0	0.3	0.3	0.0	0.5	1.1	0.0	0.0	0.0
Streblocerus serricaudatus	*Stre ser*	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Draphanotrix dentata	*Drep den*	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Acantholeberis curvirostris	*Acan cur*	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Eurycercus lamellatus	*Eury lam*	0.0	0.0	1.0	0.3	0.5	0.6	0.7	0.0	0.0
Camptocercus rectirostris	*Camp rec*	0.6	0.3	0.0	2.3	0.7	0.8	0.7	0.7	0.0
Acroperus harpae	*Acro har*	11.4	4.8	9.9	15.8	10.0	4.5	7.8	2.6	0.0
Alonopsis elongata	*Alon elo*	0.0	0.3	0.7	3.3	0.5	0.0	0.0	0.0	0.0
Alona affinis	*Alon aff*	1.0	6.5	8.5	13.2	6.5	10.1	0.7	1.5	0.4
Alona guadrangularis	*Alon gua*	0.0	0.0	1.0	0.0	0.2	0.3	0.0	1.1	0.0
Alona guttata	*Alon gut*	1.6	0.3	0.7	0.3	0.0	0.8	0.0	0.2	0.4
Alona guttata **var.** ***tuberculata***	*Alon tub*	1.6	2.6	3.4	1.3	2.1	0.8	5.3	0.4	7.4
Alona rectangula	*Alon rec*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	3.7
Alona rustica	*Alon rus*	2.2	14.8	7.8	5.3	3.0	0.5	0.0	0.0	0.0
Alona intermedia	*Alon int*	0.0	0.0	0.7	0.0	0.5	0.2	1.1	1.1	0.0
Graptoleberis testudinaria	*Grap tes*	1.0	0.0	0.0	0.0	0.0	0.6	1.1	1.1	4.9
Alonella excisa	*Alon exc*	21.9	35.5	11.9	14.5	2.8	0.9	13.8	1.7	8.2
Alonella nana	*Alon nan*	21.3	3.2	25.9	11.5	20.0	9.0	24.7	18.6	17.3
Alonella exigua	*Alon exi*	1.6	0.0	0.0	0.0	0.0	0.0	1.1	0.7	0.0
Disparalona rostrata	*Disp ros*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Pleuroxus truncatus	*Pleu tru*	0.3	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0
Peuroxus laevis	*Pleu lae*	0.3	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Pleuroxus trigonellus	*Pleu tri*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Chydorus sphaericus **s.l.**	*Chyd sph*	7.0	1.3	2.0	3.0	1.4	2.3	17.0	17.2	44.9
Chydorus piger	*Chyd pig*	0.0	0.0	0.3	1.0	2.1	0.6	0.0	0.0	0.0
Chydorus latus	*Chyd lat*	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Rhyncothalona falcata	*Rhyn fal*	0.0	0.0	0.7	0.0	0.2	0.3	0.0	0.0	0.0
Unapertura latens	*Unap lat*	1.0	0.0	0.3	0.0	0.0	0.0	0.4	0.0	0.0
Kurzia latissima	*Kurz lat*	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polyphemus pediculus	*Poly ped*	1.0	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.0
CHIRONOMIDAE										
Ablabesmyia monilis**-type**	*Abla mon*	9.6	9.2	6.6	11.6	15.6	8.1	11.9	0.7	6.9
Procladius	*Procind*	3.8	12.3	0.7	5.4	8.5	9.7	4.0	3.6	1.7
Corynoneura lobata**-type**	*Cory lob*	1.0	0.0	0.0	0.0	0.0	0.0	29.7	0.7	4.3
Corynoneura scutellata**-type**	*Cory scu*	5.8	0.0	0.7	0.0	0.0	0.0	0.0	0.0	2.6
Cricotopus bicinctus**-type**	*Cric bic*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0
Cricotopus (Isocladius) **sp.**	*Criciso*	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Cricotopus **undif.**	*Cricind*	1.9	0.0	0.0	0.0	0.0	0.0	1.0	2.2	3.4
Cricotopus **undif.**	*Cric int*	1.9	0.8	0.7	0.0	0.7	2.4	0.0	2.2	1.7
Heterotrissocladius marcidus**-type**	*Hete mar*	0.0	2.3	2.9	0.0	0.0	2.4	0.0	0.0	0.0
Heterotanytarsus apicalis**-type**	*Hett api*	0.0	1.5	7.4	0.8	9.9	0.8	0.0	0.0	0.0
Limnophyes	*Limnind*	8.7	0.0	0.0	0.0	0.0	0.0	4.0	0.0	7.8

Table II
Continued.

