

Phantom midge-based models for inferring past fish abundances

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Abstract We sampled living and subfossil phantom midge (Diptera: Chaoboridae) larvae from surface sediments of 21 small lakes in Southern Sweden to examine the influence of fish and selected abiotic variables on the abundance and species composition of chaoborid assemblages. We expected total *Chaoborus* abundance to be inversely correlated with fish abundance and *Chaoborus* species most sensitive to fish

predation to be found only in fishless lakes. We aimed to use the observed relationships to develop models to reconstruct past fish abundances from chaoborid remains and the abiotic environment. *C. flavicans* occurred in almost every lake, whereas subfossil *C. obscuripes* were found in the surface sediments of only one fishless lake. The density of living *C. flavicans* larvae correlated negatively with fish abundance, lake order and size. The concentration of *C. flavicans* subfossils was negatively associated with pH, lake size, water transparency and fish abundance. Regression models that included lake morphometry and landscape position as additional predictors of fish abundance performed better than models that used only *Chaoborus* predictors. The explained variance in fish abundance varied from 52 to 86%. Leave-one-out cross-validation indicated moderate performance of the two best models. These models explained 51 and 56% of the observed untransformed fish density and biomass, respectively. In addition, all *Chaoborus* models were unbiased in closely following the 1:1 reference line in plots of observed versus predicted values. These results are a promising step in developing midge-based paleolimnological reconstructions of past fish abundance, and the approach might be improved by including chironomid remains in the models.

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Introduction

Throughout the twentieth century, Swedish lakes have suffered from severe acidification (Brodin and Kuylenstierna 1992). By the early 1980s, approximately 18,000 lakes in Sweden, a fifth of the total number of lakes >1 ha, had a yearly minimum pH below 5.5, which is critical for the breeding success of roach (Rask et al. 1995). As a consequence, fish stocks have been affected in 9,000 of these lakes (Johansson and Nyberg 1981). A large-scale liming program was initiated in the mid-1970s (Appelberg 1998), and the Swedish government currently spends 1.8 million euros annually to lime some 5,000 lakes and 9,000 km of watercourses (Angeler et al. 2010). Although many lakes have reverted to a more natural pH, recovery of pre-disturbance plant, invertebrate, and fish communities has not been achieved. Apparently, the original non-acidified lake type (1), turns into an acidified lake type (2), and after liming to a third lake type (3), which is not equivalent to the original lake type (1) (Appelberg 1998; Guhrén et al. 2007; Angeler and Goedkoop 2010). Historical records of fish communities prior to the acidification period are sparse. Therefore, paleolimnological approaches to reconstruct past fish abundances for the time periods without direct documentation might be useful when setting targets for lake and fisheries management. As a consequence of their rarity in lake sediments, subfossil fish remains such as scales may not be feasible proxies for fish abundance (Davidson et al. 2003; Sweetman and Smol 2006), whereas abundant subfossil prey remains could be more useful.

Chaoborids are important prey for fish (Luecke 1990; Vinni et al. 2000; Horppila et al. 2008), and chaoborid species differ in their behavioural and morphological adaptations, and hence their sensitivity to fish predation (von Ende 1979; Stenson 1981; Sæther 1997; Berendonk 1999). Chaoborid communities and populations may be regulated by the combined effects of several factors, including availability of predation refugia and food resources, in addition to the predation effect of fish on the larval and pupal stages of midges (Stenson 1981). Several studies have shown the composition and abundance of phantom midge (Chaoboridae) communities of lakes to be influenced by fish predation (Wissel et al. 2003a; Sweetman and Smol 2006; Garcia and Mittelbach 2008; Kurek et al. 2010). Chaoborid larvae also leave

mandible remains that preserve well in the sediment. Hence, chaoborids are a potentially workable proxy for fish abundance in palaeolimnological applications. Phantom midge subfossils have been used to infer qualitatively the past fish population status of North American lakes (Uutala 1990; Lamontagne and Schindler 1994; Uutala and Smol 1996; Schilling et al. 2008). Only Palm and Svensson (2010) have qualitatively inferred historical changes in fish communities of European lakes using chaoborid remains. Although zooplankton-based transfer functions for quantitative reconstruction of planktivorous fish populations were developed earlier (Jeppesen et al. 1996; Amsinck et al. 2005; Davidson et al. 2010), such models using *Chaoborus* remains are still lacking.

In this study, we collected data on subfossil *Chaoborus* remains from the surface sediments of 21 small- to medium-sized (3–383 ha) lakes in southern Sweden. First, we examined the relationships between the abundance and species composition of chaoborid assemblages and environmental/ecological variables. We expected to find non-migratory *Chaoborus* species (*C. crystallinus* and *C. obscuripes*) only in fishless lakes. As the novel main objective of this study, we aimed to develop models for quantitative reconstruction of past fish abundance, using sedimentary *Chaoborus* remains alone or in combination with abiotic environmental variables.

Materials and methods

Study lakes

In April–May 2008, 21 small lakes covering extensive gradients of fish abundance and pH were sampled in southern Sweden (Fig. 1). Descriptive variables for lake morphometry and water chemistry of the study lakes (Table 1) were obtained from the database of the Swedish University of Agricultural Sciences (www.ma.slu.se).

Field sampling and laboratory analyses

Sediment and water column samples for living *Chaoborus* larvae were collected during daylight hours at the deepest spot of each lake. Five replicate samples were hauled from the sediment using a Kajak corer 5.2 cm in diameter (total area sampled

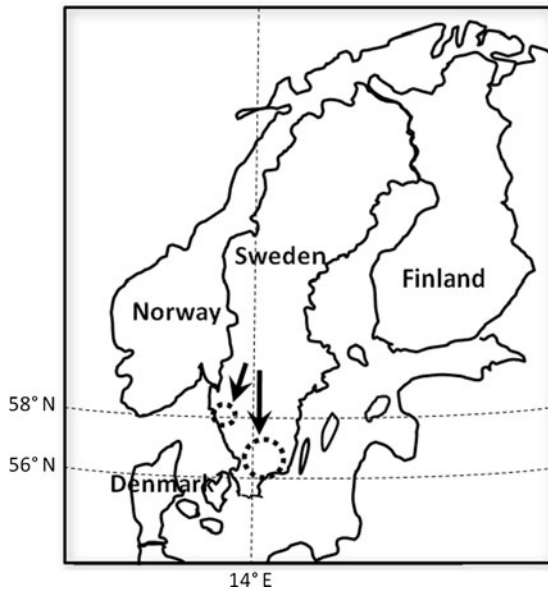


Fig. 1 Location of the study lakes

106.2 cm²). Using a heart-valve water sampler (2 l), the water column was sampled for larvae from five depth layers to integrate the whole water column. Samples were sieved through a 500- μ m mesh and preserved in 70% ethanol.

For midge remains, three replicate sediment core samples were hauled from the deepest point in each study lake using the same Kajak sampler. The top 1 cm from each replicate core was cut and pooled to form a sample with a total volume of 63 ml for each site. In the laboratory, sediment samples were homogenized and heated in 10% KOH for 20 min. After cooling, the sample was sieved through a 93- μ m mesh and preserved in 99% ethanol. *Chaoborus* mandibles were sorted under a dissecting microscope and mounted in Euparal[®] for identification of species. Three criteria were set for the sample size: (1) a minimum volume of 5 ml of wet sediment was examined, (2) at least 10 mandibles were obtained from each lake and (3) if 10 mandibles were not found when examining 10 ml of wet sediment, no additional sample volume was inspected. We consider this sample size to be representative because a minimum threshold of 5–10 subfossil mandibles has been recommended for adequate sample size and a sufficient number of mandibles can usually be recovered from <10 g of wet sediment (Quinlan and Smol 2010a).

