

Environmental determinants of chironomid communities in remote northern lakes across the treeline – Implications for climate change assessments



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ABSTRACT

Chironomids (*Diptera: Chironomidae*) in northern lakes are especially sensitive to climate change impacts. In addition, environmental factors other than direct temperature increase might play an important role in functioning of these keystone aquatic communities. We examined 31 lakes at the treeline ecotone in subarctic Finnish Lapland for their surface sediment chironomid fauna to assess the influence of different environmental factors on the communities. We aim to improve understanding of the climate-driven catchment and limnological factors, for the assessment of climate change impacts. Our results indicated that organic content of the sediment, total nitrogen, water depth and pH that are all likely to change under global warming had statistically significant influence on the chironomid assemblages and associated indicator taxa were assigned for these variables. In addition, a dissolved organic carbon (DOC) threshold (4 mg l^{-1}) was observed that divided the study sites based on their chironomid composition. Sites with high DOC concentrations and benthic microbial mats had distinctive chironomid fauna from low-DOC sites without microbial mats indicating the significance of benthic versus planktonic productivity in the structure and functioning of polar lakes. The results provide important knowledge on chironomid-environmental relationships in climate-sensitive subarctic lakes and create basis for chironomid-based environmental change assessments in remote northern areas.

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1. Introduction

Lakes have a significant role in carbon cycling, and hence they are important regulators of climate change by processing terrestrial and atmospheric as well as aquatic carbon (Williamson et al., 2009). To understand the role of lakes as sentinels of climate change, fundamental information on the climate-induced processes in lakes and their catchments is necessary. In remote northern lakes lacking direct human influence, the complex effects of climate warming propose a major threat to the ecosystems (Rühland et al., 2015). In these lakes, climate change causes reduced duration of ice-cover and warmer water temperatures (Wrona et al., 2006). However, the chemical and physical consequences of climate change vary locally

depending on the catchment characteristics, subsequently causing idiosyncratic changes in the ecological responses (Dokulil, 2014).

In addition to the apparent differences in water temperature and catchments, northern lakes have other unique climate-sensitive features compared to boreal and temperate lakes. For example, subarctic and arctic lakes may contain thick benthic microbial mats growing under an overlying nutrient-poor and transparent water column (Rautio et al., 2011). Northern ecosystems are also sensitive to the supply of organic matter through its optical and biogeochemical properties. Specifically, dissolved organic carbon (DOC) affects bacterial production, pelagic and benthic primary productivity and the exposure of aquatic organisms to ultraviolet radiation (Rautio et al., 2011). Since climate change is likely to alter the biogeochemical cycles of northern lakes and their catchments, it is important to examine these properties and their influence on aquatic organism in detail. For example, methane (CH_4) production is significantly enhanced by simultaneous increases in organic matter, nutrients and temperature (Yvon-Durocher et al., 2014). Consequently, biogenic CH_4 production provides a carbon and energy source for CH_4

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oxidizing bacteria (MOB) in microbial mats, which in turn can support food webs at higher trophic level (Ravinet et al., 2010).

Benthic *Chironomidae* larvae (*Diptera: Nematocera*) are a key component of aquatic food webs and biogeochemical cycles by consuming and recycling organic matter, which derives from allochthonous and autochthonous detritus (Pinder, 1986). Metabolically, most of the chironomid biomass can be derived from MOB production (Jones et al., 2008) suggesting that changes in organic matter, nutrients and temperature, which enhance MOB, may have significant influence on their success. Organic matter transport also influences chironomids through the humic state and related oxygen availability (Rantala et al., 2015), which in turn have complex interactions with CH₄ production and climate conditions (Van Hardenbroek et al., 2013). Therefore, these benthic macroinvertebrates are an integral part in the assessments of ecological status of freshwaters, especially in northern regions where their importance in aquatic ecosystems increases (Nyman and Korhola, 2005). The distribution and abundance of chironomids in lakes at the regional scale are determined by climate conditions, most particularly summer air temperature, which has direct influence on chironomid growth and development (Eggermont and Heiri, 2012). However, at the local and site-specific scales in temperate and boreal lakes factors related to nutrient conditions (Brooks et al., 2001; Luoto, 2011a) and hydrological variables (Mousavi, 2002; Luoto, 2010) are in dominant role for the success of particular chironomid taxa. Nutrients may directly restrict chironomid larval development (Small et al., 2011) and hydrological conditions influence their habitat and food availability and hence favor specific functional traits (Luoto and Nevalainen, 2015).

In contemporary environmental assessments, chironomids are usually used to evaluate lake nutrient status by applying different indices and classification systems (Ruse, 2010; Jyväsjärvi et al., 2014). Furthermore, fossil chironomid assemblages in the surface sediment samples (representing the present communities) have been used as calibration data for long-term assessments of both local (Brodersen and Quinlan, 2006; Luoto and Salonen, 2010) and regional variables (Heiri et al., 2011; Larocque-Tobler et al., 2015) at time periods extending beyond the observational records. In this study, we selected 31 remote lakes from northern Finnish Lapland to be examined for their chironomid assemblages in the surface sediments. Our objective was to separate non-climatic environmental factors that influence the distribution of chironomids in pristine northern lakes by minimizing the air temperature gradient in the dataset. A special focus of our study was to evaluate the indicator value of sedimentary chironomid assemblages for the assessments of the versatile climate change impacts in remote northern lakes, where traditional contemporary environmental monitoring is not practical. We hypothesize that due to the central position of chironomids in benthic food webs (Cremona et al., 2014; Nevalainen et al., 2015a) and their generally detritivory feeding habits (Merritt and Cummins, 1996), changes in carbon sources, which are climate-sensitive, are significant in determining chironomid distribution. In addition to contemporary environmental assessments, the results of this study can provide important background data for future paleolimnological investigations of natural ecological variability and long-term environmental changes in remote northern lakes.

2. Materials and methods

2.1. Study sites and sampling

31 lakes were sampled from northern Finnish Lapland (68°47'–69°55' N) covering north boreal (mixed pine and birch forest) to subarctic (mountain birch woodland to barren tundra)

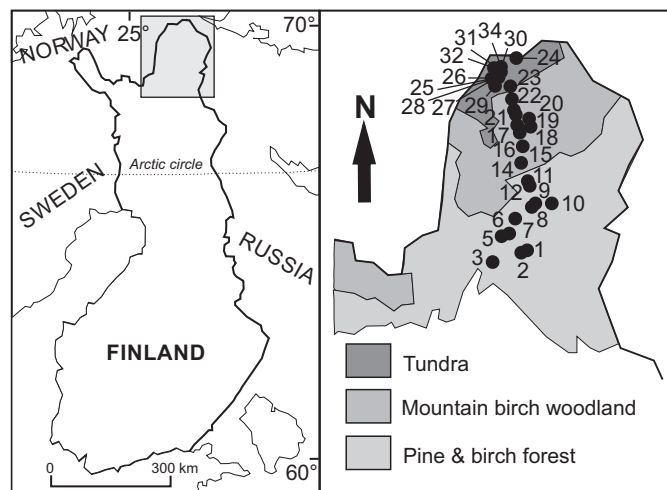


Fig. 1. Location of the study sites in northern Finland across the vegetation zones. The numbers refer to lake codes and follow Nevalainen et al. (2015b).

Table 1

General environmental characteristics of the 31 study sites in Finnish Lapland. Limnological measurements are performed from the epilimnetic waters at end of June 2014.