Tableau II
Suite.

	Code	KAL	HAU	IML	PML	ILL	TUH	JOU	HAM	KAN
Nanocladius rectinervis-type	*Nano rec*	2.9	0.0	0.0	0.0	0.7	0.0	3.0	0.0	0.9
Mesocricotopus thienemannii	*Mesc thi*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0
Orthocladius sp.	*Orthind1*	0.0	0.0	0.0	0.0	0.0	0.0	4.0	3.6	1.7
Psectrocladius (Allopsectrocladius)	*Psecall*	25.0	0.8	2.2	4.7	0.7	2.4	15.8	3.6	0.9
Psectrocladius septentrionalis-type	*Psec sep*	0.0	4.6	14.7	10.9	11.3	0.8	1.0	0.0	0.0
Psectrocladius sordidellus-type	*Psec sor*	26.0	6.2	7.4	14.7	5.7	4.0	14.9	1.5	6.0
Psectrocladius barbatipes-type	*Psec bar*	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	2.6
Micropsectra pallidula-type	*Micr pal*	0.0	0.0	0.0	0.8	0.0	0.8	0.0	0.7	0.0
Constempellina brevicosta	*Cons bre*	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0
Paratanytarsus penicillatus-type	*Part pen*	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	2.6
Paratanytarsus undif.	*Partind*	0.0	6.2	2.2	0.8	0.0	1.6	0.0	2.2	1.7
Paracladopelma	*Pardind*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Paratanytarsus austriacus-type	*Part aus*	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Zalutschia zalutschicola	*Zalu zal*	0.0	2.3	0.0	3.1	3.5	5.6	0.0	5.1	0.0
Chironomus anthracinus-type	*Chir ant*	3.8	9.2	5.1	5.4	8.5	0.8	0.0	13.1	0.9
Chironomus plumosus-type	*Chir plu*	1.0	0.8	0.7	3.9	0.7	0.0	0.0	4.4	8.6
Cladopelma lateralis-type	*Clad lat*	0.0	1.5	2.9	2.3	0.7	1.6	0.0	2.9	0.0
Dicrotendipes pulsus-type	*Dicr pul*	0.0	6.2	4.4	3.9	6.4	12.1	1.0	4.4	5.2
Einfeldia pagana-type	*Einf pag*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.6	1.7
Endochironomus albipennis-type	*Endo alb*	0.0	0.8	0.0	0.0	0.0	0.0	0.0	2.2	0.0
Endochironomus tendens-type	*Endo ten*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
Endochironomus impar-type	*Endo imp*	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
Glyptotendipes pallens-type	*Glyp pal*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	10.3
Lauterborniella agrayloides-type	*Laut agr*	1.0	0.0	1.5	2.3	0.0	0.0	0.0	1.5	1.7
Microtendipes pedellus-type	*Mict ped*	0.0	0.8	2.9	0.0	1.4	5.6	2.0	0.7	2.6
Omisus caledonicus	*Omis cal*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
Pagastiella orophila	*Paga oro*	0.0	1.5	0.0	0.0	0.7	1.6	0.0	0.0	0.0
Phaenopsectra flavipes-type	*Phae fla*	1.9	0.8	0.0	1.6	0.0	1.6	0.0	0.0	0.0
Parachironomus varus-type	*Parc var*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4
Paratendipes albimanus-type	*Patd alb*	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polypedilum sordens-type	*Poly sor*	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.7	3.4
Polypedilum nubeculosum-type	*Poly nuc*	0.0	0.8	2.9	0.8	1.4	0.0	2.0	1.5	0.9
Pseudochironomus prasinatus-type	*Pseu pra*	0.0	0.0	2.9	1.6	1.4	2.4	0.0	0.0	0.0
Cladotanytarsus mancus-type	*Clat man*	0.0	0.8	2.9	0.0	1.4	11.3	0.0	2.2	0.0
Corynocera ambigua	*Cory amb*	0.0	0.0	0.0	0.0	0.0	4.0	0.0	2.2	0.0
Rheotanytarsus	*Rhetind*	0.0	0.8	0.0	0.0	0.0	0.0	2.0	2.2	4.3
Stempellinella	*Stepind*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Tanytarsus undif.	*Tanyind*	0.0	3.8	3.7	4.7	6.4	4.8	2.0	8.0	6.9
Tanytarsus lactescens-type	*Tany lac*	0.0	4.6	3.7	0.0	0.0	0.8	0.0	0.0	0.0
Tanytarsus mendax-type	*Tany men*	0.0	10.0	14.0	7.8	4.3	4.8	0.0	6.6	0.0
Tanytarsus pallidicornis-type	*Tany pal*	0.0	9.2	2.2	12.4	8.5	1.6	0.0	5.1	1.7
Tanytarsus glabrescens-type	*Tany gla*	0.0	1.5	1.5	0.8	0.0	0.0	0.0	0.0	0.0
Tanytarsus chinyensis-type	*Tany chi*	0.0	0.8	0.0	0.0	0.7	7.3	0.0	1.5	0.0
CHAOBORIDAE										
Chaoborus flavicans	*Chao fla*	10.2	0.0	0.0	0.0	0.0	0.0	48.7	1.4	0.8
CERATOPOGONIDAE										
Bezzia-type	*Bezzind*	0.8	0.8	0.7	0.0	2.0	3.7	1.3	0.0	1.5
EPHEMEROPTERA	*Epheind*	0.8	0.0	0.0	0.0	0.0	3.7	2.2	2.1	2.3
ORIBATIDA	*Oribind*	0.0	0.0	0.7	0.0	4.6	0.0	3.5	0.7	7.6
TRICOPTERA	*Tricind*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0
Total number of taxa		**39**	**41**	**48**	**37**	**41**	**51**	**43**	**54**	**43**