Fish data

Fish abundance data (Table 2) were obtained from the database of NORS (NatiOnal Register of Survey test-fishing) of the Swedish Board of Fisheries (www.fiskeriverket.se). Using the available fish data, lake-specific catches per unit of effort (CPUE) were calculated and used as proxies for fish density (number of individuals gillnet⁻¹ day⁻¹) and biomass (g gillnet⁻¹ day⁻¹). Fish data for the lakes were obtained by the European standard test fishing methodology, using Nordic multi-mesh gillnets with mesh-sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm, in randomized order in each net (CEN 2005). The fishing procedure was based on stratified random sampling, where each lake was divided into depth strata, within which the gillnets were placed randomly. Mean CPUEs for all test fishing occasions ($n = 1-8$) during the years 2000–2007 were used as the independent and dependent variables in the models predicting *Chaoborus* abundance and in the transfer functions for fish abundance, respectively. Sedimentation rate in Swedish lakes is typically low (Guhren et al. 2007). Therefore, we considered fish data from eight previous years to correspond roughly to the years of surface sediment (0–1 cm) accumulation.

Environmental variables used in the analyses of *Chaoborus* abundance

Many environmental variables related to lake morphometry, water chemistry, fish communities, as well as lake landscape position and watercourse connectivity, were measured to examine environment-*Chaoborus*-fish relationships among the study lakes. Lake isolation has been shown to affect population dynamics of chaoborid species (Berendonk and Bonsall 2002) as well as presence/absence (Schilling et al. 2008) and community composition (Olden et al. 2001) of fish. Therefore, we included in the analyses variables related to lake landscape position and isolation: (1) altitude, (2) lake order (Riera et al. 2000) and (3) watercourse distance to the nearest downstream lake (Log₁₀ (m)) (Olden et al. 2001). To quantify accessibility of the lakes for the upstream migrating fish, we calculated (4) mean gradient (Asin ($\sqrt{0.01\%}$)) along the stream/river channel to the nearest downstream lake and (5) steepest along-channel gradient (Asin ($\sqrt{0.01\%}$)) to the nearest

Table 1 Information on location, morphometry and water chemistry of the study lakes

Lake	Liming status	N-coord. (WGS 84)	E-coord. (WGS 84)	Altitude (m asl)	Area (ha)	Max. depth (m)	Mean depth (m)	pH	P_{tot} ($\mu\text{g l}^{-1}$)	TOC (mg l^{-1})	Secchi depth (m)
Gaffeln*	N	58°03.1'	12°02.5'	122	6	16.1	5.6	5.3			
Lilla Hästevatten*	N	58°03.2'	12°01.7'	114	3	6.2	2.7	4.9			
Stavsjön	N	56°38.1'	13°35.7'	170	3	8.0	4.5	4.3	16	15.1	1.0
Liasjön	N	56°26.9'	13°59.4'	116	12	5.3	2.5	4.7	25	25.5	0.5
Gölasjön	N	56°52.1'	14°16.8'	166	6	4.2	1.3	4.8	23	32.0	0.3
Lillesjö	N	56°12.3'	14°32.4'	88	4	12.5	10.4	5.0	5	2.9	5.5
Stensjön	L (1992)	56°27.2'	14°46.0'	126	30	4.0	1.8	5.1	15	22.6	1.8
Hjärtsjön	N	57°3.2'	15°14.6'	274	128	6.0	3.4	5.3	5	4.2	5.4
Klintsjön	N	57°7.6'	14°42.0'	232	10	18.0	4.6	5.6	7	4.9	5.4
Stora Slätten	L (1980)	56°57.5'	13°35.3'	149	264	23.5	5.7	6.1	11	17.2	2.2
Bergsjön	N	57°4.6'	14°44.5'	174	326	7.0	3.4	6.1	19	11.7	2.2
Brändasjö	L	56°47.6'	14°39.0'	178	14	5.0	1.9	6.2	27	36.5	0.4
Ubbasjön	L (1983)	56°23.0'	14°22.5'	109	28	6.0	2.7	6.3	34	26.5	0.7
Römningen	L (1993)	56°34.9'	13°54.1'	121	383	4.0	1.1	6.4	20	19.2	1.3
Hultbren	L (1986)	57°7.0'	15°22.6'	240	193	3.0	1.0	6.4	26	20.0	2.2
Strönasjön	L (1983)	56°24.3'	14°23.7'	125	27	6.0	3.0	6.5	25	28.4	0.7
Gyslättsjön	L (1985)	57°6.7'	14°28.8'	226	32	10.0	2.9	6.7	14	12.2	2.0
Humlesjön	L (1985)	56°15.2'	13°34.7'	130	34	4.0	2.1	6.8	30	13.7	1.3
Hacksjön	L	57°11.9'	14°44.1'	218	45	16.0	5.4	7.1	8	7.6	4.0
Blanksjön	L (1981)	56°12.9'	15°10.8'	39	20	17.0	4.9	7.2	8	11.1	4.4
Lunksjön	L (1987)	56°25.6'	14°48.5'	98	49	8	2	7.2	16	16.1	2.2
Frösjön	L (1989)	56°30.9'	14°49.9'	140	32	6	1.5	7.2	31	21.2	0.9
Levrasjön	N	56°6.3'	14°29.5'	7	292	19.0	10.6	8.3	9	5.4	4.6

The lakes sampled during this study are arranged in ascending order along the pH gradient. Coordinates are given using the RT90 coordinate system. Liming status is given using abbreviations N = not limed and L = limed lake. Starting year of liming is given in parentheses. *Lakes sampled by Palm and Svensson (2010)

downstream lake, using available geographic information system (GIS) data (www.gis.lst.se/lanskartor/; see similar procedures used in Schilling et al. 2008). The steepest gradient to the nearest downstream lake was measured using the along-stream/river channel distance (m) between the closest altitude contours of 5 m interval. Moreover, (6) lake isolation (I) of the study lakes was calculated for those lakes situated within 1.5 km maximum distance from the study lake, using the formula of Krauss et al. (2003):

$$I = \sum e^{-d_{ij}/A_j},$$

where d_{ij} is the straight distance (km) from the neighbouring lake j to the study lake i . The probability of *C. flavicans* dispersing more than 1 km can be considered very low (Berendonk and Bonsall 2002).

Therefore, we selected 1.5 km as a suitable maximum isolation distance. A_j is the surface area (ha) of the neighbouring lake.

We included six additional variables related to lake morphometry: (7) lake surface area (A , Log_{10} (ha)), (8) lake volume (Log_{10} (m^3)), (9) maximum depth (D_{max} , Log_{10} (m)), (10) mean depth (D_{mean} , Log_{10} (m)), mean to maximum (11) depth ratio ($D_{\text{mean}}/D_{\text{max}}$) and (12) relative depth ($D_r = (D_{\text{max}} \times \sqrt{\pi}) / (20 \times \sqrt{A})$, Håkanson 1981).