	Minimum	Maximum	Mean
Latitude (N)	68°47'	69°55'	
Longitude (E)	26°31'	27°30'	
Altitude (m a.s.l.)	71	289	186
Lake percentage of the catchment area (%)	0.0	44.1	11.0
Peatland percentage of the catchment area (%)	0.0	49.3	7.5
Tundra percentage of the catchment area (%)	0.0	96.1	22.5
Forest percentage of the catchment area (%)	0.0	98.8	59.0
Catchment area (ha)	2	901	78
Lake surface area (ha)	0.3	13.2	3.6
Sampling depth (m)	0.3	7.5	2.7
Mean July air temperature (°C)	12.3	13.3	12.9
Water temperature (°C)	12.0	25.8	19.3
Loss on ignition (%)	2.3	83.6	54.5
DOC (mg l ⁻¹)	1.7	16.6	5.2
pH	5.1	8.4	7.1
TP (μg l ⁻¹)	4.7	24.1	9.3
TN (μg l ⁻¹)	138	806	416
Water color (CPU)	0	130	18

ecoregions (Fig. 1). The lakes are small and shallow and without direct anthropogenic influence due to their remote location. The mean July air temperature at the lakes varies between 12.3 and 13.3 °C, whereas the altitudinal gradient ranges from 71 to 289 m a.s.l. The catchments vary from forest and bog environments to tundra vegetation, hence the lakes have large differences in their DOC, pH and water color, for example. Environmental characteristics and limnology of the study sites are tabulated in Table 1.

Surface sediments (topmost 0–2 cm) of the lakes were sampled with a Limnos gravity corer from a rubber boat at the end of July 2014. The sampling depth at the center of the basins varied from 0.3 to 7.5 m (Table 1). The samples were stored in plastic bags in a cold room at +4 °C. Samples for water quality measurements were collected during the same fieldtrip from the epilimnion. Fieldwork, sampling methods and measurement of environmental parameters are also described by Nevalainen et al. (2015b), who examined UV exposure of meiofauna in the same study lakes. Loss on ignition was used to assess the organic content of the sediments. The samples were dried at 105 °C for 12 h and ignited in an oven at 550 °C for 2 h (Heiri, 2001).

2.2. Chironomid analysis

Subsamples for fossil chironomid analysis were prepared applying standard methods (Brooks et al., 2007). The wet sediment was gently sieved through a 100- μm mesh and the residue was examined using a Bogorov sorting tray under a stereomicroscope (32–40 \times magnification). Larval head capsules were extracted with fine forceps and mounted permanently with Euparal on microscope slides. Faunal identification was performed under a light microscope at 400 \times magnification. The minimum chironomid head capsule number per sample was set to 50 (Heiri and Lotter, 2001; Larocque, 2001). Identification of the chironomids was based on Brooks et al. (2007), which also the nomenclature follows.

2.3. Numerical methods

Detrended correspondence analysis (DCA) was applied to the chironomid assemblages (square-root transformation, down-weighting of rare species) to provide an estimation of the lengths of the first two compositional gradients (DCA axes 1 and 2). DCA was also applied to summarize the community variation among the samples. Significance of the DCA axes was estimated using the broken-stick method. Since the gradient length of the first DCA axis was larger than three standard deviations (Lepš and Šmilauer, 2003), the unimodal method of canonical correspondence analysis (CCA) was selected for further use. CCA was applied to the square-root transformed assemblages and a set of environmental variables (33 limnological, climatic and catchment parameters; Table 1) to investigate community-environment relationships. Forward selection of environmental variables was performed and the significance of each variable was tested with a Monte Carlo permutation test (999 unrestricted permutations) using the significance level of $P \leq 0.05$. The DCA and CCA analyses were performed using the program CANOCO 4.5 (ter Braak and Šmilauer, 2002).

Taxon response models were calculated using generalized linear models (GLM) to identify significant relationships (at significance level $P \leq 0.05$) between taxa with Hill's (1973) N2 (effective number of occurrences) >5 and significant environmental variables and to calculate taxon-specific response curves. The GLMs were set to quadratic degree and Poisson distribution and run with CanoDraw, a component of CANOCO. Two-way indicator species analysis (TWINSPAN) was used as a divisive technique to classify the lakes and to identify indicator taxa. Pseudospecies cut levels were set to 0, 2, 5, 10, and 20%. TWINSPAN was performed using the program WinTWINS, version 2.3 (Hill and Šmilauer, 2005).

3. Results

59 different chironomid taxa were encountered from the surface sediments of the 31 lakes. In the tundra lake at the highest altitude (lake #34), only a single taxon (*Heterotrissocladius maederi*-type) occurred and the target counting sum of 50 chironomid head capsules was not met, and therefore this sample was removed from the dataset. None of the taxa occurred in all the lakes. *Psectrocladius sordidellus*-type (0–24%) was present in 27 lakes, *Tanytarsus lugens*-type (0–19%) in 25 lakes and *Procladius* (0–7%) in 24 lakes (Fig. 2). *Dicrotendipes nervosus*-type (49%), *Psectrocladius (M.) septentrionalis*-type (45%) and *Zalutschia* type B (42%) had high dominance in particular lakes (Fig. 2).

The DCA showed gradient lengths of 3.409 SD for axis 1 and 1.919 SD for axis 2 indicating unimodal nature of the data. The first DCA axis explained 14.2% and the second axis 9.5% of the assemblage data. Both axes were significant (axis 1 $P < 0.001$, axis 2 $P = 0.026$). The subsequent CCA with forward selection of environmental variables identified loss on ignition (LOI) ($F = 2.308$,

$P = 0.002$), water depth ($F = 2.252$, $P = 0.002$), total nitrogen (TN) ($F = 1.552$, $P = 0.031$) and pH ($F = 1.442$, $P = 0.046$) as significant factors explaining chironomid community composition in the lakes (Fig. 3).

The GLMs were applied using these variables to identify significant indicator taxa. The taxon response models are shown in Fig. 5. *Dicrotendipes nervosus*-type and several *Psectrocladius* taxa were significantly associated with high-organic sediments. *D. nervosus*-type was also related to low pH lakes. *Paratanytarsus* taxa were associated with intermediate organic content and water depth and high pH. *Sergentia coracina*-type was assigned for deep waters and low TN. *Chironomus anthracinus*-type was characteristic for shallow waters together with *Cladotanytarsus mancus*-type. Lakes with high TN concentrations had indicator taxa including *Microtendipes pedellus*-type, *Polypedilum nubeculosum*-type and *Psectrocladius (M.) septentrionalis*-type.

In TWINSPAN (Fig. 5), lakes with low productivity were divided into groups of warm forest lakes and cold tundra lakes. The forest lakes had high pH and included indicator taxa *Corynocera ambigua*, *Paratanytarsus penicillatus*-type, *T. lugens*-type and *C. anthracinus*-type. *Corynocera oliveri*-type was assigned as the only indicator for the cold tundra sites. The remaining lake groups were divided based on their DOC content. The high DOC lakes had also high productivity and all the sites with benthic microbial mats present were included in this group. The humid sites included *Ablabesmyia monilis*-type, *Tanytarsus pallidicornis*-type, *Psectrocladius (M.) barbatipes*-type and *P. septentrionalis*-type as indicator taxa, whereas the indicators of the group with the most humic sites were *Tanytarsus glabrescens*-type, *Tanytarsus mendax*-type, *Dicrotendipes nervosus*-type, *P. nubeculosum*-type, *Psectrocladius (M.) calcaratus*-type and *Zalutschia* type B. The low DOC lakes were divided into a group having high pH with *Procladius*, *S. coracina*-type and *Psectrocladius sordidellus*-type as indicators and a group consisting only shallow lakes with *Paratanytarsus* as an indicator taxon.

