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ORIGINAL ARTICLE

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Both climate trends and short-term fluctuations affected algae–zooplankton interactions in a boreal lake during the late Holocene

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Abstract

1. Most studies aiming to explore the response of algae and zooplankton trophic interactions to climate variability have only been focused on unidirectional and very short-term trends in temperature changes. As a result, the non-stationary aspect of climate change (warming and cooling periods, frequencies) remains completely unstudied.
2. We studied elemental and stable isotope composition of sedimentary organic matter, photosynthetic pigments, and carbon stable isotope composition of Cladocera resting eggs in a sediment record covering the last *c.* 2,600 years. We examined how past climate change acting at different timescales affected algal biomass and community composition, and carbon assimilation by zooplankton in a boreal lake.
3. Our study revealed major effects of both long-term climate trends and shorter-term fluctuations on algae–zooplankton interactions in a boreal lake. We found the main climate trends, in particular the Little Ice Age, induced algal biomass and community composition changes and drastic changes in carbon assimilation by zooplankton. Interestingly, we found that temperature fluctuations could also contribute to regulating algae–zooplankton interactions. Specifically, we observed drastic changes in sedimentary markers and stable isotope composition of zooplankton remains during the most recent period, suggesting a strong influence of ongoing anthropogenic change on algae–zooplankton interactions.
4. Our study confirms previous findings showing close long-term linkage between the temporal dynamics of zooplankton diet and planktonic algae, and that both climate trends and short-term fluctuations are key in regulating consumer–resource trophic interactions.
5. Novel approaches that combine high temporal resolution paleolimnological reconstructions and contemporary monitoring studies are needed to better understand climate change effects on algae–zooplankton interactions and lake food webs.

KEYWORDS

algal pigments, aquatic food webs, carbon stable isotope, paleolimnology, subfossil cladocera

1 | INTRODUCTION

Climate change is altering the abiotic features of freshwaters, including complex interplays between their physico-chemical properties, and basal resources. These changes are causing wide-ranging ecological shifts, and impact consumer–resource interactions and lake food webs (Lau et al., 2020). Responses of algae–zooplankton interactions to climate variability have been studied in boreal lakes (see also Creed et al., 2018). However, most studies have focused on effects from unidirectional and very short-term changes in temperature on populations. As a result, the effects of long-term climate fluctuations (i.e. including warming and cooling periods across millennial and decadal time scale) have often been neglected.

These long-term climate changes are controlled by the joint action of numerous forcing factors that induce multidirectional long-term climate changes (Roberts, 2013). As algae and most zooplankton species have short life cycles, algae–zooplankton interactions should theoretically be strongly responsive to both such low- (millennial- to centennial-scale) and high-frequency (annual- to decadal-scale) climate variability. However, such long-term responses in lake food webs cannot be investigated using contemporary data because these time-series rarely cover more than a few decades.

Paleolimnological approaches can provide valuable insights into the effects of long-term climate change (acting at different frequencies) on consumer–resource interactions in food webs. For example, a comprehensive understanding of past dynamics of algal communities can be well captured by sedimentary algal pigments (Leavitt & Hodgson, 2002). Moreover, approaches that use stable isotope composition (mainly carbon, nitrogen, and hydrogen) of biological remains archived in lake sediments can be used to reconstruct past energy flows to primary consumers (Belle et al., 2018; van Hardenbroek et al., 2013; Wooller et al., 2012). As filter-feeding Cladocera form an important trophic link between basal resources (i.e., algae, bacteria; Havel, 2009) and higher trophic levels, changes in the stable isotope composition of their sclerotised remains (e.g. resting eggs or ephippia) provide a good proxy of food web changes in pelagic habitats (Perga, 2009). Therefore, combining sedimentary algal pigments and isotope-based approaches contributes to a mechanistic understanding of the effects of long-term climate trends and fluctuations on consumer–resource interactions in lakes.

In this study, we investigated the relationships between climate change, algal community composition, and zooplankton diet in a boreal lake over millennial to centennial time scales. This region has not undergone any significant early human impacts on vegetation composition and ecosystem changes (Bergman et al., 2004), thus facilitating the interpretation of the Lake Stor-Björsjön sediment record and subsequent quantification of climate change effects on consumer–resource interactions in the lake's food web. We analysed sediment core samples with respect to organic matter composition, photosynthetic algal pigments, and carbon stable isotope composition of cladoceran resting eggs to reconstruct past dynamics of: (1) organic matter accumulation; (2) algal biomass and community composition; and (3) carbon resources incorporated into cladoceran biomass. More specifically, we tested whether different climatic conditions induced changes in energy flows within the lake food web. We hypothesised that both climate trends and short-term fluctuations induce cladoceran carbon resources by inducing changes in algal community composition and biomass.