Variables related to water chemistry were: (13) Secchi depth, (14) total organic carbon (TOC, mg l^{-1}), (15) total phosphorus (P_{tot} , $\mu\text{g l}^{-1}$), (16) total nitrogen (N_{tot} , $\mu\text{g l}^{-1}$), (17) pH and (18) conductivity. Variables related to fish abundance were: (19) fish biomass (BM, $\text{g gillnet}^{-1} \text{ day}^{-1}$) and

Table 2 Information on *Chaoborus* densities and fish populations (mean catches \pm S.D. during the years 2000–2007) of the study lakes

Lake	Biomass (g gill-net ⁻¹ day ⁻¹)			Density (individuals gill-net ⁻¹ day ⁻¹)			<i>Chaoborus flavicans</i> Living (ind. m ⁻²)	<i>C. obscuripes</i> Remains (mandibles g of dry sed. ⁻¹)	
	Perch	Roach	Total excl. pike	Perch	Roach	Total excl. pike			
Gaffeln*	0.0	0.0	0.0	0.0	0.0	0.0		298.0	0.0
Lilla Hästevatten*	0.0	0.0	0.0	0.0	0.0	0.0		38.0	8.0
Stavsjön (1)	0.0	0.0	0.0	0	0.0	0.0	6603.8	361.6	38.0
Lillesjö (1)	0.0	0.0	0.0	0	0.0	0.0	0.0	76.7	0.0
Gölasjön (3)	128.0	0.0	128.0 \pm 33.2	1.6	0.0	1.6 \pm 0.3	943.4	687.0	0.0
Liasjön (2)	178.8	0.0	178.8 \pm 178.4	1.1	0.0	1.1 \pm 1.1	1,792.5	481.3	0.0
Ubbasjön (3)	101.6	72.3	185.7 \pm 81.7	4.1	4.6	9.2 \pm 4.9	1,320.8	57.0	0.0
Brändasjö (1)	0.0	211.4	211.4	0.0	8.9	8.9	1,792.5	61.1	0.0
Gyslättsjön (8)	137.4	240.6	418.6 \pm 100.1	5.9	3.2	9.0 \pm 2.9	2,735.8	41.7	0.0
Strönasjön (3)	45.0	58.7	424.2 \pm 307.6	2.2	3.2	6.6 \pm 4.7	660.4	105.8	0.0
Frösjön (1)	102.6	157.8	564.4	8.5	3.3	19.2	754.7	24.3	0.0
Klintsjön (3)	589.7	0.0	589.7 \pm 173.7	26.0	0.0	26.0 \pm 0.6	1,981.1	25.6	0.0
Stora Slätten (2)	805.0	40.8	974.6 \pm 128.6	10.2	2.3	14.1 \pm 2.7	0.0	5.5	0.0
Blanksjön (3)	571.8	411.2	983.0 \pm 243.6	17.5	6.5	24.0 \pm 4.8	0.0	0.0	0.0
Stensjön (1)	770.1	212.0	1,574.8	32.9	5.1	41.2	1,320.8	62.9	0.0
Römningen (1)	499.0	792.6	1,635.2	15.0	24.0	44.2	94.3	2.6	0.0
Levrasjön (1)	815.2	446.1	1,683.8	56.5	10.0	78.7	377.4	41.0	0.0
Lunksjön (1)	1,494.8	210.4	1,774.2	22.4	11.0	34.2	471.7	74.0	0.0
Hacksjön (1)	1,430.9	387.4	1,818.3	37.8	8.8	46.6	377.4	12.1	0.0
Hultbren (1)	1,370.0	488.8	1,858.8	67.1	11.6	78.8	283.0	1.4	0.0
Bergsjön (1)	1,295.8	452.7	1,932.0	38.0	26.1	68.9	0.0	21.3	0.0
Hjärtsjön (3)	2,611.2	0.0	2,611.2 \pm 466.7	38.8	0.0	38.8 \pm 7.2	0.0	0.0	0.0
Humlesjön (2)	1,319.8	2,130.1	3,860.2 \pm 300.5	56.1	134.6	191.1 \pm 76.2	943.4	109.8	0.0

Number of test fishing years is given in parentheses after the name of the lake. Lakes are arranged in ascending order of fish biomass (CPUE g gill-net⁻¹). *Data obtained from Palm and Svensson (2010)

(20) fish density (ind. gillnet⁻¹ day⁻¹) excluding piscivorous pike (*Esox lucius*), as well as biomass and densities of the three most common fish species: (21, 22) perch (*Perca fluviatilis* L.), (23, 24) roach (*Rutilus rutilus* L.) and (25, 26) bream (*Abramis brama*). Purely piscivorous pike was excluded from the analyses, because it was not considered to directly influence the abundances of chaoborids.

Statistical analyses of *Chaoborus*-environment relationships

Relationships among environmental/biological variables and the concentration of *C. flavicans* remains (number of mandibles per g dry sediment) and the

density of living midge larvae were explored using Pearson correlation analyses (Table 3). Associations of *C. flavicans* abundance with environmental variables were more thoroughly examined using univariate regression analyses. The Akaike information criterion (AIC; Akaike 1974) was used as a model selection tool among candidate models: e.g. first and second order, and one-phase exponential decay ($Y = \text{SPAN} * e^{-k*X} + \text{PLATEAU}$). AIC is based on the Kullback–Leibler information lost paradigm (Kullback and Leibler 1951) when model g is used to approximate conceptual truth, f . AIC compares residuals of the candidate models to detect the best among the alternative models. The model with the minimum (0) ΔAIC value is the best fit model. Regression

analyses were conducted using GraphPad Prism 4.00 software. Moreover, *Chaoborus*-environment relationships were examined using principal component analysis (PCA) with quartimax rotation. PCA was conducted to reduce dimensionality of the environmental data set. Quartimax rotation minimizes the number of factors needed to explain each variable, and thereby simplifies interpretation of the variables and their relationships. The analysis was performed using PASW statistics 18 software. Mandible concentrations and larval densities of *C. flavicans* were used as passive variables in the analysis. Therefore, these variables, which measure *Chaoborus* abundance, did not affect the composition of principal components, and the pure *Chaoborus*-environment relationships were demonstrated.

Construction of *Chaoborus*-fish transfer functions

Transfer functions for fish abundance were constructed using multiple regression analyses, in which the independent candidate predictors used were lake morphometry variables as well as first and second order terms of the concentrations of *C. flavicans* and *C. obscuripes* mandibles. Presence/absence (1/0) of *C. obscuripes* was also used as a dummy candidate variable in the analyses because this species has previously only been found in fishless lakes (Sweetman and Smol 2006). Variables related to lake isolation and landscape position were also included among candidate predictors. Best fit transfer functions were selected using AIC. Unique and shared proportions of variance explained by each variable were estimated using partial regression analysis (Borcard et al. 1992). Multiple regression analyses were conducted using SAM 4.0 software (Rangel et al. 2010). In addition to the data collected for the present study, appropriate literature data from Swedish lakes were also used to construct *Chaoborus*-fish transfer functions. Data on surface sediment (top 0–1 cm) densities of chaoborids in Lake Lilla Hästevatten and Lake Gaffeln were obtained from Fig. 2 of Palm and Svensson (2010) and represent a mean value of the two top sediment layers (0–0.5 and 0.5–1 cm). Information on lake morphometry was obtained from Palm and Svensson (2010) and information on isolation/connectivity of these lakes was collected using GIS tools. Leave-one-out cross-validation (Efron and Gong 1983) was used to evaluate the performance of

the established models for reconstruction of past fish abundances. In cross-validations of the models, unrealistic, negative predicted values of fish abundance were truncated to zeros.

Results

Chaoborus abundance

Chaoborus flavicans was the only species found alive in sediment samples from 16 of the 21 study lakes. Living larvae were missing from the sediment samples of Lillesjö, Hjärtsjön, Stora Slätten, Bergsjön and Blanksjön, and from water column samples of all the lakes. Densities of living *Chaoborus* tended to decrease with increasing lake order, volume and area, as well as with increasing fish abundance (Table 3, Fig. 2). Densities also correlated positively with relative depth. Abundance of living larvae correlated significantly ($r = -0.50$, $P < 0.018$) with the first PC-axis, which related positively to the variation in lake size, pH and fish abundance (Fig. 3).

