Climate-induced changes in carbon flows across the plant-consumer interface in a small subarctic lake

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Reconstructions of past food web dynamics are necessary for better understanding long-term impacts of climate change on subarctic lakes. We studied elemental and stable isotopic composition of sedimentary organic matter, photosynthetic pigments and carbon stable isotopic composition of Daphnia (Cladocera; Crustacea) resting eggs (δ13Cclad) in a sediment record from a small subarctic lake. We examined how regional climate and landscape changes over the last 5800 years affected the relative importance of allochthonous and autochthonous carbon transfer to zooplankton. Overall, δ13Cclad values were well in line with the range of theoretical values of aquatic primary producers, confirming that zooplankton consumers in subarctic lakes, even in the long-term perspective, are mainly fuelled by autochthonous primary production. Results also revealed greater incorporations of benthic algae into zooplankton biomass in periods that had a warmer and drier climate and clearer water, whereas a colder and wetter climate and lower water transparency induced higher contributions of planktonic algae to Daphnia biomass. This study thus emphasizes long-term influence of terrestrial-aquatic linkages and in-lake processes on the functioning of subarctic lake food webs.

Arctic/subarctic ecosystems are exposed to rapid and extensive changes driven by accelerated warming1, including changes in vegetation cover, biomass and productivity (i.e. the greening of the Arctic2), and permafrost thaw3. These climate-driven landscape transformations dramatically affect run-off patterns, biogeochemical cycles and organic matter dynamics, potentially triggering cascading effects acting at regional and global scales4,5. Arctic/subarctic landscapes are also characterized by a high density of lakes and water courses, exceeding 4% of the total land area6. Direct effects of warming on lakes affect both their physical (e.g. timing and duration of ice cover7), chemical (e.g. changes in organic matter inputs and nutrients run-off8,9) and biological (e.g. community composition10) properties. In northern landscapes, surface waters also play a key role in the transport of detrital materials, nutrients and organic matter11,12, thus indirectly determining the relative role of allochthonous (terrestrial) and autochthonous food resources available for aquatic consumers.

Energy flows through aquatic food webs are of fundamental importance for the function of lake ecosystems13, and are a key to our understanding of their response to global change. Biological communities in arctic/subarctic lakes are often species-poor and have simpler food webs than those of temperate lakes14. Carbon transfer through food webs is derived either from autochthonous primary production (i.e., phytoplankton and benthic algae15,16), from allochthonous detrital inputs and/or from remobilized dissolved organic carbon by bacteria17. However, due to the lack of long-term contemporary data of subarctic lakes, it is still unclear to what extent climate change affects the relative importance of these trophic processes. Hence, past dynamics of aquatic ecosystems from paleo-data provide key information that can contribute to our understanding of lake responses to changes18.

Recent paleolimnological studies conducted on subarctic lakes have shown complex relationships between changes in terrestrial vegetation in the watershed, inputs of allochthonous organic matter, changes in in-lake light regime and taxonomic shifts in the assemblages of aquatic primary producers19-21. However, identification of past energy pathways within subarctic lake food webs has been less extensively studied22. Innovative approaches using stable isotope composition (mainly carbon, nitrogen and hydrogen) of invertebrate remains archived in lake sediment records have recently been developed to reconstruct past energy flows to aquatic primary consumers22-24. Specifically, Cladocera (Crustacea) form an important trophic link between basal resources (i.e.,
primary producers, bacteria) and fish, and stable isotopic composition of their sclerotized remains (e.g. resting eggs or ephippium) is thus a good indicator of long-term changes in aquatic food webs. These paleolimnological approaches help to provide insight in future trajectories of lake food webs under ongoing climate and land-cover change in Arctic and subarctic regions.

The main objective of this study was to investigate the past relationships between climate change, landscape development and carbon flows to zooplankton in a subarctic lake. We analysed sediment composition and photosynthetic pigments, as well as carbon stable isotope composition of Daphnia (Cladocera; Crustacea) resting eggs to reconstruct past dynamics of sedimentary organic matter, autochthonous primary production and carbon resources available to Cladocera under different climatic conditions. Results were then compared with those of previous paleolimnological studies that focused on climate and landscape changes to estimate the relative importance of in-lake impacts vs. catchment-mediated processes on energy flows through subarctic food webs.