4. Discussion

4.1. Environmental controls

The generally alkaline, clear and cold-water lakes in the mountain birch woodland and barren tundra in the northernmost Lapland are known to differ significantly in their limnology compared to the more humic, warm-water lakes surrounded by forests and peatlands in the more southerly, low-altitudinal areas in Finnish Lapland (Korhola et al., 2002; Roiha et al., 2012). Also the present study sites in northeastern Lapland (Fig. 1) vary from transparent oligohumic to polyhumic lake types, along a DOC gradient of 1.7–16.6 mg l^{-1} , with all the tundra sites being low in their DOC content. Although the study area has a significant gradient in vegetation type (Fig. 1), the mean July air temperature gradient was only 1 $^{\circ}\text{C}$ (Table 1), enabling the separation of the DOC-related variables from temperature.

The current results are generally similar to the findings from northwestern Finnish Lapland (Nyman et al., 2005), where chironomid distribution was examined along a temperature gradient. This suggests that the importance of substrate type (LOI), DOC/TOC and pH, which were found as significant variables on chironomid assemblages in both studies, can be observed at different spatial scales. The present study also emphasizes the role of water depth and pH on chironomids at the local scale with a minimized temperature gradient. The results showed that there was no clear relationship between chironomid community composition and the catchment vegetation type (Fig. 2), which is in most part climate determined. In addition, according to the CCA, the community composition appeared not to be directly related to climatic variables,

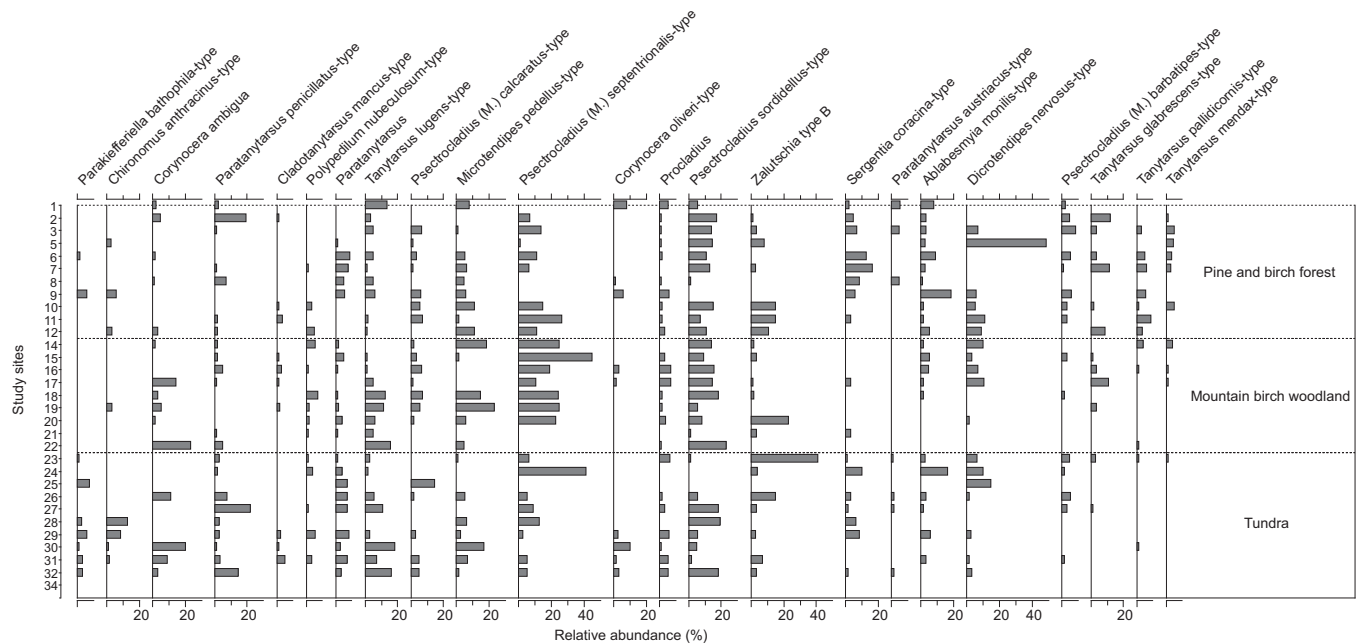


Fig. 2. Relative abundance of most common ($N_2 > 5$) chironomids in the study lakes in northern Finland. The numbers refer to lake codes and follow Nevalainen et al. (2015b). The taxa are arranged according to their preference (weighted average optima) to the specific catchment vegetation type.

such as mean July air temperature, due to the relatively short climate gradient. In common with a study from northwestern Finnish Lapland (Nyman and Korhola, 2005), the chironomid assemblages changed gradually along the environmental gradient without clear aggregates of ecological species assemblages. The CCA with forward selection of environmental variables identified LOI, water depth, TN and pH as the only significant factors explaining chironomid community composition. All these variables were more related to the second ordination axis than the first, while the first axis appeared to separate lakes with high catchment tundra percentage (Fig. 3), a variable which is associated with air temperature. However, according to the forward selection, tundra percentage was not a statistically significant explanatory factor in the dataset, though its marginal effect (tundra% as the sole constraining variable) was significant ($P = 0.009$).

Organic content and TN, which both have high axis 2 scores in CCA (Fig. 3), can be considered to represent lake productivity (Karlsson et al., 2005; Luoto and Ojala, 2014). Lake water pH can be related to productivity but also to presence of peatlands in the catchment (Weckström et al., 2010), which is apparent from the CCA ordination as the high-DOC lakes have low pH (Fig. 3). Although all the study lakes were shallow (maximum sampling depth 7.5 m, Table 1), water depth was a significant determinant of the chironomid communities. Previous studies from northeastern Finland have identified water/air temperature and LOI as the most significant factors in explaining chironomid assemblage composition (Olander et al., 1999; Nyman et al., 2005). Along an expanded latitudinal gradient, including also boreal lakes, air temperature is the most significant environmental forcing factor on chironomid community composition (Luoto et al., 2014), but also nutrient status (measured as TP) has a significant influence (Luoto, 2011a). Moreover, a study on boreal lakes in Finland (60–67°) have identified the overall impact of dystrophy and humic status to be in a significant role for dividing chironomid faunal assemblages between the oligohumic and polyhumic lake types (Luoto, 2013). A similar division between clear-water and colored lakes and their chironomid fauna has also been observed from northern Finland (Nyman and Korhola, 2005). At a more local scale, water depth and depth-related factors, such as presence of littoral vegetation,

are reported to control chironomid distribution and abundance (Luoto, 2010). Therefore, the present results are in agreement with the previous evidence on chironomid community forcing, though the environmental gradients greatly vary between the studies.

The study lakes were also allocated in the CCA ordination space according to a DOC threshold of 4 mg l^{-1} (Fig. 3). This DOC concentration is limnologically intriguing, since in low-DOC lakes ($< 4\text{--}5 \text{ mg l}^{-1}$) organic matter production is more based on autotrophic processes, while in lakes with high DOC the carbon is more allochthonous as a response of amounts of terrestrial organic matter arriving to the lakes from the catchment (Jansson et al., 2000; Forsström et al., 2013). Changes in DOC also control the underwater light milieu (Forsström et al., 2013), with the lakes under the 4 mg l^{-1} threshold being especially sensitive to UV radiation (Williamson et al., 1996; Laurion et al., 1997, 2000). In the current study, the high-DOC lakes were in most part those in which benthic microbial mats were present (Fig. 3) contrasting the assumption that these cyanobacterial-algal colonies form mainly into transparent subarctic lakes (Karlsson et al., 2009). On the other hand, the current lakes are all shallow and light penetrates to the bottom, with the exception of some of the high-DOC lakes (Nevalainen et al., 2015b). The benthic microbial production is the likely cause for these lakes having high TN concentrations, because they usually contain plenty of N-fixing cyanobacteria (Rautio et al., 2011). In boreal lakes, high TN concentrations are also closely associated with humic lakes and low TN concentrations with oligohumic lakes (Luoto, 2013), though this is not related to allocation between benthic and planktonic productivity in those systems. The high DOC lakes in the current dataset also had high organic content, which in addition to high productivity can be related to allochthonous transport of organic matter from the surrounding soils (peatlands) and vegetation. Logically, as the high-DOC lakes were polyhumic they also had low pH (Fig. 3). In Quebec, Canada, DOC was among the environmental variables that influence chironomid assemblages (Larocque et al., 2006) and in northwestern Finnish Lapland TOC was a significant explanatory variable for chironomid distribution (Nyman et al., 2005). Similar to the present study, these both dataset cover study sites over a treeline