Chaoborus remains were recovered from the surface sediments of 19 lakes. Subfossil mandibles of phantom midges were not found in Lakes Blanksjön and Hjärtsjön, both of which have high water transparency (Secchi depths 4.4 and 5.4 m, respectively) (Table 1). Fish abundances are high in Hjärtsjön and intermediate in Blanksjön (Table 2). Mandibles of *C. obscuripes* were only found in the surface sediments of Lake Stavsjön, whereas *C. flavicans* was the only species identified from the surface sediments of other study lakes, including the fishless Lillesjö. Mandible concentration of *C. flavicans* was associated negatively with lake size, pH, water transparency and fish abundance (Table 3; Figs. 2, 3); however, concentration of *Chaoborus* remains was surprisingly high in Humlesjön, which was the lake with the highest fish density.

Chaoborus-fish models

Analyses of *C. flavicans* mandible concentration-fish abundance relationships suggested that Humlesjön may be an outlier in the data set. Therefore, we first used the whole data set ($n = 23$ including data from Lilla Hästevatten and Gaffeln) and employed *Chaoborus* mandible concentration as the only predictor of

Table 3 Cross-correlations of the environmental variables, *Chaoborus flavicans* abundance (living larvae and subfossil mandible concentration) and quartimax-rotated principal component axes (eigenvalues > 1)

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Landscape position														
Altitude	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Lake order	-0.00	1	-	-	-	-	-	-	-	-	-	-	-	-
Distance to DS lake	0.24	0.17	1	-	-	-	-	-	-	-	-	-	-	-
Mean slope to DS lake	0.06	-0.37	-0.22	1	-	-	-	-	-	-	-	-	-	-
Max. slope to DS lake	-0.03	-0.34	0.20	0.75	1	-	-	-	-	-	-	-	-	-
Lake isolation	-0.48	-0.11	-0.43	-0.17	-0.27	1	-	-	-	-	-	-	-	-
Morphometry														
Lake area	0.02	0.59	0.05	-0.48	-0.43	0.22	1	-	-	-	-	-	-	-
Lake volume	-0.11	0.34	-0.09	-0.27	-0.21	0.22	0.90	1	-	-	-	-	-	-
Maximum depth	-0.20	-0.32	-0.37	0.15	0.21	0.21	0.11	0.45	1	-	-	-	-	-
Mean depth	-0.40	-0.51	-0.30	0.41	0.36	0.15	-0.05	0.36	0.73	1	-	-	-	-
Depth ratio	-0.22	-0.28	0.01	0.46	0.37	-0.26	-0.28	-0.07	-0.16	0.49	1	-	-	-
Relative depth	-0.04	- 0.60	-0.04	0.53	0.45	-0.19	- 0.72	-0.48	0.24	0.49	0.42	1	-	-
Secchi depth	0.04	-0.35	-0.12	0.37	0.33	-0.04	0.11	0.40	0.62	0.68	0.19	0.34	1	-
TOC	-0.05	0.34	0.13	-0.27	-0.27	0.07	-0.18	-0.46	- 0.56	- 0.64	-0.22	-0.33	- 0.88	1
P _{tot}	-0.06	0.43	0.32	-0.38	-0.35	-0.14	-0.04	0.34	- 0.68	- 0.65	-0.10	-0.37	- 0.86	0.76
N _{tot}	-0.31	0.59	-0.01	-0.48	-0.51	0.12	0.01	-0.25	-0.48	- 0.60	-0.31	-0.40	- 0.79	0.77
pH	-0.33	0.18	0.05	-0.28	-0.18	0.30	0.54	0.55	0.31	0.14	-0.39	-0.52	0.15	-0.18
Conductivity	- 0.68	-0.11	0.04	-0.32	-0.09	0.49	0.33	0.45	0.34	0.45	0.01	-0.23	0.23	-0.16
Fish abundance														
Fish BM	0.10	0.34	-0.01	-0.24	-0.23	-0.05	0.71	0.62	-0.01	-0.11	-0.16	- 0.57	0.28	-0.39
Fish density	0.07	0.34	0.11	-0.42	-0.37	0.02	0.74	0.62	0.05	-0.17	-0.37	- 0.66	0.22	-0.26
Perch BM	0.28	0.26	-0.11	-0.02	-0.08	-0.05	0.63	0.59	0.11	-0.04	-0.13	-0.44	0.45	-0.49
Perch density	0.11	0.26	-0.01	-0.32	-0.27	0.05	0.70	0.64	0.17	-0.05	-0.31	-0.54	0.40	-0.46
Roach BM	-0.16	0.17	0.26	-0.27	-0.15	-0.07	0.40	0.28	-0.17	-0.16	-0.09	-0.37	-0.08	-0.13
Roach density	-0.22	0.35	0.19	-0.31	-0.27	0.07	0.56	0.41	-0.16	-0.23	-0.22	- 0.56	-0.20	0.04
Bream BM	-0.13	0.35	-0.18	-0.37	-0.42	0.06	0.31	0.14	-0.24	-0.31	-0.16	-0.31	-0.23	0.17
Bream density	-0.16	0.50	-0.10	-0.41	-0.46	0.04	0.31	0.13	-0.33	-0.35	-0.13	-0.36	-0.35	0.27
Living <i>C. flav.</i> dens.	0.19	-0.47	0.18	-0.05	0.09	-0.18	- 0.57	-0.54	-0.14	-0.18	0.11	0.48	-0.32	0.14
Mandible concentration	-0.05	-0.28	0.08	0.11	0.10	0.22	- 0.55	- 0.61	-0.32	-0.10	0.20	0.23	-0.46	0.43
PCA1	0.09	0.41	0.15	-0.38	-0.30	-0.01	0.79	0.66	0.00	-0.19	-0.33	- 0.67	0.18	-0.29
PCA2	0.08	-0.50	-0.31	0.53	0.45	-0.01	-0.02	0.33	0.68	0.77	0.30	0.46	0.91	- 0.87
PCA3	- 0.79	-0.17	-0.13	-0.23	-0.11	0.60	0.17	0.33	0.37	0.54	0.12	-0.07	0.06	-0.04
PCA4	-0.28	0.15	-0.54	-0.13	-0.41	0.19	0.14	0.11	-0.12	-0.00	0.15	-0.05	-0.08	0.01
PCA5	-0.17	0.07	0.51	0.23	0.39	-0.54	-0.07	-0.01	-0.36	0.18	0.77	0.21	0.03	-0.10
PCA6	0.07	0.57	0.14	-0.27	-0.14	-0.06	0.51	0.51	0.16	0.05	-0.06	-0.27	0.08	0.03

