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Long-term effects of climate change on carbon flows through benthic secondary production in small lakes

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Abstract
1. A palaeolimnological study, covering the last c. 12,000 years, was conducted in a small subalpine lake located in the Alps to study climate change impacts on carbon flows through food webs in small lakes. We used analysis of sedimentary pigments and carbon stable isotopic composition of chironomid remains (δ13C_HC) to reconstruct past dynamics of phytoplankton community and carbon sources sustaining benthic consumers.

2. Chironomid biomass was sustained by a combination of allochthonous, autochthonous and CH4-derived organic matters, and their relative contributions were correlated to changes in temperature. Relatively high terrestrial contributions to chironomid biomass were observed during period of the Holocene when in-lake production was low. Relatively high incorporation of CH4-derived carbon to chironomid biomass was found during anoxic events co-occurring with the Holocene thermal maximum.

3. Results were then compared with those collected in a small boreal lake in Estonia. We tested the hypothesis that responses in carbon flows through benthic food web to past climate change would be similar between these lakes. We found a negative correlation between δ13C_HC values of both lakes and inferred air temperature, suggesting that temperature was the major driver to different food sources being incorporated into chironomid biomass.

4. Our study demonstrated that air temperature was the principal driver of the energy flows through benthic food web in the studied small lakes. We conjectured that carbon cycling in food webs of small lakes might be strongly sensitive to climate change.

KEYWORDS
carbon stable isotope, climate change, holocene, palaeolimnology, subfossil chironomid

1 | INTRODUCTION

Global warming (IPCC 2014) and increase in mean temperature are pointed out as one of the major threats to inland aquatic ecosystems (Goldman, Kumagai, & Robarts, 2012). While it is well-known that temperature is the driver of many processes in lakes (Wilhelm & Adrian, 2008), our understanding of ecosystem responses to climate change is still limited (Keller, 2007; Mooij et al., 2005). Indeed, effects of climate change have mainly been studied at individual level and community level (Walther, 2010). A more integrative and holistic approach is needed to better understand ecosystem responses to climate change, and to predict future trends during warmer climate.
Organic matter cycling is a key variable for understanding climate change impacts on lakes. The relative contribution between autochthonous and allochthonous organic matter inputs to lakes is strongly regulated by climatic change (Tranvik et al., 2009), affecting the availability of food sources at the base of aquatic food webs (Belle, Luoto, Kiviiä, & Nevalainen, 2017; van Hardenbroek et al., 2013). Higher temperatures can also induce oxygen depletion in the hypolimnetic zone of lakes due to longer periods of thermal stratification (Jankowski, Livingstone, Bührer, Forster, & Niederhauser, 2006), and/or an increase in bacterial activity in sediments and lake water column (Blumberg & Di Toro, 1990). Organic matter can be degraded to methane (CH₄) by methanogenic archaea (Whiticar, 1999), oxidised by methane-oxidising bacteria and used as a source of energy by aquatic consumers (Bastviken, Ejlertsson, Sundh, & Tranvik, 2003; Grey, 2016). Since sediments play a key role in the recycling of organic matter in lakes (Meyers & Ishiwatari, 1993), carbon processing in benthic food web can be seen as an integrative proxy for understanding of climate change impacts on the lake ecosystems (McGowan et al., 2016). As long-term time series of carbon processing in benthic food web are lacking, palaeolimnological approaches can provide valuable insights into historic lake dynamics.