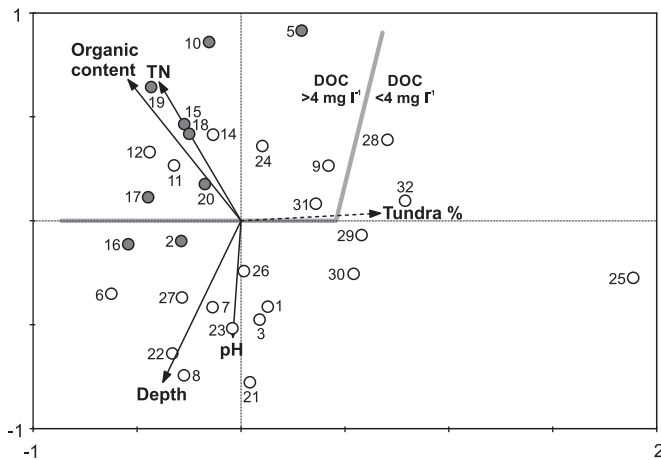


Fig. 3. Canonical correspondence analysis (CCA) results with forward-selected environmental variables in northern Finland. The percent of tundra in the catchment was not significant explanatory factor when using forward-selection, although its marginal effect on the assemblage composition was significant ($P=0.009$). Lakes with benthic microbial mats present are marked in gray and the gray line represents a dissolved organic carbon (DOC) threshold of 4 mg l^{-1} (note that sample 7 deviates from this threshold).

gradient indicating that the chironomid fauna of northern ecotones are sensitive to changes in organic carbon.

Complex species–environment relationships in shallow polymictic lakes create challenges for assessing chironomid–environment relationships along environmental gradients at different spatial scales (Medeiros and Quinlan, 2011; Wazbinski and Quinlan, 2013). The optical water properties that influence food web structure and the amount of humus that regulates lake water acidity and biological degradation are strongly related to the DOC content of lakes. Degradation of organic matter is considerably higher in humus-rich lakes than in clear-water lakes leading to decreased hypolimnetic oxygen concentrations (Schindler, 1998). Related to this, water color has been found to be important for determining the composition of chironomid communities (Walker et al., 1985). DOC itself may provide indirect nutrition for chironomids through greater food source for microbes feeding on DOC in the water column, but it may also have an inhibitory effect on their survival due to the formation of anoxic conditions (Johnson and Wiederholm, 1989; Nyman et al., 2005). The influence of other environmental factors, such as pH, food web characteristics, and substrate, may also reinforce the influence of the humic state on chironomid communities (Luoto, 2013).

4.2. Indicator value

Since organic content of the sediment (LOI), water depth, TN and pH were the significant variables in determining chironomid distribution (Fig. 3), species response models (GLMs) were produced for these variables. *Dicrotendipes nervosus*-type and *Psectrocladius* (*M.*) *calcaratus*-type showed clear preference for highly organic sediments, and also other *Psectrocladius* taxa and *Paratanytarsus* taxa had preference for organic substrates (Fig. 4) in common with observations from northwestern Finnish Lapland (Nyman and Korhola, 2005). All these taxa are associated with littoral vegetation (Brooks et al., 2007), which implies that the substrate material reflects the vegetative properties of the lakes. No statistically significant indicator taxa for minerogenic sediments were identified in this study, although *Heterotrissocladius maeae*-type, which has been found to be associated with sandy and silty substrates (Luoto et al., 2010; Shala et al., 2014), dominated the coldest tundra lake with very low organic matter content (lake #34). *Sergentia*

coracina-type was closely associated with deep sites (Fig. 4), which has also been observed from boreal and alpine lakes at different spatial scales (Luoto, 2012). Similar unimodal responses compared to previous studies were found in the depth preferences of *Paratanytarsus* taxa, *Procladius* and *Cladotanytarsus mancus*-type (Mousavi, 2002; Luoto, 2012) and also the shallow water preference of *Chironomus anthracinus*-type has been previously observed from boreal lakes (Mousavi, 2002; Luoto, 2009), hence indicating spatial uniformity in chironomid water depth optima.

In a previous study from boreal lakes in Finland, the most significant water quality variables in controlling chironomid distribution were TP (gradient $1.5\text{--}105 \mu\text{g l}^{-1}$) and TN ($110\text{--}1400 \mu\text{g l}^{-1}$) (Luoto, 2011a). In the current northern dataset, there were only oligo- and mesotrophic lakes present and the eutrophic lake type was absent. *Microtendipes pedellus*-type and *Polypedilum nubeculosum*-type were identified as indicators of high TN (Fig. 4). In agreement, these taxa have been shown to prefer mesotrophic lakes in the boreal zone (Luoto, 2011a). However, the high TN optimum for *Psectrocladius septentrionalis*-type has not been previously observed, but it may be related to the increased littoral vegetation in more nutrient-rich water bodies, or alternatively the presence of microbial mats. The taxa preferring low-TN lakes in the current dataset, including *S. coracina*-type, *Corynocera oliveri*-type and *Parakiefferiella bathophila*-type, are also previously found to thrive in oligotrophic lakes (Brooks et al., 2007; Luoto, 2011a).

pH is usually not found to have significant influence on chironomid community composition, and therefore information about the chironomid pH optima is scarce. It is possible that the influence of pH in the current lake set derives from the humic effects, which have been found to have influence on chironomid success (Saether, 1979; Luoto, 2013). The indicators of alkaline lakes were *Paratanytarsus penicillatus*-type and *P. austriacus*-type, whereas the indicators of acidic lakes included *Dicrotendipes nervosus*-type, *Psectrocladius* (*M.*) *barbatipes*-type and *Tanytarsus pallidicornis*-type (Fig. 4). In boreal lakes, *Psectrocladius* (*M.*) and *Tanytarsus* have also been found to be associated with acidic waters (Mousavi, 2002) and also *Dicrotendipes* is common in acidic lakes (Dougherty and Morgan, 1991). *Zalutschia* type B was abundant in both alkaline and acidic lakes, but absent in neutral lakes that may indicate that some other environmental factor, such as DOC concentration, is causing this distributional pattern. Usually *Zalutschia* is found from acidic sites, since it is associated with humic bog lakes with low pH (Walker and MacDonald, 1995).