**Methods**

**Study site.** Lake Diktar Erik (68°26′43″N, 18°36′50″E) is a small lake (0.1 km²) located in northern Sweden (Fig. 1A). The bedrock geology in the region is predominated by granite and its metamorphic products, while the prevailing catchment vegetation consists of mountain birch forest (Betula pubescens ssp. tortuosa). The lake is located at 375 m a.s.l. and has a maximum water depth of 16 m (Secchi depth of 6 m). The lake is oligotrophic and slightly humic, with a pH of 6.3, conductivity of 14.7 μS.cm⁻¹, and concentrations of total organic carbon of 3.6 mg.L⁻¹, total phosphorus (TP) of 5 μg P L⁻¹ and total nitrogen (TN) of 206 μg N L⁻¹ recorded in 1997. Similar
concentrations of DOC: 4.2 mg L\(^{-1}\), total phosphorus: 4 µg TP L\(^{-1}\) and total nitrogen: 270 µg TN L\(^{-1}\) for this lake were also reported by Karlsson et al.\(^{27}\). Deglaciation of the surroundings of Lake Diktar Erik was reported at approximately 9.5 ka cal. BP\(^{28–30}\). Then, favourable climatic conditions allowed rapid transition from a vegetation-free landscape to forest vegetation during the early Holocene (ca. 9.5–6.5 ka cal. BP)\(^{29–31}\). This initial phase of landscape development was followed by a climatically stable and warm period during the Holocene Thermal Maximum (ca. 6.5–3.5 ka cal. BP), marked by widespread developments of pine forests. The late Holocene period (ca. 3.5–0.05 ka cal. BP) was instead characterised by a long-term marked cooling and wetter conditions inducing a gradual replacement of pine forest by a mountain birch forest similar to that present nowadays\(^{30–32}\). Previous paleoecological studies from the area have not identified distinguishable environmental impacts in response to early human activities\(^{33}\). During the 20th century, rail tracks and road constructions have occurred along the southern, downstream shore of the lake. Thus, Holocene development of northern Sweden provides an exceptional natural experiment to study how climate and landscape changes affected terrestrial-aquatic linkages and carbon flows across the plant-consumer interface in subarctic lakes.

**Sediment sampling.** In August 2017, a 100-cm sediment core was retrieved from the largest depth of the lake using a gravity corer (9 cm of diameter; UWITEC). As terrestrial macrofossils were absent in the collected core, radiocarbon dates were determined on five bulk sediment samples measured using an accelerator mass spectrometer at the Poznan Radiocarbon Laboratory (Poland) and The Tandem Laboratory (Sweden; Table 1). In addition, we constrained the marked transition between proglacial and lacustrine sediments (Fig. 1B) using the deglaciation age (ca. 9.5 ± 0.25 ka cal. BP) reported by previous paleolimnological studies conducted in the region\(^{34,35}\). Age-depth modelling, combining calibrated radiocarbon dates and deglaciation age, was performed using simple linear interpolation (Clam package for R\(^{36}\)).

**Sedimentological and sedimentary pigment analysis.** The sediment core was vertically split in two halves, and one split core surface was covered with Ultralene\textsuperscript{®} foil to avoid desiccation and contamination, and scanned every 3 mm using an ITRAX XRF Core Scanner at the University of Stockholm (Cox Analytical Systems). XRF measurements were carried out using a Mo tube, set at 30 kV and 30 mA, for 60 s to detect relative concentrations of selected major elements (Ti, Fe, Mn, Si, Al). Elemental intensities were expressed as counts per unit time per unit area (cps).

The other split core was continuously and horizontally sliced down to 50 cm depth into 1 cm thick sub-samples that were subjected to further analyses. Organic matter concentration (OM) was analysed using the loss-on-ignition method, and results were expressed as percentage of dry weight (hereafter; % of dry weight). In
addition, sediment samples were analysed for carbon and nitrogen stable isotopes (depicted as δ13C_{OM} and δ15N_{OM} respectively), carbon and nitrogen concentrations (C_{org} and N_{tot}), and C/N weight ratios. Prior to analysis, sediment samples were dried (at 60 °C for 72 h), ground, and 3 mg of dried sediments were transferred to tin capsules. δ13C_{OM} and δ15N_{OM} were analysed using an Isotope Ratio Mass Spectrometer interfaced with an Elemental Analyser (EA-IRMS) at our Stable Isotope Laboratory (Umeå, Sweden). Results were expressed as the delta notation with Vienna Pee Dee Belemnite and atmospheric nitrogen as standards: δ13C or δ15N (‰) = [R_{sample}/R_{standard} − 1] × 1000; where R = δ13C/δ13C_{VPDB} or δ15N/δ15N_{AIR}. Sample measurement replications from internal standards (wheat and maize flour) produced analytical errors (1σ) of ±0.15‰ for both δ13C and δ15N values (n = 24).