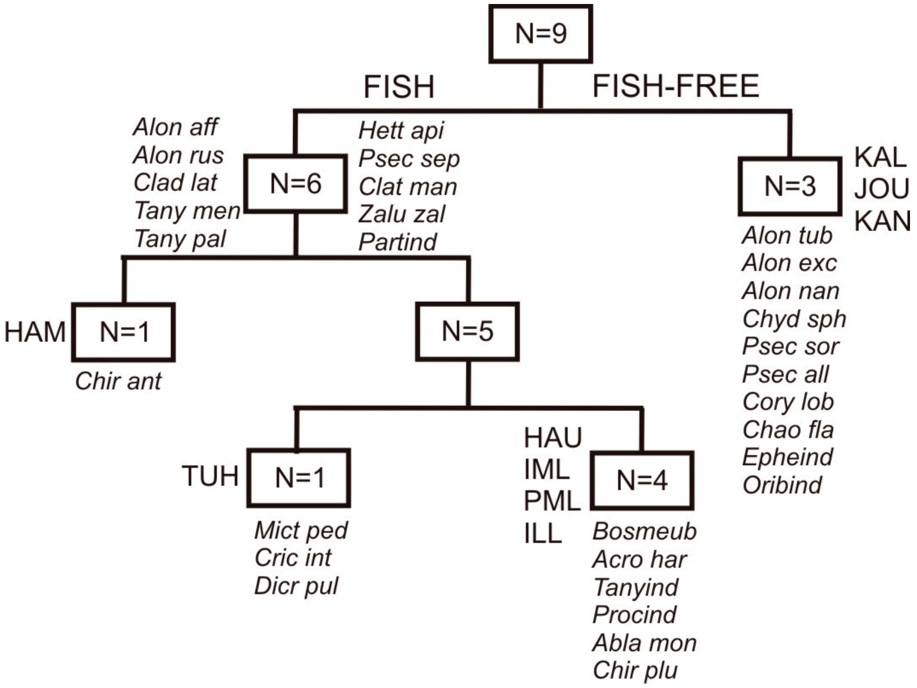

Figure 2
TWINSPAN classification of the study lakes according to their invertebrate assemblages and indicator species for each lake group. The abbreviations of the taxa are shown in Table II.

