Recent changes in chironomid communities and hypolimnetic oxygen conditions relate to organic carbon in subarctic ecotonal lakes

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Abstract

A key question in aquatic elemental cycling is related to the influence of bottom water oxygen conditions in regulating the burial and release of carbon under climate warming. In this study, we used head capsules of Chironomidae larvae to assess community and diversity change between the past (estimated as Pre-Industrial Period) and present and to reconstruct changes in hypolimnetic oxygen conditions from 30 subarctic ecotonal lakes (northeastern Lapland) using the top-bottom paleolimnological approach applying surface sediment (topmost 0-2 cm) and reference (4-5 cm) samples. Subsequently, we tested the findings against dissolved organic carbon (DOC) concentration of the sites. We found that the benthic communities were statistically dissimilar between the past and the present with largest changes occurring in the more transparent oligo-mesohumic lakes. However, murky polyhumic lakes displayed uniformly a decrease in diversity. The chironomid-inferred oxygen values showed a general decrease towards the present with largest shifts in low-DOC lakes, whereas no significant changes were found in the hypolimnetic oxygen conditions of high-DOC lakes, which were often located in wetland areas. These finding suggest that lakes associated with constant organic carbon inputs are more resilient toward climate-induced reductions in hypolimnetic oxygen.

Keywords: Chironomidae; dissolved oxygen; Lapland; DOC; paleolimnology; top-bottom approach

1 Introduction

Carbon storage in high-latitude peatlands represents a major share of the global soil carbon pool (Tranvik et al., 2009; Schuur et al., 2015). With permafrost thawing and subsequent formation of thaw lakes, larger emissions of carbon dioxide (CO_2) and methane (CH_4) are expected (Walter et al., 2006; Wauthy et al., 2018). Since lakes are important sources of greenhouse gases (Aben et al., 2017), in the context of climate change, it is essential to understand how carbon release is regulated by different levels of oxygen availability at the surface-sediment interface of lakes (Liikanen et al., 2002). Although there is CH_4 formation also in oxic water layers (Tang et al., 2016), CH_4 is mostly produced by anoxic decomposition of organic carbon and, importantly for the ongoing climate change, it has a multifold atmospheric warming potential compared to CO_2 (Deemer et al., 2016).

While in lakes with well-oxygenated bottom waters a significant part of the produced CH_4 is oxidized into CO_2 and not emitted to the atmosphere, a contrasting situation occurs in oxygen depleted lakes. In addition to hypolimnetic oxygen, there appears to be a consistent temperature dependency of CH_4 fluxes across microbial to ecosystem scales (Yvon-Durocher et al., 2014) that well-represents the cascading climate change impacts and feedback systems. In particular, methanogenesis, carried out by strictly anaerobic Archaea, is the terminal step in the remineralization of organic matter and, like most other forms of metabolism, methanogenesis is temperature-dependent (Yvon-Durocher et al., 2014). Therefore, since climate warming is emphasized in subarctic and arctic regions (Linderholm et al., 2018), northern lakes play a significant role in the ongoing climate change through their functions in carbon release and sequestration.

Chironomid (Insecta: Diptera: Chironomidae) larvae take part in benthic processes that are essential for lake ecosystem functions (Benke and Huryn, 2010; Hölker et al., 2015). Most importantly, chironomids living in the water-sediment interface have a major role in the biogeochemical cycling of carbon, nitrogen and phosphorus (Nogaro et al., 2008; Belle et al., 2017). The functional roles of chironomids are mostly reflected by their feeding preferences (Heino, 2008; Luoto and Nevalainen, 2015), but their taxonomical compositions typically respond to climate conditions at the regional scale (Brooks, 2006) and hypolimnetic oxygen and nutrient conditions at the local/site-specific scale (Brodersen and Quinlan, 2006). In Finnish Lapland, the most important environmental factors controlling chironomid distribution and abundance are temperature, organic content of the sediment, nutrients/oxygen and water depth (Olander et al., 1997; Nyman et al., 2005; Luoto et al., 2016). Hence, chironomids contribute as sensitive indicators of climate changes, limnology and elemental cycling. The influence of temperature on chironomids can be direct (metabolism) or indirect (e.g. habitat) and mediated through air (flying adults) or water (aquatic larval stage) temperature (Eggermont and Heiri, 2012), whereas the influence of hypolimnetic oxygen is related to the species-specific respiration rates and oxygen demands (Brodersen et al., 2008). Using the transfer function approach (calibration-in-space), it is possible to provide long-term quantitative reconstructions of these variables (Quinlan and Smol, 2002; Luoto et al., 2017; Wohlfarth et al., 2018).