Table 3 continued

Variable	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Landscape position														
Altitude	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lake order	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Distance to DS lake	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mean slope to DS lake	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Max. slope to DS lake	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lake isolation	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morphometry														
Lake area	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lake volume	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maximum depth	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mean depth	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Depth ratio	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Relative depth	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Secchi depth	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Water chemistry														
TOC	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P _{tot}	1	-	-	-	-	-	-	-	-	-	-	-	-	-
N _{tot}	0.79	1	-	-	-	-	-	-	-	-	-	-	-	-
pH	0.05	0.13	1	-	-	-	-	-	-	-	-	-	-	-
Conductivity	-0.10	0.00	0.68	1	-	-	-	-	-	-	-	-	-	-
Fish BM	-0.14	-0.16	0.47	0.21	1	-	-	-	-	-	-	-	-	-
Fish density	0.00	-0.03	0.66	0.34	0.91	1	-	-	-	-	-	-	-	-
Perch BM	-0.34	-0.35	0.28	0.07	0.90	0.76	1	-	-	-	-	-	-	-
Perch density	-0.21	-0.23	0.53	0.31	0.90	0.93	0.85	1	-	-	-	-	-	-
Roach BM	0.25	0.06	0.49	0.26	0.70	0.70	0.39	0.54	1	-	-	-	-	-
Roach density	0.35	0.24	0.65	0.32	0.68	0.76	0.39	0.55	0.90	1	-	-	-	-
Bream BM	0.07	0.28	-0.07	-0.10	0.30	0.30	0.10	0.26	0.19	0.30	1	-	-	-
Bream density	0.30	0.50	0.06	-0.06	0.18	0.25	-0.04	0.17	0.10	0.30	0.87	1	-	-
Living <i>C. fluv. dens.</i>	0.12	-0.02	-0.45	-0.26	-0.49	-0.50	-0.46	-0.48	-0.24	-0.34	-0.13	-0.18	1	-
Mandible concentration	0.25	0.17	-0.59	-0.23	-0.49	-0.62	-0.41	-0.53	-0.29	-0.45	-0.21	-0.25	0.41	1
PCA1	0.00	-0.06	0.63	0.28	0.95	0.97	0.80	0.91	0.75	0.79	0.27	0.21	-0.50	-0.59
PCA2	-0.92	-0.88	-0.05	0.07	0.15	-0.00	0.38	0.23	-0.19	-0.33	-0.24	-0.42	-0.12	-0.23
PCA3	-0.02	0.13	0.57	0.90	-0.08	0.05	-0.25	-0.01	0.14	0.22	-0.09	-0.01	-0.15	-0.07
PCA4	-0.10	0.18	-0.25	-0.13	0.13	0.04	0.04	0.08	-0.07	0.02	0.84	0.77	-0.11	-0.01
PCA5	0.17	-0.13	-0.18	0.01	0.05	-0.07	-0.07	-0.13	0.28	0.16	0.02	0.08	0.03	-0.12
PCA6	-0.08	0.08	0.01	0.03	-0.06	-0.03	0.07	0.03	-0.44	-0.28	0.02	0.16	-0.26	-0.28

Pearson's correlation coefficient with *P* values < 0.01 are bolded. Highest loading of each variable on the principal component axes is underlined

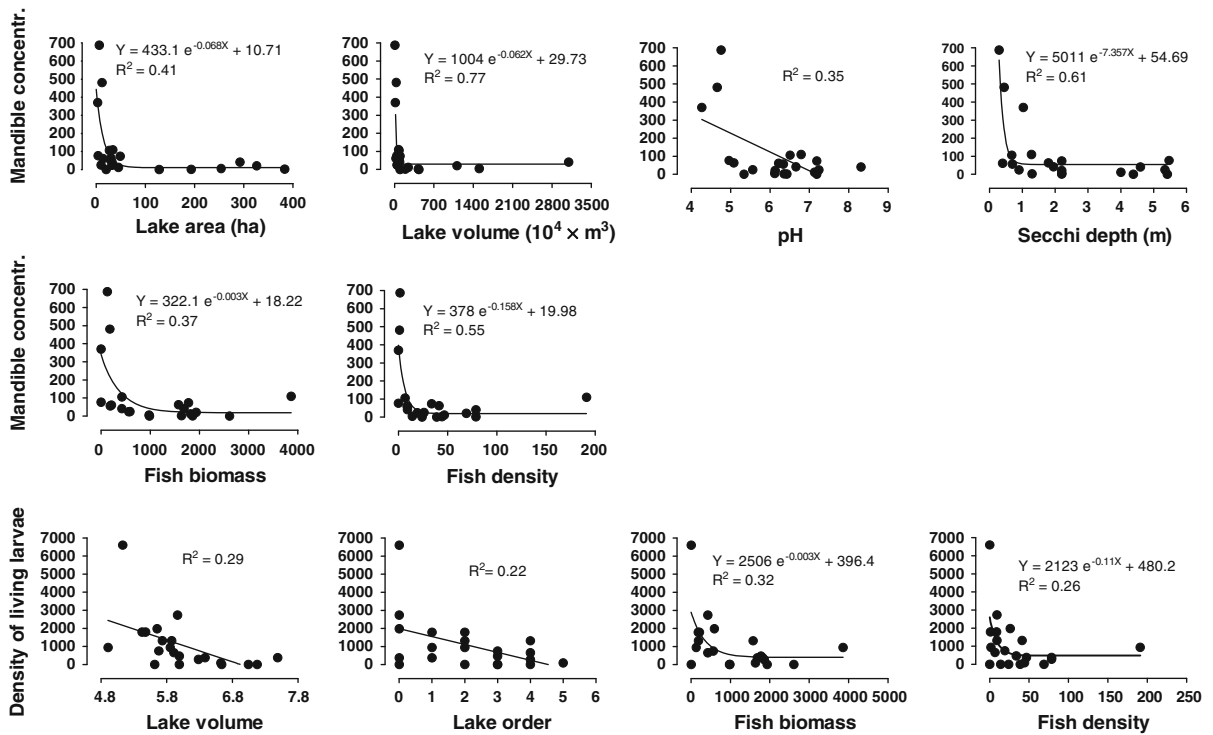


Fig. 2 Relationship between environmental variables and density of living *C. flavicans* and concentration of their subfossil mandibles in the study lakes. Best fit regression models were fitted to the data

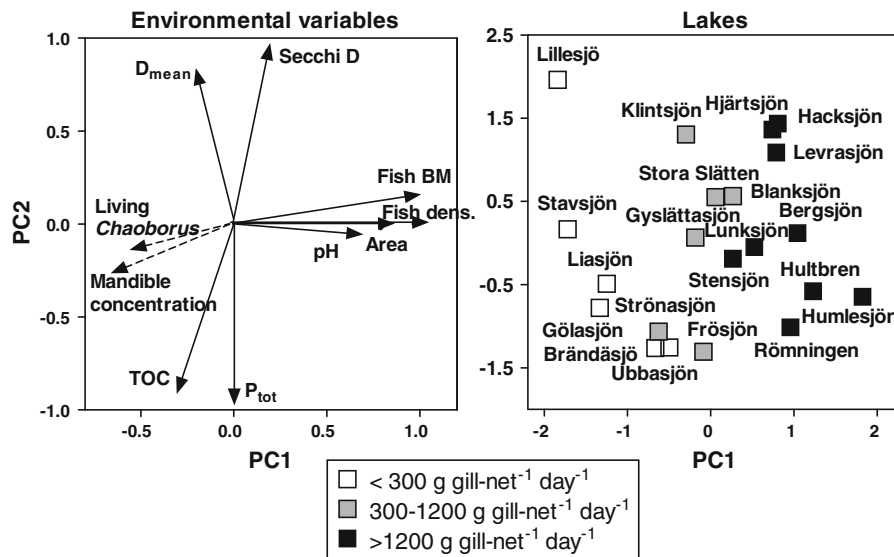


Fig. 3 PCA-ordination of the environmental-*Chaoborus* relationships

fish biomass and density in regression analyses. Second, observed fish abundances were fitted against leave-one-out predicted abundances and the outlier characteristics of Humlesjön were evaluated using