Figure 2
Classification TWINSPAN des lacs étudiés selon leurs assemblages d'invertébrés et espèces indicatrices pour chaque groupe de lacs.

Table III
RDA statistics for the tested environmental variables and invertebrate assemblages.

Tableau III
Statistiques RDA pour les variables environnementales testées et les assemblages d'invertébrés.

	$\lambda_1:\lambda_2$	*P*-value	Species-environment correlation	Cumulative variance %
Fish	1.832	0.001	0.969	37.0
pH	0.678	0.061	0.917	23.6
Conductivity	0.660	0.112	0.893	22.5
DO	1.266	0.001	0.887	29.5
Color	1.237	0.002	0.901	29.2
TP	0.688	0.050	0.924	24.0

in the RDAs were fish (presence or absence), pH, conductivity, DO, color and TP. The analysis showed that fish, DO, color and TP related significantly ($P \leq 0.05$) with the invertebrate assemblages (Table III). The assemblages were most strongly correlated with fish status ($\lambda_1:\lambda_2 = 1.832$, $P = 0.001$). In the RDA ordination for samples, taxa related to fish presence, *e.g. Cladopelma lateralis*-type, *Tanytarsus pallidicornis*-type, and *Chironomus anthracinus*-type had negative values for RDA axis 1 and low values for axis 2 (Figure 3). Of the environmental variables DO was related to fish presence, but taxa associated with high DO had negative values for both RDA axis (*e.g. Alona affinis*, *Alonopsis elongata*, *Psectrocladius sordidellus*-type, and *Heterotrissocladius apicalis*-type). At the opposite side of the ordination, taxa related to high water color and absence of fish, such as *Corynoneura lobata*-type, *Limnophyes*, *Nanocladius rectinervis*-type, *Chaoborus flavicans*, *Alonella excisa*, *Daphnia*, *Simocephalus*, and *Holopedium gibberum* had high values for RDA axis 1 and slightly