2 | METHODS

2.1 | Study site, past climate change, and sediment core sampling

Lake Stor-Björsjön (63.61455°N 12.24004°W) is a 43-ha large, oligotrophic boreal lake located at 568 m above sea level in the county of Jämtland, Central Sweden (Figure 1a). The lake has a maximum water depth of 15 m (Secchi depth of 4 m; Figure 1b). The lake stratifies in summer/winter, and has a mean pH of 7 ± 0.2, conductivity of 31 ± 8 μS/cm, total organic carbon of 4.4 ± 1 mg/L, total phosphorus (TP) of 2.7 ± 0.8 μg P/L and total nitrogen (TN) of 155 ± 33 μg N/L (mean and standard deviation for the last 5 years; see database https://miljodata.slu.se/mvm/). The catchment drains the mountains in the west and is dominated by sparse vegetation dominated by tundra shrubs and grasses in the upper reaches and by pine, spruce, and mountain birch in the lower reaches.

Tree-ring chronology of living and subfossil Scots pine (*Pinus sylvestris*) has previously been produced for the area (Figure 1a) to reconstruct summer (June–August) temperature variability during the last 3,600 years (Linderholm & Gunnarson, 2005). This reconstruction distinguishes a highly variable summer climate with warmer (e.g. 2,400–2,500 calibrated years before the present [cal. BP], and 1,050–950 cal. BP or depicted as the Medieval Warm Period), and colder periods (1,650–1,550 cal. BP, and 600–50 cal. BP depicted as the Little Ice Age).

In July 2017, a 90-cm long sediment core was retrieved from the largest depth of the lake using a gravity corer (inner diameter 9 cm; UWITEC). Radiocarbon dates were determined on two terrestrial macrofossil samples measured using an accelerator mass spectrometer at the Poznan Radiocarbon Laboratory (Poland; Table 1). Age-depth modelling, combining radiocarbon dates after calibration using the atmospheric calibration dataset IntCal13 (Reimer et al., 2013), was performed using simple linear interpolation (Clam package for R; Blaauw, 2010). All sample depths were then converted to calibrated year BP (cal. BP, with 0 cal. BP = AD 1950) according to the age–depth model.

2.2 | Sediment and pigment analysis

The retrieved sediment core was vertically split into two halves and stored cold and dark. One half of the split core was then sliced horizontally up to 60 cm core depth into 1-cm thick sediment layers that were subjected to further analyses. Sediment layers were analysed with respect to organic matter (OM) concentration using the loss-on-ignition method (% of dry mass), carbon and nitrogen stable