In this study, we investigate chironomid assemblages and changes in chironomid-inferred hypolimnetic oxygen conditions in 30 subarctic lakes in northern Finnish Lapland using the top-bottom (or before-after) paleolimnological approach (Quinlan and Smol, 2002), where the surface sediment samples (top) represent the present and the reference samples (bottom) the past. We examine the findings against the modern dissolved organic carbon (DOC) gradient of the lakes to find out potential differences caused by catchment characteristics, with special interest on the influence of peatlands.

2 Material and Methods

2.1 Study sites and sampling strategy

The study sites include 30 lakes from northeastern Finnish Lapland (68°47'–69°55'N) with a catchment gradient from mixed pine and birch forest to mountain birch woodland and barren tundra (Fig. 1). The study area is located in a sporadic permafrost region. All the lakes are small and shallow (<7.5 m) and distributed along a truncated mean July air temperature transect from 12.3 to 13.3 °C. While minimizing the temperature gradient, the lakes were sampled to characterize different catchment types from forest and bog environments to tundra vegetation to encompass a broad dissolved organic carbon (DOC) gradient from 1.7 to 16.6 mg l^{-1}. The sampling strategy was originally designed to study spatio-temporal zooplankton responses to UV radiation (the DOC screening effect) (Nevalainen et al., 2018) and to investigate the sources and controls of organic carbon in these lakes (Rantala et al., 2016a). The dataset consists of 15 oligohumic (DOC <4 mg l^{-1}), 10 mesohumic (DOC = 4-6 mg l^{-1}) and 5 polyhumic (DOC >6 mg l^{-1}) lakes. Total phosphorus in the lakes varies from 5 to 24 μg l^{-1}, total nitrogen from 138 to 806 μg l^{-1} and pH from 5.1 to 8.4. Environmental characteristics and limnology of the study sites are described in detail in Rantala et al. (2016a). The lakes and their codes (numbers) are the same as in Rantala et al. (2016a), with the exception that one tundra site (#34) was removed from this study due to low number of chironomid head capsules.

Surface (top, 0–2 cm in core depth) and reference (bottom, 4-5 cm) sediment samples were collected from the centres of the lakes using a Limnos gravity corer (Kansanen et al., 1991) in July 2014. According to several sediment cores dated from the study area (Luoto & Sarmaja-Korjonen, 2011; Luoto et al., 2017b; Rantala et al., 2016b), the average sediment accumulation in the lakes refer to past 20 years in the "top" surface sediment samples and to 150 years in the "bottom" reference samples. The top and bottom samples are discussed herein as modern and Pre-Industrial age samples, respectively, but since the samples were not independently dated, we emphasize that these general timeframes are only tentative and the bottom sample may not always represent Pre-Industrial times. Although the widely employed top-bottom (or before-and-after) approach allows for efficient spatio-temporal regional assessment of environmental change, the disadvantage of this approach is that there are no continuous data on the timing or rate of changes occurring between the two points in time represented by those samples (Smol, 2017). In addition, it cannot be assumed that there is only one Pre-Industrial/reference environmental state from which lakes have deviated (Perren et al., 2009). These limitations of the applied approach should be kept in mind when interpreting the data.

2.2 Chironomid analysis

Standard methods were applied in fossil chironomid analysis (Brooks et al., 2007). The wet sediment was sieved through a mesh (100-μm) and the residue was examined under a stereomicroscope. Larval head capsules were extracted and mounted permanently with Euparal on microscope slides. Taxonomic identification following Brooks et al. (2007) was performed under a light microscope. The minimum chironomid head capsule number per sample was set to 50 (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001). Two split head capsules were considered as one individual. The surface sediment chironomid assemblages have been previously published in Luoto et al. (2016), whereas the reference samples were analyzed in this study by the same chironomid analyst using identical methodology and taxonomy.

2.3 Numerical methods

Bray-Curtis similarity was used as a measure to assess the difference between present and past chironomid communities. In this measure, 0 refers to a completely different community and 1 to an analogous community. N2 (Hill, 1973) was used as a diversity measure, corresponding to effective number of occurrences, i.e. the effective diversity of a sample's community.