Photosynthetic sedimentary pigments were analysed as a paleo-proxy of aquatic primary production20, following the method by37. Briefly, sediment samples were freeze-dried, and pigments were extracted at −20 °C in the dark during 24 h using a solution of acetone and methanol (80:20 V:V). Extracts were then clarified by filtration through a 0.45 μm Millex-LCR hydrophilic PTFE membrane filter before chromatographic analysis. Reversed-phase high-performance liquid chromatography (RP-HPLC) was applied to separate pigments. A Shimadzu Prominence (Japan) series binary gradient system with a photodiode array (PDA) and fluorescence detectors was used (see38 for details). Peak identification and quantification were made by commercially available external standards from DHI Company (Denmark). Chlorophyll a (Chl a) and its derivative phycoerythrin a (Phe a) were selected to indicate the overall algal biomass37,39. The Chl a/Phe a ratio was used to assess pigment preservation in lake sediments, and ratios are expected to remain relatively stable over time if stable preservation conditions occur40. Taxon-specific pigments were used to indicate the biomass of aquatic primary producer’s classes: lutein (Lut) for green algae (Chlorophyceae), fucoxanthin (Fuco) for diatoms (Bacillariophyceae), alloxanthin (Allo) for cryptophytes (Cryptophytae39,) and canthaxanthin (Cantha) for cyanobacteria (Cyanophyceae41,). Pigment concentrations are expressed as nanomoles per gram of sediment organic matter (nmol g−1 OM).

**Carbon stable isotope analysis of cladoceran remains.** Stable isotope analyses were performed on resting eggs of Daphnia ssp. morphotype retained from lake sediment layers and identified using the photograph book of Szeroczyńska and Sarmaja-Korjonen42. Sediment samples were deflocculated in NaOH (10%) solutions, resting eggs of Daphnia ssp. morphotype retained from lake sediment layers and identified using the photograph book of Szeroczyńska and Sarmaja-Korjonen42. Resting eggs were sorted out under a dissection microscope until approximately 50 eggs or a mesh according to standard protocol of Perga22. Resting eggs were sorted out under a dissection microscope until approximately 50 eggs or a

**Table 1.** Radiocarbon dates (± 1 standard deviation) of the sediment sequence (Lake1_17_C1) from Lake Diktar Erik. In column Model, ‘R’ refers to rejected date, and ‘I’ to included dates.

| Depth (cm) | Lab code | Material | yr BP    | Model |
|------------|----------|----------|----------|-------|
| 9          | Ua-62416 | Bulk     | 1356 ± 31 | I     |
| 10         | Poz-99924| Bulk     | 2685 ± 30 | R     |
| 19         | Ua-62417 | Bulk     | 2147 ± 31 | I     |
| 29         | Poz-99925| Bulk     | 3145 ± 30 | I     |
| 49         | Poz-99926| Bulk     | 4885 ± 35 | I     |

**Data analysis.** Two separate principal component analyses (PCA) were performed on sediment and pigment data, respectively. PCA axis significance was checked using the broken-stick model31. Pigment concentrations and sediment composition were expected to have significant, and potentially non-linear, influences on food resources for zooplankton and, therefore, δ13C_{Clado} values. Statistical relationships between δ13C_{Clado} values and PCA1 scores performed on sedimentological and pigment data (PCA1_{sed} and PCA1_{pig}, respectively) were examined using a generalized additive model (GAM; fitted using the mgcv package for R(R)) approach, with a continuous-time, first-order autoregressive process to account for temporal autocorrelation55. Significance of fitted trends was checked using standard statistical inferences for GAM. All statistical analyses and plots were performed using the R 3.5.2 software46.