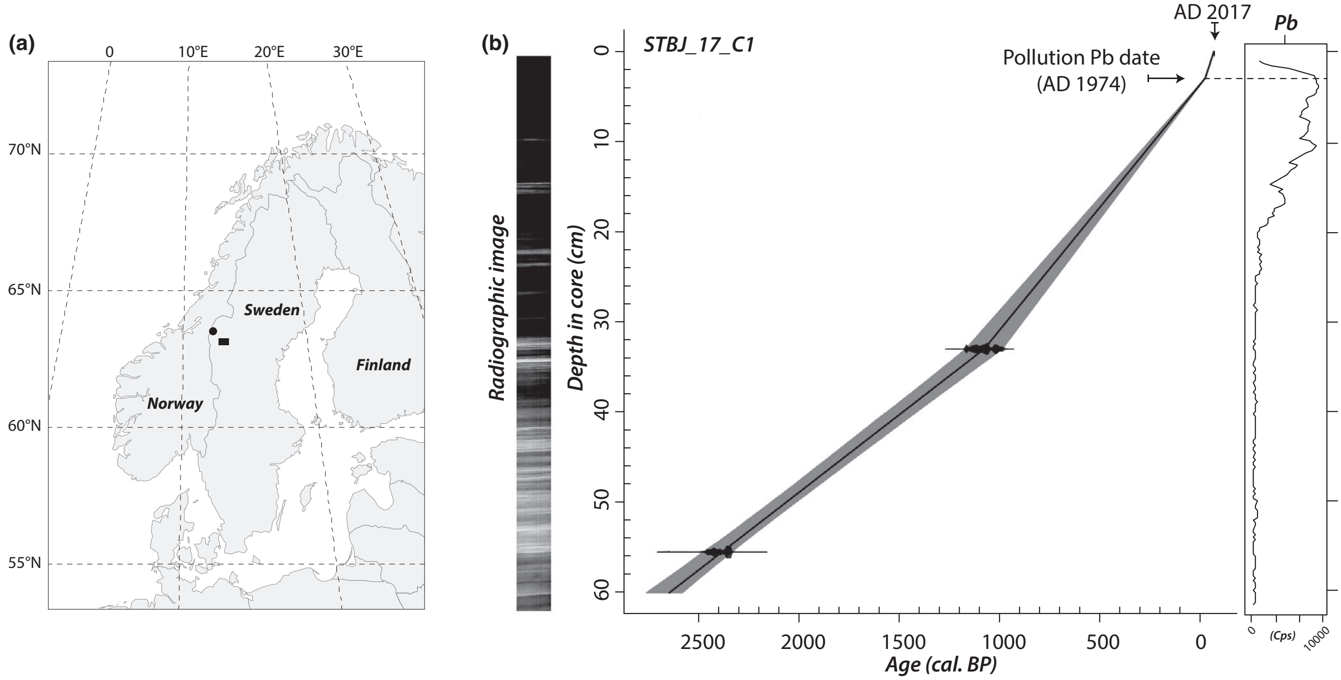

FIGURE 1 (a) Location of the study region showing the sampling site (black circle; Lake Stor-Björsjön), and area considered for previous paleo-climate reconstruction (black rectangle; Linderholm & Gunnarson, 2005). (b) Radiographic image, age–depth model (linear interpolation) and lead record (Pb, XRF measurements) in the sediment core (STBJ_17_C1) retrieved from Lake Stor-Björsjön. The age-depth model indicates an average sedimentation rate of 0.23 mm/year

TABLE 1 Radiocarbon dates and material dated in sediment core STBJ_17_C1 from Lake Stor-Björsjön

Depth (cm)	Lab code	Material	year BP
33	Poz-110509	Leaf	1,160 ± 30
55.5	Poz-110510	Leaf	2,355 ± 30

isotopes (depicted as $\delta^{13}C_{OM}$ and $\delta^{15}N_{OM}$, respectively), and organic carbon (C_{org}) and total nitrogen concentrations using elemental analysis (N_{tot}), as well as C/N weight ratios. Sediment samples were dried (60°C; 72 hr), ground, packed in tin capsules (3 mg), and analysed using an isotope ratio mass spectrometer interfaced with an elemental analyser at SLU's Stable Isotope Laboratory (Umeå, Sweden). Results were expressed as the delta notation and using Vienna Pee Dee Belemnite and atmospheric nitrogen as standards: $\delta^{13}C$ or $\delta^{15}N$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1{,}000$; where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. Sample measurement replications from internal standards (wheat and corn flour) produced analytical errors (1σ) of ±0.15‰ for both $\delta^{13}C$ and $\delta^{15}N$ values ($n = 24$).

Sedimentary pigments were analysed as a paleo-proxy of aquatic primary producer biomass and algal community composition (Reuss et al., 2010), following the method by Leavitt and Hodgson (2002). Briefly, sediment samples were freeze-dried, and pigments were extracted at −20°C in the dark for 24 hr using a solution of acetone and methanol (80:20 V:V). Extracts were then clarified by filtration through a 0.45-µm membrane filter (Millex-LCR hydrophilic PTFE) before chromatographic analysis. Reversed-phase high-performance liquid chromatography using a Shimadzu Prominence (Japan) series binary gradient system with a photodiode array and fluorescence detectors was used (see Tamm et al., 2015 for details) and applied to separate pigments. Peak identification and quantification were made by commercially available external standards from DHI Company (Denmark). Chlorophyll *a* (Chl *a*) and its derivative pheophytin *a* (Pheo *a*) were used as indicators of overall algal biomass (Leavitt & Hodgson, 2002; Waters et al., 2013). The Chl *a*/Pheo *a* ratio was used to assess pigment preservation in lake sediments, and ratios are expected to remain constant over time if stabile preservation conditions prevail (Ady & Patoine, 2016). Taxon-specific marker pigments were used to indicate the biomass of major algal groups: i.e. lutein for green algae (Chlorophyceae), fucoxanthin for diatoms (Bacillariophyceae), alloxanthin for cryptophytes (Cryptophytae, Roy et al., 2011; Waters et al., 2013), and canthaxanthin for cyanobacteria (Cyanophyceae, Deshpande et al., 2014). Fucoxanthin and lutein can also be present in chrysophytes and in higher plants but to a lesser extent (Roy et al., 2011; Waters et al., 2013). Pigment concentrations were expressed as nmol/g of dry mass sediment OM.