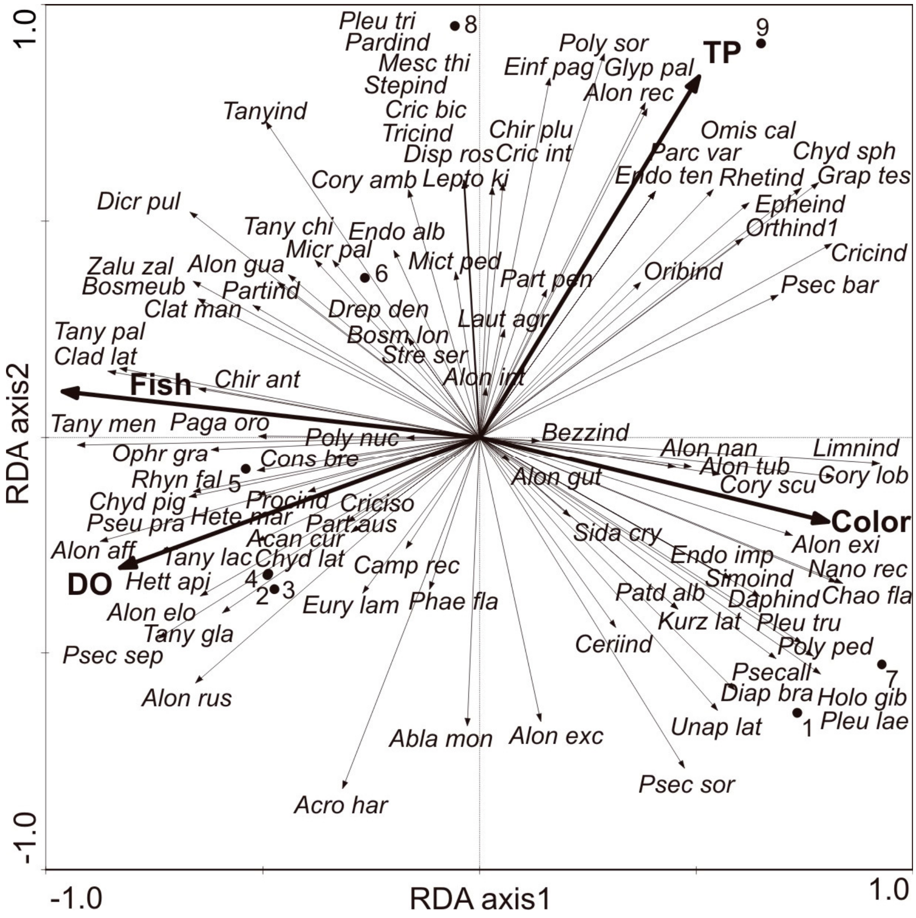

Figure 3
RDA ordination for samples (lakes 1–9 according to Table I), environmental variables, and invertebrate taxa. The abbreviations of the taxa are shown in Table II.

Figure 3
Ordination RDA des échantillons (lacs 1–9 selon le tableau I), variables environnementales et taxons d'invertébrés. Les abréviations des taxons sont celles du tableau II.

negative values for axis 2. Relationship between taxa (*e.g. Glyptotendipes pallens*-type and *Alona rectangular*) and TP were shown as high values for both RDA axes.

DISCUSSION

The TWINSPAN classification of the nine study lakes according to their invertebrate assemblages showed that the three lakes with no permanent fish stocks were grouped together (Figure 2), suggesting that the faunal assemblages in fish-free lakes differ from those with fish. The indicator species for fish-free lakes included Oribatida, Ephemeroptera, and *Chaoborus flavicans.* This is not surprising, since Oribatida (oribatid mites) and Ephemeroptera (may flies) are large-sized and therefore easily caught by fish for consumption. *Chaoborus flavicans* (the phantom midge) is known to co-occur with fish only in deep and stratified lakes, which provide refugia in the hypolimnion, in clay-turbid lakes that prevent visual predation by fish (Liljendahl-Nurminen, 2006), and in humic brown-watered lakes that have reduced fish predation potential due to their light-, oxygen-, and temperature profiles (Paasivirta, 1982). In fish-free lakes invertebrates, such as *Chaoborus* larvae may become the top predators (Nyberg, 1998) and in small and shallow lakes the presence or absence of *C. flavicans* is suggested to be regulated by fish predation (Luoto and Nevalainen, 2009). Therefore, *Chaoborus flavicans* seems to be a good indicator species of fish-free environments in the current data set of small shallow lakes (Figure 2), coherently with the results from the above mentioned previous studies.

According to the TWINSPAN analysis, small species of the family Chydoridae of the Cladocera; *Chydorus sphaericus* s.l., *Alonella nana*, *Alonella excisa*, and *Alona guttata* var. *tuberculata* were indicators of the fish-free lakes (Figure 2), although they occurred in all the lakes (Table II). This result is contradictory to many other results, since usually large and visible cladoceran species, such as *Daphnia* spp., succeed in fish-free waters (Kerfoot, 1974; Jeppesen *et al.*, 2001b) in the expense of small cladocerans (Arnott and Vanni, 1993). Therefore, it is possible that the small chydorid species are not actually indicators of the absence of fish, but such limnological conditions that inhibit success of fish. For example, two of the three fish-free lakes are humic lakes (Kalatoin and Jousjärvi), which contain only a narrow photic and oxygenated epilimnion and therefore suffer from oxygen depletion during winters. Lake Kangaslampi, on the other hand, is extremely eutrophic and disturbed basin and therefore summer algal blooms and winter oxygen depletion restrain permanent inhabitation of fish. In fact, the small chydorids may actually be indicators of fish-free lakes when *Chaoborus* is the top predator. Fitting well with this interpretation, Irfanullah and Moss (2005) showed that a relatively small cladoceran species, *C. sphaericus* succeeded and remained unaffected by *Chaoborus* predation due to its high reproductive rate compensating predation loses.