Grubbs’s test for outlier detection (Grubbs 1969). Grubbs’s test uses the Z-ratio, which is calculated from differences between observed values and model predictions ($Diff_i = Y_i - X_i$) as follows:

Table 4 Transfer functions for fish abundances

Models & predictors	Coefficients	t/F	VIF	P	Unique R ²	R ²
Fish density						
Only chaoborid predictors						
Constant	1.69	11.45		<0.001		
<i>C. flavicans</i> mandible concentr. (Log ₁₀ X + 1) ²	-0.18	-4.43	1.05	<0.001	0.37	0.50
<i>C. obscuripes</i> recovered or not (0/1)	-0.87	-2.71	1.05	0.014	0.14	0.27
Model		16.98		<0.001		0.64
Morphometry + landscape position						
Constant	0.41	1.33		0.200		
Lake area (log ₁₀ ha + 1)	0.67	3.97	2.25	<0.001	0.20	0.69
Relative depth	-0.02	-2.46	2.09	0.025	0.08	0.58
Lake order	-0.08	-1.39	1.61	0.184	0.02	0.17
Model		20.67		<0.001		0.78
Morphometry, landscape position + chaoborid predictors						
Constant	1.23	3.38		0.004		
Relative depth	-0.03	-3.51	2.16	0.003	0.10	0.58
<i>C. flavicans</i> mandible concentr. (Log ₁₀ X + 1) ²	-0.11	-3.11	1.82	0.007	0.08	0.50
Lake area (log ₁₀ ha + 1)	0.40	2.39	3.18	0.029	0.05	0.69
Lake order	-0.10	-2.10	1.64	0.052	0.04	0.17
Model		25.42		<0.001		0.86
Fish biomass						
Only chaoborid predictors						
Constant	0.92	8.35		<0.001		
<i>C. flavicans</i> mandible concentr. (Log ₁₀ X + 1) ²	-0.12	-3.79	1.05	0.001	0.36	0.46
<i>C. obscuripes</i> recovered or not (0/1)	-0.40	-1.65	1.05	0.116	0.07	0.16
Model		10.47		<0.001		0.52
Morphometry						
Constant	-1.55	-2.49		0.023		
Lake volume	0.37	3.70		0.002	0.24	0.58
Relative depth	-0.01	-2.13		0.047	0.08	0.42
Model		18.63		<0.001		0.66
Morphometry + chaoborid predictors						
Constant	-0.60	-0.86		0.404		
Lake volume	0.25	2.46	1.84	0.025	0.09	0.58
<i>C. flavicans</i> mandible concentr. (Log ₁₀ X + 1)	-0.18	-2.24	1.52	0.039	0.07	0.47
Relative depth	-0.01	-2.15	1.41	0.047	0.07	0.42
Model		16.72		<0.001		0.74

$$Z_i = \frac{|\overline{Diff_i} - Diff_i|}{SD}$$

where $\overline{Diff_i}$ is the mean of the differences ($Diff_i$) between observed and predicted values, and SD is the standard deviation of the differences. From the models for fish biomass and density, calculated Z values for

Humlesjön were 2.85 and 2.41, respectively. Using Grubbs's test, the observed fish biomass ($t = 3.64$, $df = 22$, $P < 0.002$) and density ($t = 2.83$, $df = 22$, $P < 0.01$) in Humlesjön significantly differed from the values predicted by the model using the whole data set. Therefore, Humlesjön was determined to be an outlier in the data set, and was removed from

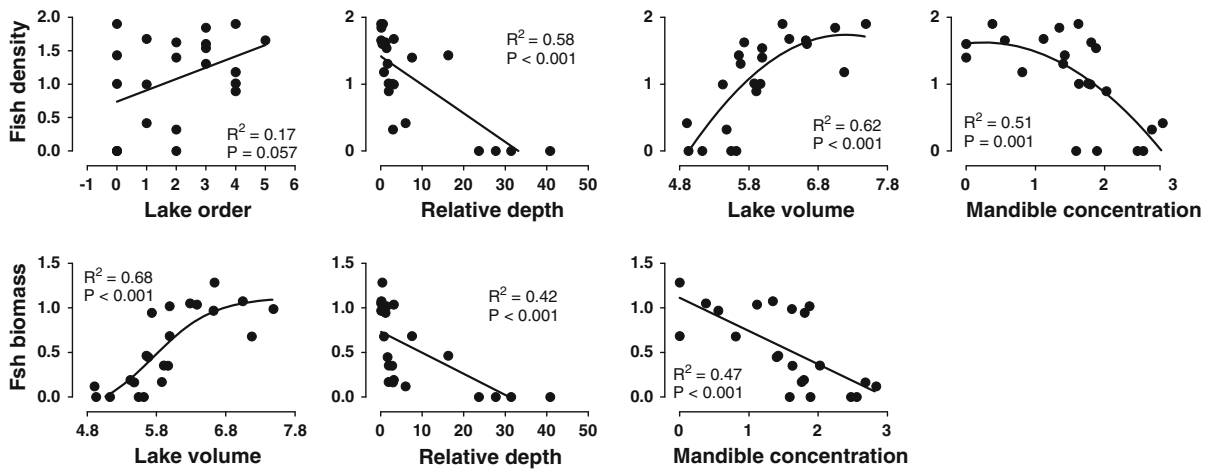


Fig. 4 Relationships between total fish abundance and environmental variables and mandible concentration

subsequent development of fish abundance transfer functions, which reduced the data set to 22 lakes.

The best model for fish density, based on AIC and using only chaoborid predictors, accounted for 64% of the observed variance (Table 4). This model included the second order term of *C. flavicans* mandible concentration and presence/absence of *C. obscuripes* as predictors of fish density. The best *Chaoborus*-fish density model, using both *Chaoborus* remains and other predictors, included negative and positive linear relationships with lake basin shape (relative depth) and area, respectively (Fig. 4). Moreover, the fish density model included negative associations with lake order and the second order term of *C. flavicans* mandible concentration (Table 4). This model explained 86% of the variation in fish density. Relative depth and mandible density accounted for 10 and 8% unique shares of total variation. Smaller unique shares of variation were explained by surface area and lake order, 5 and 4%, respectively.

The best fitting model for fish biomass using only chaoborid predictors included the second order term of *C. flavicans* mandible concentration and presence/absence of *C. obscuripes*. This model explained 52% of the variation in fish biomass. The best *Chaoborus*-morphometry model for fish biomass included positive association with lake volume and negative relationships with the *C. flavicans* mandible density and relative depth. This model accounted for 74% of the variance in fish biomass (Table 4). A large proportion of the variation in the model was shared

among the predictors (51%), while their unique shares of variations were small (7–9%).