2.3 | Carbon stable isotope analysis of cladoceran remains

Carbon stable isotope analyses were performed on empty resting eggs of *Daphnia* spp. morphotypes retained from lake sediments and identified using Szeroczyńska and Sarmaja-Korjonen (2007) and Vandekerkhove et al. (2004). For the extraction of resting eggs, sediment samples were deflocculated in NaOH (10% V/V) solution, pre-treated using washing with HCl (10% V/V) solution and sieved through a 100-µm mesh according to Perga (2009). The HCl rinse was used to remove potential carbonate contaminations and allow for better comparisons with previously published paleolimnological studies. Resting eggs were sorted under a dissection microscope until approximately 50 ephippia or a mass of 60 µg was reached. If resting egg abundance was too low in a single sediment layer, resting eggs from the next consecutive sediment layer were used to make a pooled sample. Carbon stable isotopic composition of resting eggs ($\delta^{13}C_{Clado}$) was analysed using an isotope ratio mass spectrometer interfaced with an elemental analyser at INRA Nancy (Champenoux; France), and the results were expressed according to the delta notation (see above). Replicate measurements of laboratory standards produced analytical errors (1σ) of ±0.2‰ ($n = 15$).

2.4 | Data analysis

Sediment depth zones, defined by major temporal trends in sedimentological data and sedimentary pigment concentrations, were determined by constrained hierarchical cluster analysis using a Canberra and Bray–Curtis distance and a CONISS linkage method (*Rioja* package for R). Distinct zones were identified using the broken-stick model (Bennett, 1996). Bayesian change point analysis was also used on $\delta^{13}C_{Clado}$ data to identify changes in mean and variance of univariate time series data using the *bcp* package for R (Wang & Emerson, 2015).

Detrended correspondence analysis was performed on sediment and pigment datasets separately to estimate among-samples variability and to select the appropriate ordination method, resulting in a linear approach (Legendre & Birks, 2012). Two separate principal component analyses were therefore performed on sediment and pigment data and principal component (PC) axis significance was tested using the broken-stick model (Bennett, 1996). The $\delta^{13}C_{Clado}$ data were then added to each PC factorial map as a supplementary (passive) variable to identify factors potentially associated with $\delta^{13}C_{Clado}$ variability. Statistical relationships between first PC axis scores applied on sediment ($PC1_{sed}$) and pigment ($PC1_{pig}$) datasets, respectively, were assessed using a generalised additive model (GAM) approach (fitted using the *mgcv* package for R; Wood, 2011). Finally, statistical relationships between $\delta^{13}C_{Clado}$ values and explanatory variables were examined using a GAM approach (following similar approach described by Simpson & Anderson, 2009). All statistical analyses were performed using the R 3.5.2 software (R Core Team, 2018), which also produced graphics.

3 | RESULTS

3.1 | Temporal changes in sediment composition

All calibrated radiocarbon ages consistently increased with depth in the sediment core (Figure 1b and Table 1), and revealed that 60 cm of sediment depth covered the last *c*. 2,600 years, corresponding to an average sedimentation rate of 0.23 mm/year. OM concentration ranged 11.1%–21.8%, while C_{org} and N_{tot} concentrations in sediments ranged 4.2%–10.6% and 0.3%–0.7%, respectively (Figure 2a). Overall, OM, C_{org}, and N_{tot} concentrations showed relatively high temporal variability and no clear trend. The sediment C/N ratio ranged 14.3–17.3, except for the lowest values of 9.6 observed at 39 cm depth in the sediment (Figure 2a). The $\delta^{15}N_{OM}$ values ranged 1.2–2.3‰, and those of $\delta^{13}C_{OM}$ ranged from −28.7 to −27.7‰. Temporal trends of $\delta^{13}C_{OM}$ and $\delta^{15}N_{OM}$ followed opposite patterns and were divided into four distinct zones with transitions occurring at 50 cm (*c*. 2,000 cal. BP), 20 cm (600 cal. BP) and 3 cm (*c*. 1950 AD; Figure 2a).