**Results**

**Past changes in sediment composition.** The transition from proglacial to lacustrine sedimentation could be well observed in our sediment core as a colour-change from dark grey at the bottom to dark brown towards the surface (Fig. 1B). All calibrated radiocarbon ages consistently increase with depth in core, except at 10 cm (Table 1); and this radiocarbon age was therefore not included in the final model as it would lead to age-reversal and/or abrupt change in sedimentation rates not supported by sedimentological observations (Fig. 1B). This radiocarbon age also conflicted with another date at 9 cm depth (Table 1) which fits well the age model. Hence, 81 cm of sediments from Lake Diktar Erik covered the last ca. 9500 years, corresponding to an average sedimentation rate of about 0.08 mm.yr−1. Titanium intensities in lake sediments were relatively stable at approximately 4500 cps from 50 to 10 cm sediment depth, and then gradually decreased to 2000 cps at the sediment surface (Fig. 2A). Organic matter concentration (OM) ranged 19.1–36.5%, while C_{org} and N_{tot} concentrations in sediments ranged 6.9–16.9% and 0.5–1.2%, respectively (Fig. 2A). Overall, OM, C_{org} and N_{tot} concentrations
were higher in the oldest part of the record (ca. 5.8–3.5 ka cal. BP), and followed a gradual decrease over time (from ca. 3.5 to 0.05 ka cal. BP). Interestingly, however, these declining trends reversed and showed conspicuous peaks in the most recent sediment layers. The sediment weight C/N ratio ranged 12.5–16.0 with the highest values observed from ca. 5.8 to 3.5 ka cal. BP (Fig. 2A). δ¹⁵NOM values ranged 1.6–3.1‰, and those of δ¹³COM ranged from −28.5 to −27.2‰. δ¹³COM and δ¹⁵NOM temporal trends were similar, with gradual increases over time, except for the uppermost samples where instead decreases were noted (Fig. 2A).

The first two PCA axes explained 61.8% and 19.5%, respectively, of the total variance of sediment data. PCA₁sed axis was strongly correlated with OM, Ntot, Corg, δ¹⁵NOM and δ¹³COM (Fig. 3A). Negative values on PCA₁sed axis represented organic-rich sediment layers with low δ¹⁵NOM and δ¹³COM values. PCA₂sed axis predominantly explained C/N ratios (Fig. 3A), with negative values representing samples with low C/N ratios. PCA₁sed scores followed a gradual increase over time, switching from negative to positive values at ca. 3.4 ka cal. BP (Fig. 2B), whereas PCA₂sed scores showed no specific temporal trend, except a conspicuous decrease observed from 8 cm and upward (Fig. 2B).

Trends of sedimentary pigment concentrations. Chl a/Phe a ratios showed high values in deep sediment layers, but gradually declined from 50 to 13 cm depth in the core (Fig. 4A). The highest photosynthetic pigment concentrations, 132.0 nmol g⁻¹ OM and 43.1 nmol g⁻¹ OM, respectively, were found for Phe a and Chl a (Fig. 3A). Allo and Lute, indicating cryptophytes and green algae, respectively, were the most concentrated taxon-specific pigments (ranging 2–9 nmol g⁻¹ OM, Fig. 4A). Temporal trends of pigments were almost consistently similar, higher during the oldest part of the record (ca. 5.8–3.5 ka cal. BP), and then decreasing gradually to present-day. However, Fuco instead showed slightly higher values from ca. 3 ka cal. BP to present-day, indicating an increase in diatoms. The first two axes of the PCA applied to sedimentary pigment data accounted for 53.1% and 35.0% of the total variance, respectively. PCA₁pig axis explained Chl a, Allo, Cantha and Lute (Fig. 3B). Negative values on the PCA₁pig axis represent pigment-rich sediment layers. PCA₂pig axis predominantly explained Pheo a and Fuco (Fig. 3B), with positive values representing sediment samples with high Fuco and Pheo a concentrations. PCA₁pig scores followed a gradual increase over time, switching from positive to negative values around 3.5 ka cal. BP (Fig. 4B) suggesting a decline in concentrations of Chl a, Allo, Cantha and Lute, whereas PCA₂pig scores followed a small increase over time (Fig. 4B).