In the TWINSPAN classification the four oligotrophic lakes (Hauklampi, Iso Majaslampi, Pieni Majaslampi, Iso Lehmälampi) currently inhabited by fish form a separate cluster (Figure 2, Table I). All these lakes experienced severe acidification and related fish kills during the 1980s. This separate cluster with species such as cladoceran *Bosmina (Eubosmina)* and chironomid *Procladius* may indicate limnological and ecological conditions where recent fish introductions have taken place causing distict invertebrate assemblages to succeed or where slow biological recovery following the acidification is under process (Holt and Yun, 2003; Nyberg *et al.*, 2010).

The multivariate RDA ordination for environmental variables and invertebrate taxa in the case of *C. flavicans* (Figure 3) is in accordance with the TWINSPAN classification (Figure 2), showing that *C. flavicans* is successful in fish-free environments. The ordination also revealed a relationship between many planktonic cladoceran species and fish absence. Large and visible planktonic taxa *Daphnia* spp., *Ceriodaphnia* spp., *Simocephalus* spp., *Holopedium gibberum* and *Diaphanosoma brachyurum* occurred mostly in fish-free lakes, since they easily fall prey to fish and are an important part of the fish diet (*cf.* Brooks and Dodson, 1965; Zaret, 1972). However, the remains of planktonic cladocerans were rare, as *e.g*. *Daphnia* and *Simocephalus* were found only in one lake (Table II). Many of the study lakes are very acidic and have an acidification history that may have affected the infrequency of *Daphnia* in the dataset. Recently, Jeziorski *et al.* (2008) showed that acidic deposition and lack of calcium in Canadian boreal shield lakes, comparable to boreal lakes in Finland, nearly extirpated some *Daphnia* species. Therefore, the cause behind scarcity of *Daphnia* may be the chemical composition of the water. In addition, the preservation of *Daphnia* remains may also vary among lakes, possibly connected to water chemistry (Sarmaja-Korjonen, 2007). Thus, according to the present results from the nine lake data set, no significant conclusions can be made about whether these taxa are truly related to fish-free environments in shallow basins.

The RDA statistics showed a high and significant correlation between fish and invertebrate assemblages (Table III), indicating good potential to infer past changes in fish status when the data set is expanded in the future. In the future, more fish-free lakes should be added into the data set and, in overall, the future calibration set should have evenly distributed environmental gradients, including similar amount of lakes with and without fish present. When the data set is expanded with limnologically variable sites, it is more probable that the signal of the influence of fish on invertebrate communities can be separated from those of other limnological conditions. Since the presence and absence of fish is indicated by binary codes, not as actual size of fish stocks, it cannot represent the actual abundance of fish, but rather the trends in fish status when reconstructed from downcore fossil invertebrate assemblages.

In this respect, the fish index to be developed can be regarded as a semi-quantitative method to detect changes in fish status of lakes and should be enlarged to cover at least 30 lakes for reliable validations and regional applicability. Although the determination of fish presence in lakes is very difficult and time-consuming, partly due to the uncommonness of fish-free lakes, it is still utmost important to carefully assess the lake-specific fish status.

As suggested by Sweetman and Smol (2006), multi-proxy investigations of fossil invertebrate remains may allow paleolimnological interpretations of past changes in fish status in lakes. Our results of local invertebrate assemblages in surface sediments of the nine lakes imply that the use of various ecologically different faunal groups and numerous taxa together may allow tracking of presence and absence of fish and therefore support the proposal of Sweetman and Smol (2006). To conclude, the present tentative implications may further enhance the knowledge of internal and long-term food-web processes in lakes, although plenty of work in enlarging the data set will be required before applicable reconstructions at different regions can be performed.

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