Minimum hypolimnetic dissolved oxygen (DO) was reconstructed using a 30-lake chironomid-based calibration model for Finland, where the calibration sites range from anoxic (O_2<0.5 mg l^{-1}) to hypersaturated sites (O_2=18.1 mg l^{-1}) (Luoto and Nevalainen, 2011; Luoto and Salonen, 2010). The weighted averaging partial least squares model has a cross-validated (leave-one-out) coefficient of determination of 0.74 and a root mean squared error of prediction of 2.3 mg l^{-1}. The suitability of the calibration model for the chironomid assemblages in the surface and bottom samples were assessed using representation of fossil taxa in the calibration set (cutoff for good representativeness 95%) and the modern analogue technique (MAT) using squared chi-square distances of the 10 closest modern analogues (cutoff for a good modern analogue 5% squared chi-square distance) (Birks et al., 2014). Furthermore, Generalized Linear Modeling (GLM) was used to assess taxa that significantly ($P \leq 0.05$) respond to oxygen conditions. The GLMs were run using Poisson distribution. Samples where majority of the taxa have significant relationship with the environmental variable of interest can be considered to produce reliable reconstructions (Rees et al., 2008; Luoto et al., 2010).

3 Results

The counting sum of chironomid individuals varied between 50 and 60 in the sediment samples. The most common and abundant chironomids in the bottom samples were the same as in the surface sediment samples (Fig. 2), including *Psectrocladius septentrionalis*-type (bottom = 27 occurrences, mean abundance 12.6%, maximum abundance 48.9%; top = 23, 12.0%, 45.2%), *P. sordidellus*-type (bottom = 28, 12.4%, 39.3%; top = 27, 10.2%, 23.6%) and *Tanytarsus lugens*-type (bottom = 28, 8.0%, 28.3%; top = 25, 5.9%, 19.0%). The most common taxa with largest decreases in their mean abundance from bottom to top samples included *Polypedilum nubeculosum*-type (-2.5%), *P. sordidellus*-type (-2.2%) and *T. lugens*-type (-2.1%), whereas the largest increases were observed with *Paratanytarsus penicillatus*-type (3.2%), *Microtendipes pedellus*-type (2.1%) and *Tanytarsus glabrescens*-type (2.0%). *Protanypus*, which was present in 11 bottom samples, was encountered only in a single surface sample. On the contrary, *Tantarsus mendax*-type that was absent in the bottom samples appeared in 10 surface samples.

According to the similarity analysis, oligotrophic tundra lakes had the largest shifts in taxa assemblages between the past and present (average Bray-Curtis similarity 0.44), whereas polyhumic lakes, located in pine and birch forest (0.50) and mountain birch woodland (0.55), exhibited less changes (Table 1; Fig. 3). However, unlike oligohumic and mesohumic sites, the polyhumic sites showed consistently decreased diversity (Table 1; Fig. 3).

The chironomid-inferred hypolimnetic oxygen varied between 3.0 and 13.5 mg l^{-1} in the surface samples and between 6.6 and 17.1 mg l^{-1} in the bottom samples (Fig. 3). In all, the average chironomid-inferred oxygen for the surface sediments was 9.4 mg l^{-1} and for the bottom samples 12.6 mg l^{-1}. According to the MAT, all the surface and bottom samples had good modern analogues (<5% squared chi-square distance) in the calibration set. However, the surface sample from lake #27 had taxa representativeness slightly less than the cutoff value of 95% due to absence of *Paratendipes nudisquama*-type from the calibration set. Nonetheless, since 94.7% of the fossil taxa were present in the calibration set, this did not produce a significant error source for the reconstruction. In the surface sediment samples, 71.7-100% (average 91.0%) of the taxa present (relative community abundance) had significant relationship with oxygen conditions, whereas in the reference samples 73.1-100% (average 89.3%) were significantly associated with oxygen. Hence all samples had the needed coverage of statistically significant oxygen indicators. The most abundant taxon without significant relationship with hypolimnetic oxygen was *Procladius*, which occurred in the samples with a relatively low mean abundance of 2.4% (maximum abundance 7.4%). When comparing the shifts in inferred oxygen values and their relative change (Fig. 4), the polyhumic sites showed no significant changes, mesohumic sites showed decrease with only one exception (an outlier lake with a pH of 5.1) and the oligohumic sites illustrated a coherent decrease in oxygen.