Stable C isotope in cladoceran resting eggs. δ¹³C values of Daphnia resting eggs ranged from −30.6 to −27‰ (Fig. 5C), and the lowest δ¹³C_Clado value was found for the uppermost sediment layer (−30.6‰; Fig. 5C). Based on the temporal trends, two distinct patterns were identified in the uppermost 50 cm of the core. The
δ<sup>13</sup>C<sub>Clado</sub> values first increased from −30.6 to −28.8‰ between 5.8 and ca. 3 ka cal. BP, and then decreased to values around −30.2‰ after ca. 3 ka cal. BP. GAM showed that PCA1<sub>sed</sub> and PCA1<sub>pig</sub> covariates explained 56.9% of the overall variability of δ<sup>13</sup>C<sub>Clado</sub> values (p-value < 0.001). Relationships between δ<sup>13</sup>C<sub>Clado</sub> values and covariates were non-linear (Fig. 6). PCA1<sub>sed</sub> showed a monotonic and positive relationship with δ<sup>13</sup>C<sub>Clado</sub> values (F = 7.2; edf = 1.39; Fig. 6A), whereas PCA1<sub>pig</sub> scores were unimodally related to them (F = 7.9; edf = 1.89; Fig. 6B). The PCA1<sub>pig</sub> fitted function showed a positive relationship with δ<sup>13</sup>C<sub>Clado</sub> values for negative PCA1<sub>pig</sub> scores, and a negative relationship with δ<sup>13</sup>C<sub>Clado</sub> values for positive PCA1<sub>pig</sub> scores. Therefore, major shift in pigment response curve occurred for PCA1<sub>pig</sub> scores observed at ca. 3.5 ka cal. BP (Figs. 5 and 6).

**Discussion**

We reconstructed the long-term development of Lake Diktar Erik over the last 5800 years based on sedimentary organic matter and photosynthetic pigment analyses. Our results showed that during the Holocene Thermal Maximum (5.8–3.5 ka cal. BP), steady organic matter inputs from the surrounding watershed were revealed by high OM and C<sub>org</sub> concentrations and high C/N ratios in Lake Diktar Erik sediment core (Fig. 2). Moreover, the highest pigment concentrations in the Lake Diktar Erik record were also observed during this period (Fig. 4), a period that otherwise showed a general decline in all pigment concentrations (Fig. 4). This decline in autochthonous primary production was likely driven by the onset of the cooling phase around 5 ka cal. BP in Fennoscandia (Fig. 5D; but see also 21,28,29). Then, the climate during the late Holocene period (ca. 3.5–0.05 ka cal. BP) was characterised by long-term cooling and wetter conditions (Fig. 5D), inducing a gradual replacement of pine forest by a mountain birch forest similar to that present nowadays (Fig. 5E–H)30–32. These results were well in line with successional developments of similar lakes in northern Sweden (see also 28,30,32), and showed three distinct development phases. Our results also showed a strong decline in OM and pigment concentrations (Figs. 2 and 4), suggesting marked decreases in both terrestrial and aquatic productivity, as previously reported from pigment and diatom dynamics21,28 and sedimentological records from other subarctic lakes30,31. Moreover, the ongoing trend towards more oligotrophic conditions revealed from long-term monitoring of Swedish lakes corroborate this observation. Whereas the overall trend in PCA1<sub>sed</sub> scores followed a gradual increase over time, switching from negative to positive values, the uppermost sediment sample instead showed the most negative PCA1<sub>sed</sub> value of the time series (Fig. 5A), likely due to the effects of diagenetic alteration of both elemental and isotopic compositions of sedimentary organic matter (see also 48,49).

The δ<sup>13</sup>C values of *Daphnia* resting eggs (δ<sup>13</sup>C<sub>Clado</sub>) ranged from −30.6 to −27‰, and were lower than those of organic matter (Fig. 5C), implying that zooplankton utilised an isotopically lighter food source than the overall sedimentary organic matter. δ<sup>13</sup>C<sub>OM</sub> values have been widely used as a reliable proxy of sediment composition, reflecting the relative contribution of organic matter from aquatic and terrestrial origins, as autochthonous primary producers usually exhibit lower δ<sup>13</sup>C values than those of terrestrial organic matter20. Therefore, *Daphnia* of
Lake Diktar Erik likely has preferentially assimilated $^{13}$C-depleted aquatic primary producers, and our study thus confirms that zooplankton consumers in subarctic lakes, even in the long-term perspective, have been mainly fuelled by autochthonous primary production (see also 51–54). The $\delta^{13}$C$_{Clado}$ values were also closely correlated to changes in sediment composition (PCA1 sed scores) and in-lake primary production (PCA1 pig scores), but we found a major change in their relationships with in-lake primary production occurring at ca. 3.5 ka cal. BP (Figs. 5B and 6B). This pattern suggest a strong influence of autochthonous primary production on Daphnia feeding habits, and these results could strengthen previous findings that zooplankton diet and algal dynamics are closely linked in subarctic food webs.