The first two PC-axes explained 51.1% and 27.2%, respectively, of the total variation in the sediment data. The $PC1_{sed}$ axis was strongly correlated with OM, N_{tot}, and C_{org} (Figure 2b). Positive values on the $PC1_{sed}$ axis represented organic-rich sediment layers, while the $PC2_{sed}$ axis predominantly explained $\delta^{15}N_{OM}$, $\delta^{13}C_{OM}$ and C/N ratios. Negative values on the $PC2_{sed}$ axis represented samples with low C/N ratios and high $\delta^{15}N_{OM}$ and $\delta^{13}C_{OM}$ values. No strong temporal trend was found for either $PC1_{sed}$ or $PC2_{sed}$ scores, except for the four most recent samples. Additional projection of the $\delta^{13}C_{Clado}$ values in the PC factorial map suggested a correlation with $\delta^{13}C_{OM}$ values (Figure 2b).

3.2 | Temporal trends in sedimentary pigment concentrations

Ratios of chlorophyll *a* to pheophytin *a* were constant throughout the sediment core suggesting stable pigment preservation over the studied period (Figure 3a). The highest photosynthetic pigment concentrations were 101.4 nmol/g OM for pheophytin *a*, and 23.1 nmol/g OM for chlorophyll *a*. Alloxanthin and lutein, indicating planktonic cryptophytes and green algae, respectively, were the taxon-specific pigments with the highest concentrations, ranged 2–9 nmol/g OM. Cluster analysis on individual pigment concentrations (Bray–Curtis distance and CONISS linkage method) revealed three significant zones with transition at 50 cm (*c*. 2,000 cal. BP) and 20 cm (600 cal. BP) sediment depth. All pigments showed the lowest concentrations in the oldest zone (before *c*. 2,000 cal. BP), but then gradually increased during the period between 50 and 20 cm (from *c*. 2,000 to 600 cal. BP; Figure 3a). After *c*. 600 cal. BP, concentrations of alloxanthin, an indicator for cryptophytes (one of the predominant algal groups in this period) and fucoxanthin, an indicator pigment for diatoms, drastically increased, while canthaxanthin, indicating cyanobacteria, showed a slight decrease during this time period.

The first two axes of the PC applied to pigment data accounted for 45.3% and 25.8% of the total variance, respectively. The $PC1_{pig}$ axis explained pheophytin *a*, alloxanthin, and fucoxanthin, while negative values on this $PC1_{pig}$ axis represented pigment-rich sediment layers (Figure 3b). The $PC2_{pig}$ axis represented a gradient in chlorophyll *a* and lutein, with positive values representing samples with high concentrations. Samples were mainly distributed along the first $PC1_{pig}$ axis,