4 Discussion

4.1 Ecological change

The chironomid assemblages in the 30 study sites in northern Lapland showed clear shifts when comparing the reference (tentative age estimate 150 years in average) and modern surface sediment samples. *Paratanytarsus penicillatus*-type, which was rare in the bottom samples, showed increase especially in the low-DOC lakes (Fig. 2). Also several other collector-filterers consistently increased, such as *Tanytarsus mendax*-type and *T. glabrescens*-type, though remaining relatively low in their abundances. When interpreting the community changes, it should be noted, according to the species-area relationship (Lomolino, 2000), that the time-intervals between the top and bottom samples may differ and cause uncertainties in comparisons of rare taxa occurrences. Nonetheless, the recent increase of *T. mendax*-type is very typical in the northern lakes in the area (Shala et al., 2014). *T. mendax*-type has a high modern temperature optimum in Lapland (Luoto et al., 2014) and elsewhere in Europe (Heiri et al., 2011). Therefore, this taxon appears to represent an example of a chironomid that clearly benefits from climate warming. In contrast, the cold-indicating *Protanypus* has disappeared from the surface sediments of the study sites suggesting that the temperature range of the lakes is no longer suitable for it to survive. In addition to temperature, *T. mendax*-type and *Protanypus* have strict preferences for meso-eutrophic and oligotrophic lakes, respectively (Luoto, 2011; Medeiros and Quinlan, 2011). For chironomids, the influence of nutrient conditions is in most part mediated through the direct physiological effects of hypolimnetic oxygen conditions (Brodersen and Quinlan, 2006), as oligotrophic lakes tend to be well-oxygenized and eutrophic lakes often oxygen depleted.

According to the Bray-Curtis similarity, the polyhumic study sites with DOC >9 μg l^{-1} had smallest and the oligo-mesohumic lakes largest community changes (Fig. 3). While displaying relatively little change in community assemblages, the polyhumic sites appeared to have uniformly suffered a loss in their diversity. Hence, the chironomid communities of the polyhumic sites have not significantly changed in their dominating taxa, instead there have been general decreases in the less abundant taxa (Fig. 2). As all the current lakes are situated in an ecotonal area, the ecological impacts of climate change are typically magnified (Pienitz and Vincent, 2000). Therefore, the larger community shifts occurring in the low-DOC lakes (Fig. 3) are not surprising owing to oligohumic and oligotrophic lakes being generally poorly buffered against environmental perturbations (Gunn et al., 2001). Overall, the findings from the chironomid assemblages suggest that ecological changes in taxonomic composition and/or diversity occur between the reference samples and the present, with direction and magnitude depending on the lake type. As the status of aquatic ecosystems as carbon sinks or sources is very likely to change owing to the ongoing climate change, the biodiversity of freshwater ecosystems across most of the Arctic will also likely be altered (Wrona et al., 2006). Accordingly, our results provide further evidence that these changes are proceeding in subarctic lakes of Lapland, where chironomids play a significant functional role through regulation of organic matter decomposition, and subsequently, take a major part in the biogeochemical cycling of nutrients (including carbon).

4.2 Oxygen change

As the chironomid assemblages had good modern analogues in the calibration set according to the MAT and based on the GLMs the taxonomic compositions included sensitive oxygen indicators

(Luoto and Salonen, 2010), such as the low-oxygen *Sergentia coracina*-type and high-oxygen *Tanytarsus lugens*-type and *Psectrocladius* taxa, we were able to reliably reconstruct the hypolimnetic oxygen conditions from the top and bottom samples of the study sites. The results showed differences in chironomid-inferred oxygen levels between different lake types in past and modern samples (Fig. 3). Whereas the oxygen decrease from the estimated Pre-Industrial Age was 3.2 mg l^{-1} on average, which clearly exceed the model's prediction error, largest reductions were observed in the oligohumic lakes (Figs 3-4). With the outlier (lake #5 with anomalous pH) excluded, also mesohumic lakes distinctly suffered from decreased oxygen levels. On contrast, the polyhumic lakes with present-day DOC >6 mg l^{-1} had no or little change in their oxygen levels between the past and the present. Therefore, the larger oxygen change in the oligo-mesohumic lakes compared to polyhumic lakes is probably due to their generally poorer buffering ability against environmental changes (Gunn et al., 2001). The lower buffering ability, or resilience, of low-DOC lakes most probably relates to their light environment (more transparent water column), trophic status (less nutrients), variable limnological conditions (such as in pH) and diverse catchment characteristics compared to the murky, low-pH polyhumic lakes with boggy catchments (Korhola et al., 2002; Rautio et al., 2011; Rantala et al., 2016a).