The TWINSPLAN results, which can be considered to provide guidelines for regional lake classification in assessments for environmental change, divided low-productivity sites into cold tundra sites and warm forest sites according to their chironomid communities (Fig. 5). The indicator for tundra environment was *Corynocera oliveri*-type, which is a cold-adapted taxon (Brooks et al., 2007). The warm (relative to the study area) forest sites also had high pH. The indicator taxa for these lakes included *C. ambigua*, *Tanytarsus lugens*-type, *C. anthracinus*-type and *M. pedellus*-type. These taxa have also previously been found to commonly occur together in Finnish and Swedish Lapland (Larocque et al., 2001; Nyman et al., 2005). However, there is some controversy in the ecological preferences of *C. anthracinus*-type between the present study and results from boreal lakes in Finland, where the taxon is found to be more common in acidic lakes (Luoto, 2011b). This may be due to nutrient related factors because the low-pH lakes in the current subarctic lakes have also high productivity, whereas in the boreal dataset the low-pH lakes have low-productivity. The current results also shed light on the enigmatic ecology of *C. ambigua* by assigning it to the relatively warm, low-productive and high-pH lake group (Fig. 5). Against most other evidence, the taxon has been shown to occur sporadically in productive temperate lakes in Denmark

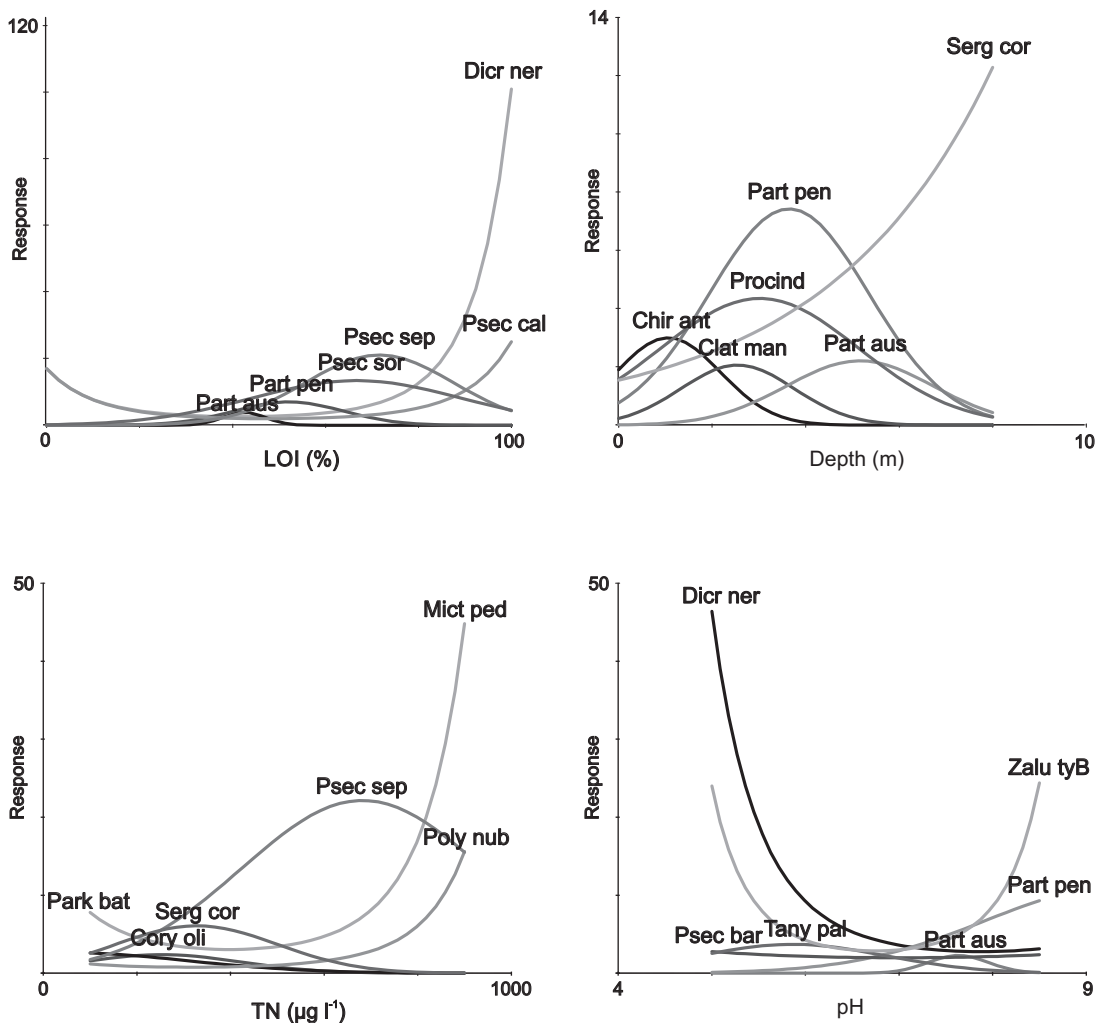


Fig. 4. Species response models based on generalized linear modeling (GLM) for chironomid indicator taxa ($N_2 > 5$, $P < 0.05$) of sediment organic content (loss on ignition, LOI), water depth, total nitrogen (TN) and pH. The taxa codes are abbreviated from the first four letters of the genus names and first three letters of species names.

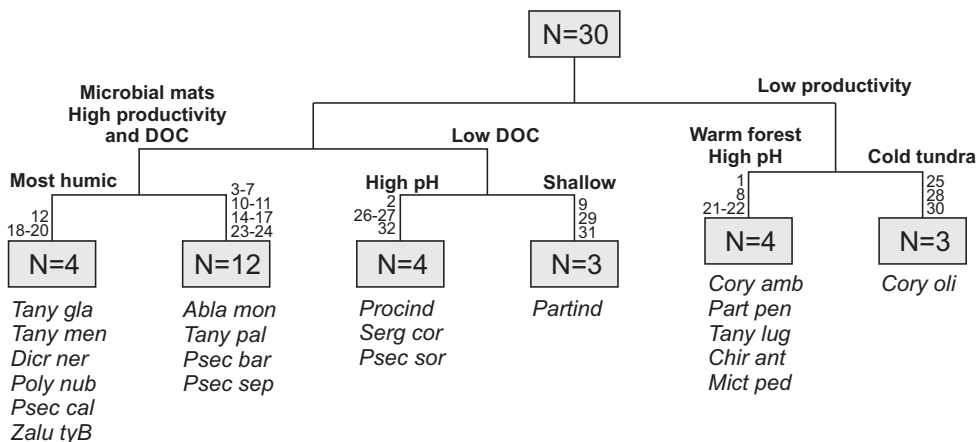


Fig. 5. Grouping of 30 Finnish Lapland lakes according to two-way indicator species analysis (TWINSpan) based of chironomid assemblages. The taxa codes are abbreviated from the first four letters of the genus names and first three letters of species names.

(Brodersen and Lindegaard, 1999). In distributional datasets, the taxon has been usually assigned for relative cold lakes (north boreal, subarctic) (Gajewski et al., 2005; Luoto et al., 2012) and in paleolimnological investigations it has been shown to increase in abundance during environmental disturbances (Engels et al., 2014; Shala et al., 2014; Pawłowski et al., 2015). Therefore, the species probably

benefits in situations where environmental conditions in subarctic lakes generally change.

In addition to the low-productivity sites, TWINSpan divided the study lakes into low DOC and high DOC groups (Fig. 5). The low-DOC lake type was further divided into shallow (*Paratanytarsus*) and high-pH (*Procladius*, *Sergentia coracina*-type and

P. sordidellus-type) lake groups. Controversially, the indicator taxa of the high-pH lake group have previously been found to be associated with mildly acidic boreal lakes in Finland (Luoto, 2011b). This controversy may be related to differences in the limnology of boreal and subarctic lakes or to the fact that pH is not the most important environmental determinant of these taxa. The high-DOC lakes had increased productivity and also included benthic microbial mats. The indicators for this lake group were *Ablabesmyia monilis*-type, *T. pallidicornis*-type, *P. barbatipes*-type and *P. septentrionalis*-type, whereas the most humic lakes in this group were characterized by the presence of *Tanytarsus glabrescens*-type, *T. mendax*-type, *D. nervosus*-type, *P. nubeculosum*-type, *P. calcaratus*-type and Z. type B. DOC can influence aquatic communities by attenuating light penetration and by changing the thermal stratification of lakes (Vincent and Roy, 1993; Karlsson et al., 2009). Carbon has also direct influence on chironomid growth through their feeding habits (Wilcox et al., 2005), and hence differences in carbon sources might explain these patterns in distribution.