Chironomidae (Diptera, Nematocera) are non-biting midges whose larvae can grow in superficial lake sediments (Armitage, Cranston, & Pinder, 1995), and are often a dominant group in the profundal fauna of lakes. Furthermore, chironomid larvae contribute to the recycling of organic matter (Nogaro et al., 2009) and form an important trophic link between settling primary producers and fish (benthic–pelagic coupling, Goedkoop & Johnson, 1996; Wagner, Volkman, & Dettinger- Klemm, 2012). The most sclerotised part of their exoskeleton (the head capsules, HC) is archived in sediments after each larval moulting (Walker, 2001). The chemical composition of chironomid remains is well-preserved in sediments (Verbruggen et al., 2014), allowing for the analysis of their carbon stable isotopic composition (δ¹³CHC; Heiri, Schilder, & van Hardenbroek, 2012). Due to differences in isotopic fractionation by primary producers (Rounick & Winterboum, 1986) and bacteria (e.g., methanogenesis and methanotrophy; Whiticar, 1999), food at the base of aquatic food webs often differs in their carbon stable isotopic compositions. Analysis of carbon stable isotope ratios (δ¹³C) of aquatic animals is widely used to track carbon flows through food webs (Grey, 2006). Moreover, the trophic fractionation, that is the difference between δ¹³C values of a single food resource and a consumer, can be low or negligible for chironomid larvae (Goedkoop, Akerblom, & Demandt, 2006), while the offset between larvae and head capsule is assumed to be constant (Frossard, Belle, Verneaux, Millet, & Magny, 2013). δ¹³CHC values can therefore provide a reliable long-term reconstruction of past changes in carbon resources for Chironomidae (Belle, Verneaux, Mariet, & Millet, 2017; Frossard, Verneaux, Millet, Magny, & Perga, 2015; van Hardenbroek, van Lotter, Bastviken, Andersen, & Heiri, 2014; Wooller et al., 2012).

The objective of this study was to determine the relationship between temporal changes in carbon flows through benthic consumers and Holocene climate change in a small subalpine lake. Using analyses of sedimentary pigments and carbon stable isotopic composition of chironomid head capsules, we reconstructed the Holocene dynamics of phytoplankton composition and carbon resources fueling chironomid biomass. Results were then compared with those collected in a similarly sized lake (Lake Tollari; Estonia) to test the hypothesis that temperature is the major driver of food availability at the base of benthic food web in small lakes. Accordingly, we expected that the relationship of carbon processing through benthic food web to temperature change would be similar for both lakes.

## Methods

### Study site and climate reconstruction

Lake Colbricon (46°17′10″N, 11°45′56″E; 1914 m a.s.l.) is located in the subalpine vegetation belt of the Dolomites massif of the Alps (Italy). The bedrock of its small catchment (36 ha; ratio of catchment to lake ratios = 25.7) is composed of quartziferous porphyry and sandstone. Sediment cores were retrieved from the deepest part of the lake (Figure 1b), and details concerning coring and dating methods were previously reported by Leys et al. (2014). The number, name and non-calibrated age of each radiocarbon date are summarised in Table S1. The total length of the sediment core was 3.6 m and covered the last c. 12,000 years, corresponding to an average sedimentation rate of about 0.3 mm/year (Figure 1c). All sample depths were converted to calibrated year BP (expressed hereafter in 1000 calibrated years before present: kyr cal. BP, with 0 cal. BP = AD 1950) according to the age-depth model (Figure 1c). Mean July air temperature (Tₘₒ) over the Holocene period in Lake Colbricon area was assumed to match with the climate reconstruction based on chironomid assemblage records provided by Heiri, Ilyashuk, Millet, Samartin, and Lotter (2015).

### Sedimentological and chironomid analyses

Sediment cores were sliced into 1 cm thick layers to characterise temporal changes in the sediment composition. To assess overall organic matter inputs to lake’s sediment, organic matter content in sediments (OM) was analysed in each sediment layer using the loss-on-ignition method and expressed as percentage of dry weight (% of dry weight). To track temporal changes in aquatic primary production, photosynthetic pigments were extracted, keeping samples overnight under nitrogen, from about 1 g of fresh sediments using a solution of acetone (90%). Samples were then centrifuged at c. 2700 g for 10 min and filtered through a 0.45-µm pore size filter (Gualizzi et al., 2011). Total carotenoids (TC) and chlorophyll derivatives (CD) were then quantified from extracts via spectrophotometry (as described by Gualizzi et al., 2011). Pigment concentrations were expressed as milligrams per gram of organic matter (mg/g of OM), and as units per gram of organic matter (U/g OM), respectively.