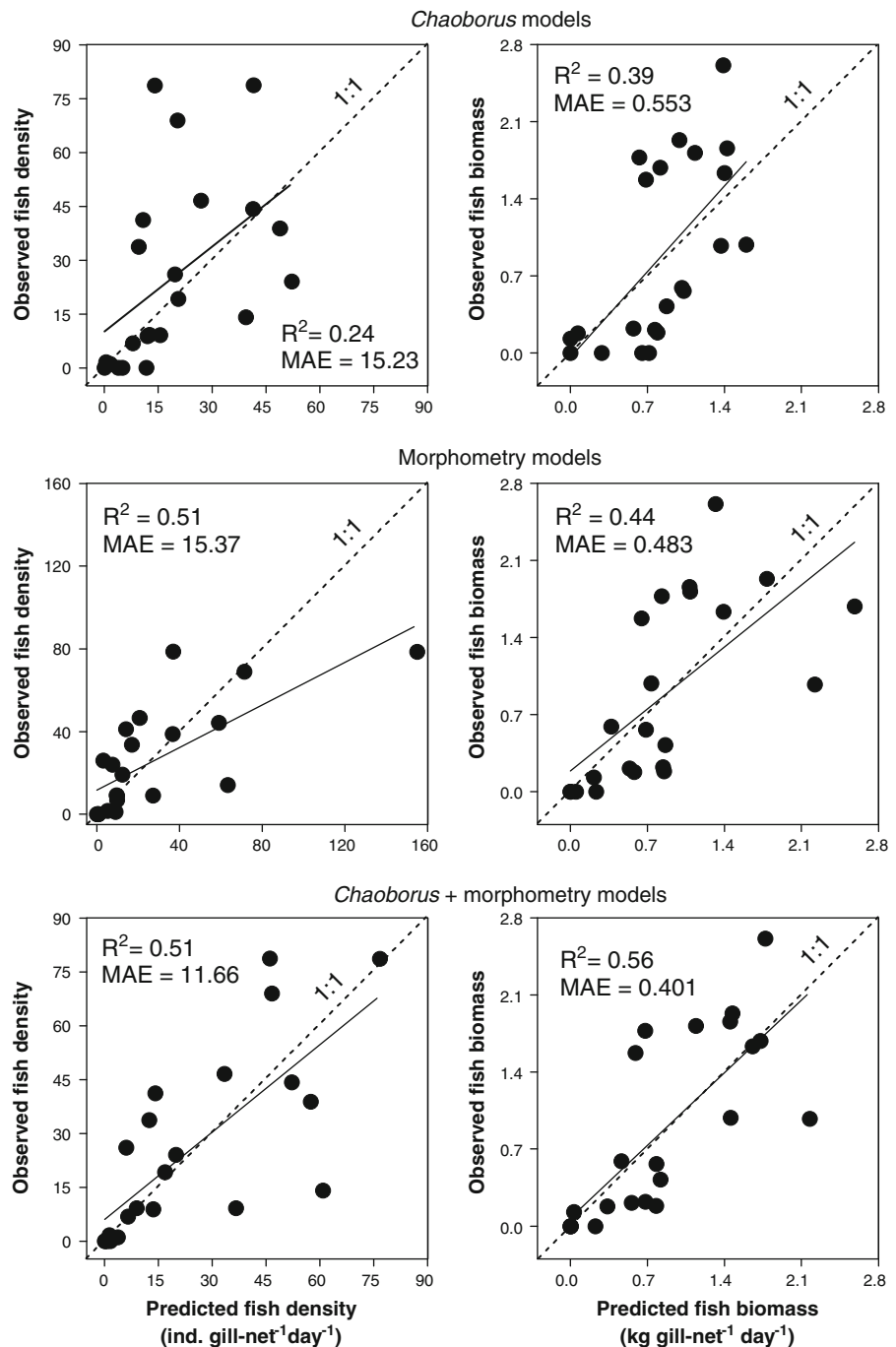
In leave-one-out cross-validations, models using both chaoborid and morphometry predictors performed better than “chaoborids only” or “morphometry only” models (Fig. 5). The predicted values of “*Chaoborus* + other predictors” models accounted for 51 and 56% of the observed fish density and biomass, respectively. Mean absolute errors (MAE, Schaeffer 1980) of the predictions were 11.7 individuals and 401 g per gill-netting day for fish density and biomass, respectively.

Discussion

Environmental determinants of the abundance and species composition of chaoborid assemblages

We observed highest phantom midge population abundances in lakes with low water transparency and pH, small volume and low to zero fish abundance. The density of living, sediment-dwelling *C. flavicans* larvae correlated negatively with fish abundance, lake volume and area, as well as with lake order. The total lack of live *Chaoborus* larvae in the water column samples may be related to the daytime position of larvae in the sediment (Sæther 1997). Swimming larvae might also have been able to avoid our small-volume (2-l) sampler. Mandible concentration of *C. flavicans* decreased with increasing lake size, pH,

Fig. 5 Leave-one-out cross-validations of *Chaoborus*–fish transfer functions



water transparency and fish abundance. It was not possible, however, to differentiate between the effects of fish abundance and lake morphometry on the phantom midge abundance, because these variables were strongly inter-correlated in the data set.

Previous studies have stated that fish predation can control chaoborid assemblages in lakes (Wissel et al.

2003a; Sweetman and Smol 2006) and that only smaller-sized *Chaoborus* species (e.g. *C. flavicans*) with diel vertical migrations are adapted to coexist with fish (Wissel et al. 2003a). *C. flavicans* is commonly found in lakes with fish, where larvae and pupae of *C. flavicans* have been reported in the diets of cyprinid (Vinni et al. 2000), percid (Kålas 1995) or salmonid (Luecke 1990)

fish species. In addition to predation, many other factors may cause mortality at various life stages of phantom midges. Early larval instars are vulnerable to cannibalism and predation by other invertebrate predators (Sæther 1997). Lower reproductive investment as a cost of predator avoidance (Hammill and Beckerman 2010) may also reduce the recruitment of early instar larvae in lakes containing abundant fish populations. Survival of fast-growing, but gape-limited and easily starving, first- and second-instar larvae has been observed to vary widely (from 1 to 80%), depending on the availability of suitable rotifers for food (Neill and Peacock 1980). Therefore, multiple sources of variation, either with parallel or counteracting survival effects, may confound observed patterns in chaoborid-fish relationships.

Lake Humlesjön was an outlier in the data set, with high abundance of living *C. flavicans* larvae, subfossil mandibles and fish in the same lake. We hypothesize that one explanation for this unexpected finding in the cyprinid-dominated lake may be high near-bottom turbidity as a consequence of sediment resuspension by detritivorous/benthivorous fish (Breukelaar et al. 1994). Turbid water may serve as a refugium and improve survival of phantom midges in shallow lakes with dense fish populations. In addition, intense feeding by benthivorous fish can directly release sediment-bound nutrients via bioturbation (dredging behaviour; Breukelaar et al. 1994) and/or transmit nutrients from the sediments to the water column via excretion (Brabrand et al. 1990). By disturbing sediment, dense detritivorous fish populations can also prevent sediment consolidation, and therefore facilitate resuspension of sediments by wave action (Scheffer et al. 2003). Nutrients released from the sediment, together with fish-generated resuspension of settled algal cells from the sediment (Roozen et al. 2007), may further boost lake productivity and could, therefore, increase the amount of zooplankton food suitable for chaoborid larvae. Zooplankton communities of eutrophic lakes with dense fish populations (like Humlesjön) are usually dominated by small taxa, which are suitable food for *Chaoborus*. Although shallow Humlesjön lacks a hypolimnetic refuge, chaoborid larvae are able to penetrate into the sediment during light hours (Sæther 1997). Therefore, unique or interacting effects of these several factors may explain the relatively high abundance of *C. flavicans* larvae in Humlesjön, in spite of high fish abundance.