4.3. Implications for climate change assessments

The climate forcing on physical properties of northern lakes include changes in thermal regime and mixing, underwater solar radiation and water depth, volume and residence time (Williamson et al., 2009). The geochemical changes are related to changes in dissolved oxygen, nutrients (P, N), dissolved organic matter and organo-metal complexes, whereas the climate forcing on the biological environment includes changes in biodiversity, biomass and production, food web structure and trophic relationships (Williamson et al., 2009). In aquatic biogeochemical cycles, benthic chironomids are in the hotspot due to their mainly detritivorous behavior recycling organic matter. The current results emphasize the role of chemical environment on chironomid distribution and suggest that they are sensitive indicators for these environmental parameters (Figs. 3–5).

Climate change scenarios for Finland project major increase in air temperature and precipitation (Carter et al., 2004; Jylhä et al., 2004). The expected changes in Finland will have a greater affect during winters than summers (Luoto et al., 2013), critically influencing factors such as the development and duration of the snow cover. Winter snow accumulation is an important climate change feedback mechanism and provides a critical ecological threshold for ecosystem health (Smol and Douglas, 2007). In addition to the cascading effects of the increased temperatures in the future, the increased precipitation in Finland will cause more frequent and larger flooding, especially during the spring snowmelt season through changes in surface runoff and lake levels.

The impact of climate change on catchment vegetation affects limnology of ecotonal lakes, such as the current sites, in various ways. Northern lakes are especially sensitive to climate-induced changes because climate change effects are amplified in polar regions (Bekryaev et al., 2010) and the treeline ecotone is experiencing noticeable changes as the forest line advances further north and higher on the fjelds (Harsch et al., 2009). Increase in surface temperatures causes also higher weathering rates and longer hydraulic residence times (Maher, 2010). Increased precipitation can lead to higher ground water levels that could subsequently increase peatland areas and thereby promote higher levels of organic matter in lakes (Evans et al., 2006). This is especially important in the current study site, where peatlands already cover vast areas. On the opposite scenario to what has been projected for Finland (Jylhä et al., 2004), if surface water levels were to decline the bog areas could expand northwards over present fen area and cause changes in humic matter decomposition and release rates and affect acidity and water color of lakes (Korhola et al., 2002). In any case, the expansion of forests and mires proposes a

serious threat to treeline lakes, which are typically naturally low in humic substances and have hence clear water, causing increased humus content and water color. Therefore, the existence of clear-water lakes, which were also represented in the present dataset and are characteristic of the tundra areas of Lapland, are threatened along with their climate-sensitive aquatic ecosystems. This phenomenon has already been observed in the subarctic Sweden (Callaghan et al., 2010). Furthermore, nutrient and carbon enrichment will enhance nutrient cycling and productivity, and alter the generation and consumption of carbon-based trace gases consequently causing changes in the status of aquatic ecosystems as carbon sinks or sources (Wrona et al., 2006; Jutinen et al., 2013). The high share of lakes in northern Lapland makes the present study area particularly important for carbon cycling. Enhanced carbon (including DOC) loads may increase turbidity reducing photosynthesis and the subsequent rise in the availability of organic matter will probably result in a concomitant increase in benthic microbial respiration, which produces CO₂ (Ramlal et al., 1994). Furthermore, CH₄ production is accelerated by simultaneous increases in organic matter, nutrients and temperature (Yvon-Durocher et al., 2014) boosting carbon and energy availability for MOB in microbial mats, and consequently supporting higher trophic level food webs (Jansson et al., 2008; Ravinet et al., 2010).

Since the present study sites were selected so that the temperature gradient is truncated (mean July temperature range = 1 °C), we were able to separate the non-climatic forcing on chironomid communities in these natural high latitude lakes. The results show that the chironomid distribution and abundance in northern Lapland is mostly determined by factors related to catchment properties, lake productivity and particular physical characteristics (Fig. 3). These environmental factors are all, at least partly, climate-driven. Therefore, in addition to the direct influence of temperature on chironomids (Eggermont and Heiri, 2012), climate warming and increasing precipitation will influence chironomids indirectly through the climate change impacts on catchments and limnology and food web functioning. The identified indicator taxa for particular environmental variables (Figs. 4 and 5) are likely to be most sensitive to these indirect influences of climate change. The influence of humic substances on chironomids and benthic food webs, presence of benthic microbial mats and the DOC threshold of 4 mg l⁻¹, around which significant changes between lakes are expected, should be studied in more detail in the future. This is important, since projected increases in water temperature and inputs of carbon arising from climate change are very likely to affect the structural and functional dynamics of the microbial food web, and are likely to increase rates of carbon processing (Wrona et al., 2006).

5. Conclusions

The results suggest that chironomid assemblages are significantly related to environmental factors that are sensitive to climate change, such as catchment characteristics, lake productivity and water depth. We were able to assign indicator taxa for sediment organic content, TN, pH and water depth, since these variables were those that significantly explained chironomid community composition. Furthermore, a DOC threshold (4 mg l⁻¹) important for chironomids was identified, which is closely related to a lake type where benthic primary production dominates creating microbial mats to the sediment-water interface. We project that these polar lakes will have cumulative environmental responses in the future due to the superimposed effects of increased temperatures and climate-induced catchment and limnological changes. The results are useful for future assessments of climate change impacts on remote northern lakes through estimations of ecosystem status

and evaluation of past, present and future climate change using limnological and paleolimnological approaches.