Based on long-term trends in Lake Diktar Erik and previous paleolimnological investigations of other lakes from the area, we identified the potential mechanisms of these observed patterns. Between 5.8 and ca. 3.5 ka cal. BP, $\delta^{13}$C$_{Clado}$ values increased from $-30.6$ to $-28.8\%$o, and were positively correlated to a decrease in autochthonous primary productivity (Fig. 6A). This increase in $\delta^{13}$C$_{Clado}$ values could thus reflect a slight increase in the relative contribution of $^{13}$C-enriched terrestrial organic matter to Daphnia biomass. Our study thereby strengthens previous findings that the relative contribution of allochthonous organic matter to consumer biomass largely increased in unproductive lake food webs (Fig. 6B). After ca. 3.5 ka cal. BP, $\delta^{13}$C$_{Clado}$ values decreased and correlated negatively with pigment data (Fig. 6B). Several studies of similar subarctic lakes during this period have demonstrated a taxonomic shift in algal assemblage composition (from benthic- vs. pelagic-dominated algal assemblages) induced by increased inputs of terrestrial DOC and a decline in the phototrophic zone of the lake19,21. Specifically, there is evidence that cooler and wetter climate conditions reported in Fennoscandia

**Figure 5.** (A) Sediment PCA1 scores, (B) pigment PCA1 scores, (C) carbon stable isotopic composition of cladoceran remains in sediment core Lake1_17_C1 from Lake Diktar Erik ($\delta^{13}$C$_{Clado}$‰), (D) pollen-based temperature variability for Northern Europe47, percentage of pollen from (E) *Pinus sylvestris* and (F) *Betula pubescens* in sediment core of Vuolep Njakajaure (letter A in Fig. 1B), percentage of pollen from (G) *Pinus sylvestris* and (H) *Betula pubescens* in sediment core of Vuoskkujávri (letter B in Fig. 131), and (I) vertical dashed lines dividing the stratigraphy into 4 phases: initial landscape development (ca. 9.5–6.6 ka cal. BP), catchment stabilization (ca. 6.6–3.4 ka cal. BP), long-term cooling (ca. 3.4–0 ka cal. BP) and ongoing climate change (adapted from 28).
during the late Holocene induced a change in catchment vegetation, increased transport of DOC to lakes and a subsequent functional predominance of benthic to pelagic algae\textsuperscript{19,21}. Our observed trends in sediment composition and pigment concentrations (Figs. 2 and 4) are typical for this type of lakes\textsuperscript{19,21}, and we therefore conjecture that a similar shift from a benthic- to a pelagic-dominated algal assemblages occurred in Lake Diktar Erik during this period. As phytoplankton usually is more \textsuperscript{13}C-depleted than benthic algae\textsuperscript{57,58} and terrestrial organic matter\textsuperscript{49}, an observed decrease in $\delta^{13}C_{\text{clado}}$ values would therefore indicate a higher contribution of planktonic algae to zooplankton biomass. Results suggested that the diet of \textit{Daphnia} in subarctic lakes, even in the long-term perspective, depends on both availability (i.e. standing stock) and quality of food resources (i.e. allochthonous vs. autochthonous; benthic vs. pelagic), as previously demonstrated at seasonal scale (see also\textsuperscript{59}). Our study thus revealed the long-term influence of terrestrial-aquatic linkages and in-lake processes on the functioning of subarctic food webs.

In this study, we examined how regional climate and landscape changes over the last 5800 years affected the relative importance of allochthonous and autochthonous carbon transfer to zooplankton in a subarctic lake. Our study revealed complex interplays between climate-induced change in in-lake (through algal productivity and assemblage composition) and catchment-mediated (through changes in allochthonous DOC and vegetation composition) processes in the functioning of planktonic food webs of a small subarctic lake. The results showed greater incorporations of benthic primary production into zooplankton biomass in periods that had a warmer and drier climate and clearer water, whereas colder and wetter climates and lower water transparency led to higher relative contributions of planktonic algae into zooplankton biomass. Hence, our results demonstrate that paleolimnological studies can be a powerful approach for further exploring impacts of climate change on biogeochemical cycles and terrestrial-aquatic linkages in subarctic environments.

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**Author contributions**
S.B., T.V., J.N. and W.G. designed the study. S.B. analysed all samples with the exception of pigment analysis performed by I.T. and R.F. S.B. wrote the paper with substantial contribution from all co-authors.

**Competing interests**
The authors declare no competing interests.

**Additional information**

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