Small humic and eutrophic lakes are susceptible to hypolimnetic oxygen deficiency that favours *Chaoborus* larvae that are very tolerant of low oxygen concentrations (Quinlan and Smol 2010b). As an anti-predator behaviour against fish, phantom midge larvae migrate between the epilimnion and their oxygen-poor, hypolimnetic, profundal refugium (Sæther 1997). In addition to species-specific behavioural differences, the extent of vertical migration behaviour of *Chaoborus* depends on the larval stage and its vulnerability to fish predation. First and second instars are non-migratory, while third and fourth instars have been observed to perform incomplete and wide-range vertical migrations, respectively (Gliwicz et al. 2000). We lacked oxygen concentration data from our study lakes, but the assumption that *Chaoborus* abundance correlates negatively with hypolimnetic oxygen concentration is supported by observations of *Chaoborus*-lake morphometry associations. Highest midge densities were observed in small lakes with small hypolimnetic volumes. In our lake data set, *Chaoborus* abundance did not correlate significantly with TOC. The three lakes with highest chaoborid abundance were, however, humic and displayed low water transparency (Table 1). Therefore, our observations offer support for earlier findings that population densities of phantom midge larvae are commonly high in brown-coloured, humic lakes (Wissel et al. 2003b). Low water transparency is known to favour phantom midge larvae by decreasing predation efficiency of visually feeding fish in coloured or turbid water (Wissel et al. 2003b; Liljendahl-Nurminen et al. 2008).

The concentration of subfossil *C. flavicans* remains correlated negatively with lake order. Rather than being related to a species colonization/dispersal effect, the lake order effect on *Chaoborus* abundance may instead be a consequence of water chemistry differences such as lower hypolimnion oxygen concentration and pH (Quinlan et al. 2003) or lower fish abundance in low order lakes, as observed among our study lakes. We did not observe a significant correlation between lake isolation and phantom midge densities ($r = 0.27$, $n = 21$, $P = 0.241$). *C. flavicans* has been observed to exhibit mainland-island meta-population structure with large habitat patches (large populations) and a network of small habitat patches (islands) within the species dispersal range (Beren-donk and Bonsall 2002). The probability of the species

dispersing further than 1 km is considered to be very low (Berendonk and Bonsall 2002). Therefore, dispersal may be important for species colonization, but to affect densities, possible mass-effects of dispersal from neighbouring population(s) would require short between-lake distances, and large differences in size between the source and receiving populations (Mouquet and Loreau 2003).

Our data did not indicate other strong water quality effects on the abundance of phantom midges, except negative (likely indirect) effects of water transparency and pH. Phantom midge larvae are very tolerant of low pH (Walker et al. 1985). Therefore, only indirect acidity effects on chaoborid abundance can be met within the pH range of this study. Phantom midges are favoured by acidification due to a loss or decline of the fish feeding on them (Kurek et al. 2010). Although we did not observe a significant relationship between lake productivity and density of phantom midges, earlier studies indicated that chaoborids probably benefit from a moderate increase in phytoplankton productivity (Yan et al. 1985). This may be related to better survival of early instar larvae in meso-eutrophic lakes (Neill and Peacock 1980).

Chaoborus–fish models and their critical evaluation

An ecological premise of prey-predator transfer functions is that mortality of the prey organism, or in the case of multi-species models, proportional abundances within the guild of prey organisms (e.g. cladocerans, chironomids or chaoborids), should change as a consequence of fish predation. Specifically, abundances of some species should decline relative to species “favoured” or less affected by the predation. Our results demonstrated the decrease of *C. flavicans* abundance along the gradient of fish abundance, although predation effects on phantom midges are obviously alleviated by low water transparency and the presence of an oxygen-poor hypolimnion. Many studies have shown that the abundance, size distribution, species and species trait composition of prey change along the temporal (Uutala 1990; Blumenshine et al. 2000; Palm and Svensson 2010) and spatial (Blumenshine et al. 2000; Garcia and Mittelbach 2008) gradients of fish abundance, as well as along the spatial gradients of refuge availability (Tolonen et al. 2003). Morphological, chemical and

behavioural defences, e.g. use of refugia, have been shown to alleviate the effects of predation (Stenson 1981; Hershey 1987; Dawidowicz et al. 1990; Luecke 1990; Berendonk 1999). Therefore, variation in refuge availability for prey species, e.g. an oxygen-poor hypolimnion for chaoborids, may decrease the explanatory power of prey-fish transfer functions if the measures/proxies of refugia availability or their spatial extent cannot be incorporated into the transfer functions.

Using data from southern Sweden, we developed chaoborid-fish regression models for fish density and biomass. These models demonstrated moderate usability of chaoborid remains for the reconstruction of past fish abundances. The models explained 52–86% of the variation in fish abundance with moderate prediction errors (Fig. 5). The relatively large residuals between observed and predicted values in our study lakes with moderate or high fish abundance may be related to among-lake variation in sedimentation rates, because high and low sedimentation rates dilute or concentrate subfossil remains, respectively, and hence tend to over- or under-predict fish abundance, respectively. Decreasing linear or curvilinear fish abundance relationships with concentrations of *C. flavicans* remains were included in all transfer functions. In addition, the models included negative associations of fish abundance with the presence/absence of *C. obscuripes* remains, lake order and relative depth, as well as positive relationships with lake surface area and volume. A negative association between relative depth of the basin and fish abundance may be due to the more extensive littoral zone with abundant food resources, spawning sites and sheltering habitats for fish in lakes with flat cross-sections, compared to caldron-shaped, deeper lakes. In addition to water chemistry, lake morphometry has been shown to be a critical factor in regulating abundance, species composition and size structure of fish (Holmgren and Appelberg 2000; Olin et al. 2002; Mehner et al. 2005). Like Olin et al. (2002), we observed that total abundance of fish positively correlated with lake size.

Our model covered a large gradient of fish abundance, from zero to very high abundance. The maximum fish catch per gill-net was approximately 4 kg. Appelberg (2000) estimated that saturation of multi-mesh gill-nets may not affect the outcome of test fishing until 6 kg of fish have been caught. Efficiency

of similar gill-nets, however, has been shown to decrease with much smaller catches, even catches >1.3 kg of fish per gill-net (Olin et al. 2004). Therefore, the magnitude of the difference in fish densities and biomasses between low- and high-fish-abundance lakes may have been underestimated in this, as well as other studies, that used gill-net CPUE comparisons. Furthermore, underestimation of fish abundance is more likely in clear-water lakes, where catchability decreases, with fewer fish caught than in turbid or humic lakes (Olin et al. 2004).

We emphasize that lake size may limit the usability of our chaoborid-fish transfer functions because our study was limited to fairly small lakes (3–383 ha). Because lake size and morphometry are important factors governing fish abundance and community composition (Olin et al. 2002; Mehner et al. 2005), we caution that our transfer functions might apply only to fairly small lakes with a surface area less than 4 km². If fishless lakes and cyprinid-dominated Brändasjö are excluded from our data, all other lakes in our model calibration data set were percid-dominated. Therefore, the performance of our models may be poor in cyprinid-dominated eutrophic lakes.

Conclusions and suggestions for further studies

Results of this as well as other studies suggest that chaoborid assemblage composition is mainly governed by the presence/absence and abundance of fish (Wissel et al. 2003a; Garcia and Mittelbach 2008). On the other hand, abundance of *C. flavicans*, a species well adapted to co-exist with fish, is mainly determined by the interactive effects of fish abundance, water transparency and lake morphometry (presence/absence and extent of oxygen-poor hypolimnetic refuge). So far, little is known about the interactive effects of fish abundance versus water transparency and fish abundance versus oxygen-poor refuge on the plasticity of habitat use behaviour (benthic vs. planktonic), and vertical distribution of phantom midge larvae in their natural environments.

We achieved moderately performing chaoborid-fish transfer functions, which could be used in conjunction with the cladoceran-rotifer model of Jeppesen et al. (1996) to reconstruct population abundances of omnivorous and planktivorous fish. Moreover, future inclusion of chironomid subfossils in midge-fish transfer functions might improve the

reconstruction of fish population abundances (Brodersen and Quinlan 2006).

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