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References

- Bekryaev, R.V., Polyakov, I.V., Alexeev, V.A., 2010. Role of polar amplification in long-term surface air temperature variations and modern Arctic warming. *J. Clim.* 23, 3888–3906.
- Brodersen, K.P., Lindegaard, C., 1999. Mass occurrence and sporadic distribution of *Corynocera ambigua* Zetterstedt (Diptera, Chironomidae) in Danish lakes Neand and palaeolimnological records. *J. Paleolimnol.* 22, 41–52.
- Brodersen, K.P., Quinlan, R., 2006. Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. *Quat. Sci. Rev.* 25, 1995–2012.
- Brooks, S.J., Bennion, H., Birks, H.J.B., 2001. Tracing lake trophic history with a chironomid – total phosphorus inference model. *Freshw. Biol.* 46, 513–533.
- Brooks, S.J., Langdon, P.G., Heiri, O., 2007. The Identification and Use of Palaeoarctic Chironomidae Larvae in Palaeoecology. QRA Technical Guide No. 10. Quaternary Research Association, London, 276 pp.
- Callaghan, T.V., Bergholm, F., Christensen, T.R., Jonasson, C., Kokfelt, U., Johansson, M., 2010. A new climate era in the sub-Arctic: accelerating climate changes and multiple impacts. *Geophys. Res. Lett.* 37, L14705, <http://dx.doi.org/10.1029/2009GL042064>.
- Carter, T.R., Fronzek, S., Bärlund, I., 2004. FINSKEN: a framework for developing consistent global change scenarios for Finland in the 21st century. *Boreal Environ. Res.* 9, 91–107.
- Cremona, F., Timm, H., Agasild, H., Tönno, I., Feldmann, T., Jones, R.I., Nöges, T., 2014. Benthic foodweb structure in a large shallow lake studied by stable isotope analysis. *Freshw. Sci.* 33, 885–894.
- Dougherty, J.E., Morgan, M.D., 1991. Benthic community response (primarily Chironomidae) to nutrient enrichment and alkalization in shallow, soft water humic lakes. *Hydrobiologia* 215, 73–82.
- Dokulil, M.T., 2014. Impact of climate warming on European inland waters. *Inland Waters* 4, 27–40.
- Eggermont, H., Heiri, O., 2012. The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. *Biol. Rev.* 87, 430–456.
- Engels, S., Self, A.E., Luoto, T.P., Brooks, S.J., Helmens, K.F., 2014. A comparison of three Eurasian chironomid-climate calibration datasets on a W-E continental gradient and the implications for quantitative temperature reconstructions. *J. Paleolimnol.* 51, 529–547.
- Evans, C.D., Chapman, P.J., Clark, J.M., Monteith, D.T., Cresser, M.S., 2006. Alternative explanations for rising dissolved organic carbon export from organic soils. *Global Change Biol.* 12, 2044–2053.
- Forsström, L., Roiha, T., Rautio, M., 2013. Microbial food web responses to increased allochthonous DOM in an oligotrophic subarctic lake. *Aquat. Microb. Ecol.* 68, 171–184.
- Gajewski, K., Bouchard, G., Wilson, S.E., Kurek, J., Cwynar, L.C., 2005. Distribution of Chironomidae (Insecta: Diptera) head capsules in recent sediments of Canadian Arctic lakes. *Hydrobiologia* 549, 131–143.
- Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* 12, 1040–1049.
- Heiri, O., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *J. Paleolimnol.* 25, 101–110.
- Heiri, O., Lotter, A.F., 2001. Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. *J. Paleolimnol.* 26, 343–350.
- Heiri, O., Brooks, S.J., Birks, H.J.B., Lotter, A.F., 2011. A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. *Quat. Sci. Rev.* 30, 3445–3456.
- Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427–432.
- Hill, M.O., Šmilauer, P., 2005. TWINSPLAN for Windows, Version 2.3. Centre for Ecology and Hydrology, University of South Bohemia, Huntington & České Budějovice.
- Jansson, M., Hickler, T., Jonsson, A., Karlsson, J., 2008. Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in subarctic Sweden. *Ecosystems* 11, 367–376.
- Jansson, M., Bergström, A.K., Blomqvist, P., Drakare, S., 2000. Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in clear-water and humic lakes. *Ecology* 81, 3250–3255.
- Johnson, K., Wiederholm, T., 1989. Classification and ordination of profundal macroinvertebrate communities in nutrient poor, oligo-mesohumic lakes in relation to environmental data. *Freshw. Biol.* 21, 375–386.
- Jones, R.I., Carter, C.E., Kelly, A., Ward, S., Kelly, D.J., Grey, J., 2008. Widespread contribution of methane-cycle bacteria to the diets of lake profundal chironomid larvae. *Ecology* 89, 857–864.
- Juutinen, S., Väiliranta, M., Kuutti, V., Laine, A.M., Virtanen, T., Seppä, H., Weckström, J., Tuittila, E.S., 2013. Short-term and long-term carbon dynamics in a northern peatland-stream-lake continuum: a catchment approach. *J. Geophys. Res. Biogeosci.* 118, 171–183.
- Jylhä, K., Tuomenvirta, H., Ruosteenoja, K., 2004. Climate change projections for Finland during the 21st century. *Boreal Environ. Res.* 9, 127–152.
- Jyväsjärvi, J., Aroviita, J., Hämäläinen, H., 2014. An extended Benthic Quality Index for assessment of lake profundal macroinvertebrates: addition of indicator taxa by multivariate ordination and weighted averaging. *Freshw. Sci.* 33, 995–1007.
- Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of nutrient-poor lake ecosystems. *Nature* 460, 506–509.
- Karlsson, J., Jonsson, A., Jansson, M., 2005. Productivity of high-latitude lakes: climate effect inferred from altitude gradient. *Glob. Change Biol.* 11, 710–715.
- Korhola, A., Weckström, J., Blom, T., 2002. Relationships between lake and land-cover features along latitudinal vegetation ecotones in arctic Fennoscandia. *Arc. Hydrobiol.* 139, 203–235.
- Larocque, I., 2001. How many chironomid head capsules are enough? A statistical approach to determine sample size for palaeoclimatological reconstructions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 172, 133–142.
- Larocque, I., Hall, R.I., Grahn, E., 2001. Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). *J. Paleolimnol.* 26, 307–322.
- Larocque, I., Pienitz, R., Rolland, N., 2006. Factors influencing the distribution of chironomids in lakes distributed along a latitudinal gradient in northwestern Quebec, Canada. *Can. J. Fish. Aquat. Sci.* 63, 1286–1297.
- Larocque-Tobler, I., Filipiak, J., Tylmann, W., Bonk, A., Grosjean, M., 2015. Comparison between chironomid-inferred mean-August temperature from varved Lake Żabińskie (Poland) and instrumental data since 1896 AD. *Quat. Sci. Rev.* 111, 35–50.
- Laurion, I., Ventura, M., Catalan, J., Psenner, R., Sommaruga, R., 2000. Attenuation of ultraviolet radiation in mountain lakes: factors controlling the among- and within-lake variability. *Limnol. Oceanogr.* 45, 1274–1288.
- Laurion, I., Vincent, W.F., Lean, D.R.S., 1997. Underwater ultraviolet radiation: development of spectral models for northern high latitude lakes. *Photochem. Photobiol.* 65, 107–114.
- Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press.
- Luoto, T.P., 2013. Dystrophy in determining midge community composition in boreal lakes. *Ecosystems* 20, 391–398.
- Luoto, T.P., 2012. Spatial uniformity in depth optima of midges: evidence from sedimentary archives of shallow Alpine and boreal lakes. *J. Limnol.* 71, 228–232.
- Luoto, T.P., 2011a. The relationship between water quality and chironomid distribution in Finland – a new assemblage-based tool for assessments of long-term nutrient dynamics. *Ecol. Indic.* 11, 255–262.
- Luoto, T.P., 2011b. Indicator value of midge larvae (Diptera: Nematocera) in shallow boreal lakes with a focus on habitat, water quality, and climate. *Aquat. Insect* 33, 351–370.
- Luoto, T.P., 2010. Hydrological change in lakes inferred from midge assemblages through use of an intralake calibration set. *Ecol. Monogr.* 80, 303–329.
- Luoto, T.P., 2009. A Finnish chironomid- and chaoborid-based inference model for reconstructing past lake levels. *Quat. Sci. Rev.* 28, 1481–1489.
- Luoto, T.P., Nevalainen, L., 2015. Climate-forced patterns in midge feeding guilds. *Hydrobiologia* 742, 141–152.
- Luoto, T.P., Ojala, A.E.K., 2014. Paleolimnological assessment of ecological integrity and eutrophication history for Lake Tiiläänjärvi (Askola Finland). *J. Paleolimnol.* 51, 455–468.
- Luoto, T.P., Salonen, V.-P., 2010. Fossil midge larvae (Diptera: Chironomidae) as quantitative indicators of late-winter hypolimnetic oxygen in southern Finland: a calibration model, case studies and potentialities. *Boreal Environ. Res.* 15, 1–18.
- Luoto, T.P., Kaukolehto, M., Weckström, J., Korhola, A., Väiliranta, M., 2014. New evidence of warm early-Holocene summers in subarctic Finland based on an enhanced regional chironomid-based temperature calibration model. *Quat. Res.* 81, 50–62.
- Luoto, T.P., Helama, S., Nevalainen, L., 2013. Stream flow intensity of the Saavajoki River, eastern Finland, during the past 1500 years reflected by mayfly and caddisfly mandibles in adjacent lake sediments. *J. Hydrol.* 476, 147–153.
- Luoto, T.P., Nevalainen, L., Salonen, V.-P., 2012. Midge distribution patterns at multiple spatial scales in shallow Finnish lakes revealed through sedimentary records. *Entomol. Fennica* 23, 83–94.
- Luoto, T.P., Kultti, S., Nevalainen, L., Sarmaja-Korjonen, K., 2010. Temperature and effective moisture variability in southern Finland during the Holocene quantified with midge-based calibration models. *J. Quat. Sci.* 25, 1317–1326.
- Maher, K., 2010. The dependence of chemical weathering rates on fluid residence time. *Earth Planet. Sci. Lett.* 294, 101–110.
- Medeiros, A.S., Quinlan, R., 2011. The distribution of the Chironomidae (Insecta: Diptera) along multiple environmental gradients in lakes and ponds of the eastern Canadian Arctic. *Can. J. Fish. Aquat. Sci.* 68, 1511–1527.
- Merritt, R.W., Cummins, K.W. (Eds.), 1996. An Introduction to the Aquatic Insects of North America. Kendall-Hunt, Dubuque.