When observing the oxygen change since the estimated Pre-Industrial Age to the present (Fig. 4) in the light of climate warming, it becomes apparent that polyhumic lakes are less influenced. This is probably due to the fact that polyhumic sites have generally been subjected to low oxygen conditions through their polyhumic lake state, especially during the winter season when oxygen is consumed under ice following the excessive decay of plant material derived from the catchment wetlands (Mathias and Barica, 1980). It has been shown that while colored lakes are typically naturally oxygen depleted, the profundal oxygen values have a weak relationship with lake trophic state (Crisman et al., 1998). Instead, the oxygen conditions in lakes are closely connected with temperature. For example, oxygen conditions were generally improved during the cold Little

Ice Age (~1300-1900 CE) but deteriorated during the warm Medieval Climate Anomaly (800-1300 CE) and also under the present climate warming in oligohumic and polyhumic boreal lakes of Finland (Luoto and Salonen, 2010). The current results show that even though the hypolimnetic oxygen levels have decreased in the oligo-mesohumic lakes, none of the lakes have become anoxic thus far (Fig. 3). However, despite the fact that the bottom reference samples represent a time period that may correspond to the Little Ice Age and may consequently represent naturally higher values, the decreasing oxygen trend in these lakes is evident, and the future therefore holds a potential risk that the lakes may become oxygen depleted as climate warming proceeds.

5 Conclusions

The chironomid assemblages in the past and modern sediment samples of the 30 lakes showed dissimilar communities between the past and the present with largest shifts in the more transparent oligo-mesohumic lakes. Although there was no significant change in the taxonomic communities of the murky polyhumic lakes, they displayed a decrease in diversity driven by disappearance of rare specialized taxa. The chironomid-inferred hypolimnetic oxygen values generally decreased from the Pre-Industrial Age to the present, with largest change in low-DOC lakes but no significant changes were found in the oxygen conditions of high-DOC lakes. Since the polyhumic study lakes were often located in wetland areas, our findings suggest mechanisms that prohibit oxygen decline in sites associated with continual organic carbon inputs making them more resilient against climate-induced reductions in hypolimnetic oxygen. Consequently, although contributing less to the total carbon release from northern lakes when compared to polyhumic lakes, the low-DOC oligohumic lakes of the northern treeline are generally more prone to climate change impacts with increased potential of higher CH_4 emissions under reduced bottom water oxygen levels.

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8 Tables

Table 1 Mean values and range (in brackets) in present-day wetland coverage and dissolved organic carbon (DOC) in the 30 subarctic lakes in northeastern Finnish Lapland in comparison with Bray-Curtis similarity and changes in N2 diversity and hypolimnetic oxygen between the surface (top) and reference (bottom) samples.

	Pine and birch forest	Mountain birch woodland	Tundra
Wetland area of catchment (%)	5.8 (0…16.6)	15.6 (0.1…49.3)	2.9 (0…8.9)
DOC (mg l^{-1})	4.8 (2.2…9.6)	7.6 (2.5…16.6)	3.4 (1.7…7.4)
Similarity (Bray-Curtis)	0.50 (0.37…0.68)	0.55 (0.40…0.71)	0.44 (0.27…0.58)
Effective diversity change (N2)	0.12 (-5.03…2.35)	-1.69 (-7.64…6.54)	-0.74 (-8.61…7.59)
Oxygen change (mg l^{-1})	-3.0 (-7.0…4-0)	-1.9 (-7.0…0.5)	-4.5 (-9.6…-0.2)

9 Figure captions

Fig.1 Map. Study sites along the northern forest zones in northeastern Finnish Lapland. The numbers present lake codes, which are the same as in Rantala et al. (2016a).

Fig. 2 Community compositions. Chironomid assemblages in the surface (top = gray) and reference (bottom = black) sediment samples in the 30 lakes in northeastern Finnish Lapland. The lakes are arranged according to their modern dissolved organic carbon (DOC) concentration and the threshold of 4 mg l^{-1} (between oligo- and mesohumic) is marked with a dashed line.

Fig. 3 Ecological changes. Bray-Curtis similarity (0 = dissimilar, 1 = similar) between the surface and reference chironomid assemblages in lakes in northeastern Finnish Lapland compared with Hill's (1973) N2 effective number of occurrences (diversity) and chironomid-inferred hypolimnetic oxygen along the dissolved organic carbon (DOC) gradient in the surface (top = gray) and reference (bottom = black) sediment samples.

Fig. 4 Oxygen changes. Difference between chironomid-inferred hypolimnetic oxygen in the surface and reference sediment samples (negative values refer to decreased oxygen towards the present) compared with modern measured dissolved organic carbon (DOC) in the 30 lakes in northeastern Finnish Lapland. The samples are colored according to DOC thresholds of 4 and 6 mg l^{-1} (separating oligo-, meso- and polyhumic sites) and the site with anomalously high pH (an outlier) is marked with an x.