The reconstruction of carbon flows through benthic consumers was estimated by analyses of carbon stable isotopic composition of
chironomid HC that were extracted from sediment samples collected every 3 or 4 cm. In total, 100 sediment samples were pre-treated using successive washings with NaOH (10%) and HCl (10%) solutions and sieved through a 100 \( \mu \)m mesh following the recommendations by Schimmelmann and DeNiro (1986) and van Hardenbroek et al. (2009). The Chironomus anthracinus-type morphotype (based on classification provided by Brooks, Langdon, & Heiri, 2007) was selected because it is a deposit-feeder that feeds on phytoplankton deposits, terrestrial detritus and associated bacteria (Johnson 1985), and can be used as an indicator of the recycling of organic matter in lake sediments. To avoid misleading interpretations due to incomplete carbon turnover, only HC belonging to the fourth larval instar were selected (Frossard et al., 2013). Approximately 15 HC were packed into tin capsules to form samples of at least 20 \( \mu \)g (van Hardenbroek et al., 2009). When HC concentrations in a single sediment sample were too low, a few consecutive samples were pooled together. The new sample age corresponded then to the average age of the pooled sediment layers. A total of 67 chironomid samples were analysed. Carbon stable isotopic composition of these samples was then analysed using an isotope ratio mass spectrometer interfaced with an elemental analyser at INRA Nancy (Champenoux; UMR INRA 1137). Results were expressed according to the delta notation with Vienna Pee Dee Belemnite as the standard: \( \delta^{13}C (\%o) = (R_{\text{sample}}/R_{\text{standard}}) - 1 \times 1,000; \) where \( R = ^{13}C/^{12}C \). Replication of sample measurements from internal laboratory standards (with a target weight of 20 \( \mu \)g) produced analytical errors (1\( \sigma \)) of \( \pm 0.2^{\circ/o} \) (\( n = 12 \)).

2.3 | The Lake Tollari dataset
Lake Tollari (57°45'6"N, 26°20'32"E; 97 m a.s.l.) is a 5.7 ha large lake located in the Karula upland (Estonia; Figure 1a). This lake has been studied using similar methods by Belle, Poska, Hossann, and Tonno (2017), including carbon stable isotopic analyses of Chironomus anthracinus-type morphotype head capsules. To track only the influence of climate change on benthic food web, the uppermost 2.5 m (corresponding approximately to the last 1.5 kyrs) of the Lake Tollari core was excluded due to strong human impacts (Belle, Poska, et al., 2017). The comparison of the two small lakes, located at different altitudes and in two different climate zones, allows us to test the hypothesis of similar responses between climate and carbon flows through benthic consumers. For Lake Tollari, a pollen-inferred reconstruction of the mean warm months’ (May, June, July and August) air temperature has been provided by Poska A. (in Belle, Poska, et al., 2017). The comparison of the two small lakes, located at different altitudes and in two different climate zones, allows us to test the hypothesis of similar responses between climate and carbon flows through benthic consumers. For Lake Tollari, a pollen-inferred reconstruction of the mean warm months’ (May, June, July and August) air temperature has been provided by Poska A. (in Belle, Poska, et al., 2017). Subfossil pollen and chironomid remains have been widely used to reconstruct air temperature change over the post-glacial period (Bigler, Larocque, Peglar, Birks, & Hall, 2002). Comparative studies in the arctic/boreal area revealed strong similarities between reconstructions based on pollen and chironomid...
2.4 Statistical analysis