- Mousavi, S.K., 2002. Boreal chironomid communities and their relations to environmental factors—the impact of lake depth, size and acidity. *Boreal Environ. Res.* 7, 63–75.
- Nevalainen, L., Luoto, T.P., Manca, M., Weisse, T., 2015a. A paleolimnological perspective on aquatic biodiversity in Austrian mountain lakes. *Aquat. Sci.* 77, 59–69.
- Nevalainen, L., Luoto, T.P., Rantala, M.V., Galkin, A., Rautio, M., 2015b. Role of terrestrial carbon in aquatic UV exposure and photoprotective pigmentation of meiofauna in subarctic lakes. *Freshw. Biol.* 60, 2435–2444.
- Nyman, M., Korhola, A., 2005. Chironomid-based classification of lakes in western Finnish Lapland. *Boreal Environ. Res.* 10, 239–254.
- Nyman, M., Korhola, A., Brooks, S.J., 2005. The distribution and diversity of *Chironomidae* (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. *Global Ecol. Biogeogr.* 14, 137–153.
- Olander, H., Birks, H.J.B., Korhola, A., Blom, T., 1999. An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *Holocene* 9, 279–294.
- Pawłowski, D., Plóciennik, M., Brooks, S.J., Luoto, T.P., Milecka, K., Nevalainen, L., Peyron, O., Self, A., Ziełiński, T., 2015. A multiproxy study of Younger Dryas and Early Holocene climatic conditions from the Grabia River palaeo-oxbow lake (central Poland). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 438, 34–50.
- Pinder, L.C.V., 1986. Biology of freshwater *Chironomidae*. *Annu. Rev. Entomol.* 31, 1–23.
- Ramlal, P.S., Hesslein, R.H., Hecky, R.E., Fee, E.J., Rudd, J.W.M., Guildford, S.J., 1994. The organic carbon budget of a shallow arctic tundra lake on the Tuktoyaktuk Peninsula, NWT, Canada: Arctic lake carbon budget. *Biogeochemistry* 24, 145–172.
- Rantala, M.V., Luoto, T.P., Nevalainen, L., 2015. Late Holocene changes in the humic state of a boreal lake and their associations with organic matter transport and climate dynamics. *Biogeochemistry* 123, 63–82.
- Rautio, M., Dufresne, F., Laurion, I., Bonilla, S., Vincent, W.F., Christoffersen, K.S., 2011. Shallow freshwater ecosystems of the circumpolar Arctic. *Écoscience* 18, 204–222.
- Ravinet, M., Syväranta, J., Jones, R.I., Grey, J., 2010. A trophic pathway from biogenic methane supports fish biomass in a temperate lake ecosystem. *Oikos* 119, 409–416.
- Roiha, T., Tirola, M., Gazzanelli, M., Rautio, M., 2012. Carbon quantity defines productivity while its quality defines community composition of bacterioplankton in subarctic ponds. *Aquat. Sci.* 74, 519–525.
- Rühland, K.M., Paterson, A.M., Smol, J.P., 2015. Lake diatom responses to warming: reviewing the evidence. *J. Paleolimnol.* 54, 1–35.
- Ruse, L., 2010. Classification of nutrient impact on lakes using the chironomid pupal exuvial technique. *Ecol. Indic.* 10, 594–601.
- Saether, O.A., 1979. Chironomid communities as water quality indicators. *Ecography* 2, 65–74.
- Schindler, D.W., 1998. Sustaining aquatic ecosystems in boreal regions. *Conserv. Ecol.* 2, 18.
- Shala, S., Helmens, K.F., Luoto, T.P., Väiliranta, M., Weckström, J., Salonen, J.S., Kuhry, P., 2014. Evaluating environmental drivers of Holocene changes in water chemistry and aquatic biota composition at Lake Loitsana, NE Finland. *J. Paleolimnol.* 52, 311–329.
- Small, G.E., Wares, J.P., Pringle, C.M., 2011. Differences in phosphorus demand among detritivorous chironomid larvae reflect intraspecific adaptations to differences in food resource stoichiometry across lowland tropical streams. *Limnol. Oceanogr.* 56, 268–278.
- Smol, J.P., Douglas, M.S., 2007. From controversy to consensus: making the case for recent climate change in the Arctic using lake sediments. *Front. Ecol. Environ.* 5, 466–474.
- ter Braak, C.J., Smilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination* (version 4.5).
- Van Hardenbroek, M., Heiri, O., Parmentier, F.J.W., Bastviken, D., Ilyashuk, B.P., Wiklund, J.A., Hall, R.I., Lotter, A.F., 2013. Evidence for past variations in methane availability in a Siberian thermokarst lake based on $\delta^{13}\text{C}$ of chitinous invertebrate remains. *Quat. Sci. Rev.* 66, 74–84.
- Vincent, W.F., Roy, S., 1993. Solar ultraviolet-B radiation and aquatic primary production: damage, protection and recovery. *Environ. Rev.* 1, 1–12.
- Walker, I.R., MacDonald, G.M., 1995. Distributions of *Chironomidae* (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arct. Alp. Res.* 27, 258–263.
- Walker, I.R., Fernando, C.H., Peterson, C.G., 1985. Associations of *Chironomidae* (Diptera) of shallow, acid, humic lakes and bog pools in Atlantic Canada, and a comparison with an earlier paleoecological investigation. *Hydrobiologia* 120, 11–22.
- Wazbinski, K.E., Quinlan, R., 2013. Midge (*Chironomidae*, *Chaoboridae*, *Ceratopogonidae*) assemblages and their relationship with biological and physicochemical variables in shallow, polymictic lakes. *Freshw. Biol.* 58, 2464–2480.
- Weckström, J., Seppä, H., Korhola, A., 2010. Climatic influence on peatland formation and lateral expansion in sub-arctic Fennoscandia. *Boreas* 39, 761–769.
- Wilcox, H.S., Wallace, J.B., Meyer, J.L., Benstead, J.P., 2005. Effects of labile carbon addition on a headwater stream food web. *Limnol. Oceanogr.* 50, 1300–1312.
- Williamson, C.E., Saros, J.E., Vincent, W.F., Smol, J.P., 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnol. Oceanogr.* 54, 2273–2282.
- Williamson, C.E., Stemberger, R.S., Morris, D.P., Frost, T.M., Paulsen, S.G., 1996. Ultraviolet radiation in North American lakes: attenuation estimates from DOC measurements and implications for plankton communities. *Limnol. Oceanogr.* 41, 1024–1034.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M., Vincent, W.F., 2006. Climate change effects on aquatic biota, ecosystem structure and function. *Ambio* 35, 359–369.
- Yvon-Durocher, G., Allen, A.P., Bastviken, D., Conrad, R., Gudasz, C., St-Pierre, A., Thanh-Duc, N., Del Giorgio, P.A., 2014. Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. *Nature* 507, 488–491.