Since temperature and organic matter contents were expected to have a significant, and potentially nonlinear, influence on carbon processing by chironomids, statistical relationships between explanatory variables (OM and T_Jul) and the response variable (δ^{13}C values) were examined using a generalised additive model approach (GAM; fitted using the mgcv package for R; Wood, 2011). To account for temporal autocorrelations, a continuous-time first-order autoregressive process was introduced to the model (Simpson & Anderson, 2009). A forward selection was used to add explanatory variables in the model. Statistical significance (p-value; with α < 0.05) of each explanatory variable was used to select terms, and Akaike information criterion (AIC) helped to select the best model. Finally, a similar GAM procedure was also performed on merged reconstructed air temperature and δ^{13}C values from both Lake Tollari and Lake Colbricon. For graphical displays, main temporal trends were visually tracked by smoothing the time series using LOESS-regression (LOESS parameters: span = 0.2; polynomials degree = 2). All statistical tests and graphical displays were performed using R 3.4.0 statistical software (R Core Team, 2017).

3 RESULTS

Organic matter content (OM) of sediment samples ranged from 8.3% to 46.6% for Lake Colbricon (Figure 2). Its temporal trend followed a gradual increase from the beginning of the Holocene until c. 4.5 kyr cal. BP, but OM then decreased up to the uppermost part of the core (Figure 2). Chlorophyll derivatives (CD) ranged from 16 to 82.6 U/g of OM, and TC from 0.1 to 0.6 mg/g of OM (Figure 2). The temporal trends were characterised by dramatic increases in pigment concentrations (of both CD and TC) from 12 to c. 8.5 kyr cal. BP with values ranging from the lowest to the highest values (Figure 2). Then, pigment concentrations either remained almost constant over time (CD, Figure 2) or followed a gradual decrease interrupted by a small increase from c. 4 to 1 kyr cal. BP (TC, Figure 2). Subfossil chironomid δ^{13}C values (δ^{13}C_{chc}) ranged from −39.8‰ to −21.8‰ for Lake Colbricon (Figure 2). The heaviest δ^{13}C_{chc} values (or the less 13C-depleted, ranging from −28.7 to −21.8‰) occurred in the period before 10.5 kyr cal. BP, whereas lightest values (more 13C-depleted; ranging from −39.8 to −36‰) were observed between c. 9.5 and 6.4 kyr cal. BP (Figure 2) during the warmest period of the Holocene. δ^{13}C_{chc} values decreased during the first part of the Holocene and then followed an increasing trend during the second part (Figure 2), matching well with the temporal trend previously reported in Lake Tollari (Belle, Poska, et al., 2017).

A GAM approach was applied to the δ^{13}C_{chc} values of Lake Colbricon to identify controlling factors of their temporal trend. GAM model residuals followed a normal distribution, allowing the use of a Gaussian family distribution in our modelling approach. The final model built on δ^{13}C_{chc} values of Lake Colbricon (Table 1) showed strong negative relationships with T_Jul (F = 16.9; edf = 1.19) and OM content (F = 15.8; edf = 1.54), explaining 71% of the δ^{13}C_{chc} variability (Figure 3). Combined, δ^{13}C_{chc} values from Lake Colbricon and Lake Tollari were negatively correlated with reconstructed air temperature (F = 57.1; edf = 1.51; Figure 4), explaining 48.5% of the δ^{13}C_{chc} variability, with no significant differences in slopes and intersects of the two lakes (p-value > .3). However, the distribution of reconstructed air temperature values suggested that the coldest temperatures were likely under-sampled in our study (Figure 4).

**FIGURE 2** The temporal dynamic of mean air temperature reconstruction (chironomid-inferred temperature of July, T_Jul expressed in °C; Heiri et al., 2015), organic matter content (OM; %), sedimentary pigments (chlorophyll derivatives (CD) and total carotenoids (TC), expressed U/g of OM and in mg/g of OM, respectively) and carbon stable isotopic composition of chironomid remains (δ^{13}C_{chc}; ‰) of Lake Colbricon. The grey surface displays the standard error of the temperature inference.
TABLE 1 Summary of statistics for the general additive model (GAM) fitted with a Gaussian distribution to $\delta^{13}$C$_{HC}$ values. The response variables were organic matter content in sediments (OM), and summer mean air temperature ($T_{Jul}$). “edf” refers to the effective degrees of freedom.

<table>
<thead>
<tr>
<th>Lake Colbricon</th>
<th>Intercept</th>
<th>$t$-value</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta^{13}$C$<em>{HC} = s(T</em>{Jul}) + s(OM)$</td>
<td>-35.4</td>
<td>-173.4</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>$R^2 = 0.71$</td>
<td>Terms</td>
<td>edf</td>
<td>$F$</td>
</tr>
<tr>
<td>$s(T_{Jul})$</td>
<td>1.19</td>
<td>16.9</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>$s(OM)$</td>
<td>1.54</td>
<td>15.8</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

4 | DISCUSSION

4.1 | Past temperature change in Europe

Comparable patterns of air temperature changes for the two studied areas have been reported for the Holocene (Figure 2, Heiri et al., 2015; Holmström, Ilvonen, Seppä, & Veski, 2015; Belle, Poska, et al., 2017). These patterns can be divided into three climatic periods: (1) from c. 11.7 to 8.2 kyr cal. BP (Early Holocene) when the Holocene coolest temperatures were observed, followed by a rapid warming, (2) maximal and stable temperatures during the Holocene thermal maximum (from c. 8.2 to 4.2 kyr cal. BP) and (3) since c. 4.2 kyr cal. BP (Late Holocene) when a slight gradual cooling was observed. Air temperature reconstructions used in this study were inferred from two different proxies: chironomid assemblages (Lake Colbricon area: Heiri et al., 2015) and pollen analysis (Lake Tollari; Belle, Poska, et al., 2017). Inter-proxy comparisons in the boreal/arctic region have previously revealed strong similarities between temperature reconstructions for the main temporal trends (Bigler et al., 2002; Rosén et al., 2003). Therefore, we assumed that the pollen-based climate reconstruction from Lake Tollari was comparable to a chironomid-based inference in this area, and allowed for the comparison of the two air temperature reconstructions. Precipitation patterns are also an important component of climate variability (Luoto & Nevalainen, 2017), and changes in precipitation patterns could affect lake carbon cycling (Nevalainen, Kivilä, & Luoto, 2016). Further studies are needed to understand the impact of Holocene changes in precipitation patterns and its impact on carbon flows through food webs.

4.2 | Carbon processing in benthic food webs and climate change

Climate (in particular air temperature) is known to have a strong influence on inputs of allochthonous organic matter to lakes (Staß, 1998), on autochthonous primary productivity (Anderson et al., 2008) and the production of CH$_4$-derived biomass during anoxic events (Duc, Crill, & Bastviken, 2010). Therefore, food availability for benthic deposit-feeding invertebrates can be closely related to long-term temperature fluctuations and were expected to be highly variable over time (Belle, Luoto, et al., 2017; van Hardenbroek et al., 2013). In this study, temporal trends in sedimentary pigments (CD and TC) and OM records suggest an increase in the lake’s trophic state from c. 11 kyr cal. BP, induced by a period of rapid warming between c. 11 and 4.5 kyr cal. BP (Figure 2). During this periods, the amount of organic matter available for chironomid larvae as well as the aquatic organic matter proportion in lake sediments dramatically increased during the first part of the Holocene (Figure 2), as reflected by increased sedimentary pigments concentrations.

The comparison between $\delta^{13}$C$_{HC}$ values and carbon stable isotopic baselines and sedimentary pigment records provided valuable insights into carbon flows through chironomid larvae. Our results show that chironomid biomass appeared to be sustained by a combination of allochthonous, autochthonous and CH$_4$-derived organic matters, and their contributions were correlated to temperature change (Figure 4). The $\delta^{13}$C$_{HC}$ values ranged from $-35^{\circ}_{om}$ to $-31^{\circ}_{om}$ in this study (Figure 4), which was indicative of a strong reliance on autochthonous organic matter, as $\delta^{13}$C of pelagic primary producers usually ranges from $-36^{\circ}_{om}$ to $-25^{\circ}_{om}$ (Vuorio, Meili, & Sarvala, 2006; Wang, Liu, Peng, & Wang, 2013). Our study thus supports the conjecture that aquatic consumers are mainly fuelled by autochthonous primary production (Holgerson, Post, & Skelly, 2016; Lau, Sundh, Vrede, Pickova, & Goedkoop, 2014; Tanentzap et al., 2017). However, relatively heavy $\delta^{13}$C$_{HC}$ values (from $-28.7$ to $-21.8^{\circ}_{om}$) were

FIGURE 3 Fitted smooth function between explanatory variables (OM and $T_{Jul}$) and $\delta^{13}$C$_{HC}$ values of Lake Colbricon from general additive models (GAM), with a continuous-time first-order autoregressive process to account for temporal autocorrelations. Grey surface marks the 95% uncertainty interval of the fitted function. On the x-axis, black ticks show the distribution of observed values. Numbers in brackets on the y-axis are the effective degrees of freedom (edf) of the smooth function.
provide better insight in the long-term temporal changes in $\delta^{13}C$ baselines in lake sediments, and quantify the contribution of food sources (autochthonous versus allochthonous) to chironomid larvae. In addition, the analysis of the hydrogen stable isotope as a second isotopic tracer for chironomid remains could better highlight the allochthonous contribution to benthic consumers (Doucett, Marks, Blinn, Caron, & Hungate, 2007; Belle, Verneaux, Millet, Parent, & Magny, 2015.)

Finally, very light $\delta^{13}C_{HC}$ values (lighter than $-37\permil$) were reported during the warmest period of the Holocene (Figures 2 and 4). Due to high fractionation by methanogens, biogenic CH$_4$ exhibits very light $\delta^{13}C$ values (Whiticar, 1999), leading to a characteristic $^{13}$C-depletion for aquatic consumers feeding on CH$_4$-derived carbon (Grey, 2016). Our study suggests that the incorporation of CH$_4$-derived carbon into chironomid biomass was directly and/or indirectly enhanced by warm temperature as previously reported from boreal and arctic lake records (Belle, Poska, et al., 2017; van Hardenbroek et al., 2009; Wooller et al., 2012). The CH$_4$-based pathway was detected during the Holocene thermal maximum of two small lakes located at different altitudes and in two different climate zones (Figure 4). We suggest that the dependence on CH$_4$-derived carbon could be a widespread phenomenon in small lakes in warm climates. Moreover, given that a significant part of the biogenic CH$_4$ produced in small lakes is released into the atmosphere (Bastviken, Tranvik, Downing, Crill, & Enrich-Prast, 2011), our study also suggests that freshwater ecosystems were important contributors to the global carbon budget during the warmest Holocene period.

### 4.3 Functional response to long-term climate change

Ecosystems can have alternative stable states and exhibit nonlinear responses (known as a regime shift) when environmental conditions change (Scheffer & Carpenter, 2003). As Jones et al. (2008) found a nonlinear relationship between oxygen dynamics and the contribution of CH$_4$-derived carbon to aquatic consumers, we expected a threshold in the correlation between $\delta^{13}C_{HC}$ values and air temperature. While our study found several changes in carbon flows through benthic consumers (allochthonous versus autochthonous reliance, CH$_4$-based food web, etc.), the data did not reveal such an abrupt change. Instead, changes were more linearly correlated to long-term temperature fluctuations (Figure 4). Further studies of carbon processing in aquatic food webs of small lakes are needed to better understand the mechanisms by which climate change affects carbon cycling in small lakes.

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