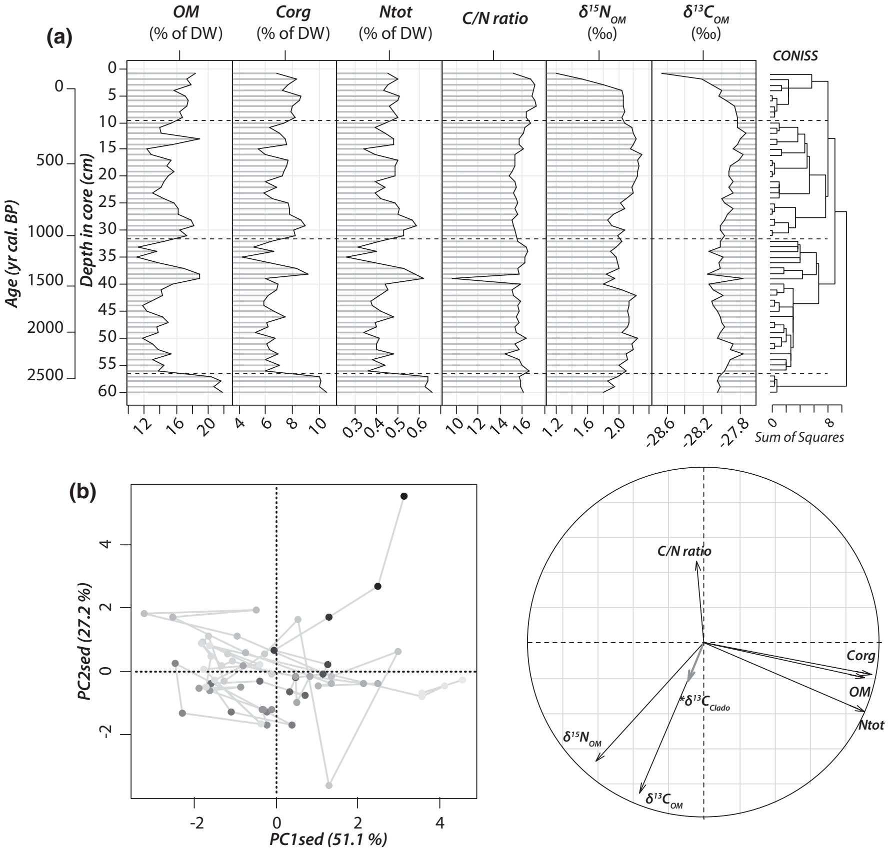

FIGURE 2 (a) Trends in organic matter concentration (OM; % of dry weight), total nitrogen (N_{tot}; % of dry weight), total organic carbon (C_{org}; % of dry weight), atomic ratio of organic carbon to total nitrogen (C/N), stable nitrogen isotope composition of sedimentary organic matter ($\delta^{15}N_{OM}$; ‰), stable carbon isotope composition of sedimentary organic matter ($\delta^{13}C_{OM}$; ‰), and carbon stable isotope composition of cladoceran remains in sediment core STBJ_17_C1 from Lake Stor-Björsjön ($\delta^{13}C_{Clado}$; ‰). Age and depth scales are both given on y-axes. Dendrogram is based on the sediment data and constructed by hierarchical clustering analysis (Canberra distance, CONISS linkage method). Horizontal dashed lines indicate significant zones defined by major patterns. (b) Factorial map of principal component analyses ($PC1_{sed}$ vs. $PC2_{sed}$) performed on sedimentological data. A grey-scale was used to identify the sample age ranging from light-grey colours for the oldest samples, to black symbols for the youngest samples. The $\delta^{13}C_{Clado}$ values have been added to the correlation circles as a passive variable (grey arrow). Correlation circles representing variable contributions to the first two axes of the PC

suggesting changing concentrations of alloxanthin, pheophytin *a*, and lutein and, to a lesser extent, canthaxanthin. Additional projection of the $\delta^{13}C_{Clado}$ values in the factorial map showed good agreement with $PC1_{pig}$, suggesting high correlations with fucoxanthin, and low correlations with pheophytin *a* and alloxanthin. Finally, the $PC1_{sed}$ scores were strongly and positively correlated with those of $PC1_{pig}$ (Figure 4; $edf = 1.926$; $F = 13.91$; $p\text{-value} < 0.001$).

3.3 | Delta-^{13}C in cladoceran resting eggs

The $\delta^{13}C$ of cladoceran resting eggs ranged from −35.2‰ to −30.9‰ (Figure 5a), with the lowest value found for the uppermost sediment layer. Bayesian change point analysis revealed a strong increase in $\delta^{13}C_{Clado}$ values occurring 20 cm depth in the core, and a significant decrease in $\delta^{13}C_{Clado}$ values occurring at 1 cm, corresponding to the period between *c*. 600 cal. BP and the early 21st century, respectively (Figure 5b). The $\delta^{13}C_{Clado}$ values ranged from −35.2‰ to −31.3‰ for the 60–20-cm and 1–0-cm layers being slightly more negative than those observed for the 20–1-cm period (that ranged from −33.7‰ to −30.9‰). When plotted together, $\delta^{13}C_{Clado}$ values and potential causal variables coincided (Figure 6). Synchronous changes in $\delta^{13}C_{Clado}$ and the explanatory variables occurred during the onset and end of the Little Ice Age (*c*. 600 cal. BP). GAM showed non-linear and positive effects of $PC1_{pig}$ and $\delta^{13}C_{OM}$ on $\delta^{13}C_{Clado}$ values, explaining 38.8% of the $\delta^{13}C_{Clado}$ variability (Table 2). High $PC1_{pig}$ scores, referring to high abundance of cryptophytes and diatoms, and high $\delta^{13}C_{OM}$ values, indicating high terrestrial inputs, positively correlated with $\delta^{13}C_{Clado}$ values (Figure 6).

4 | DISCUSSION

4.1 | Long-term changes in algal biomass and community composition

Sediment composition showed high variability over the past 2,600 years (Figure 2). Observed temporal patterns in C/N ratio,

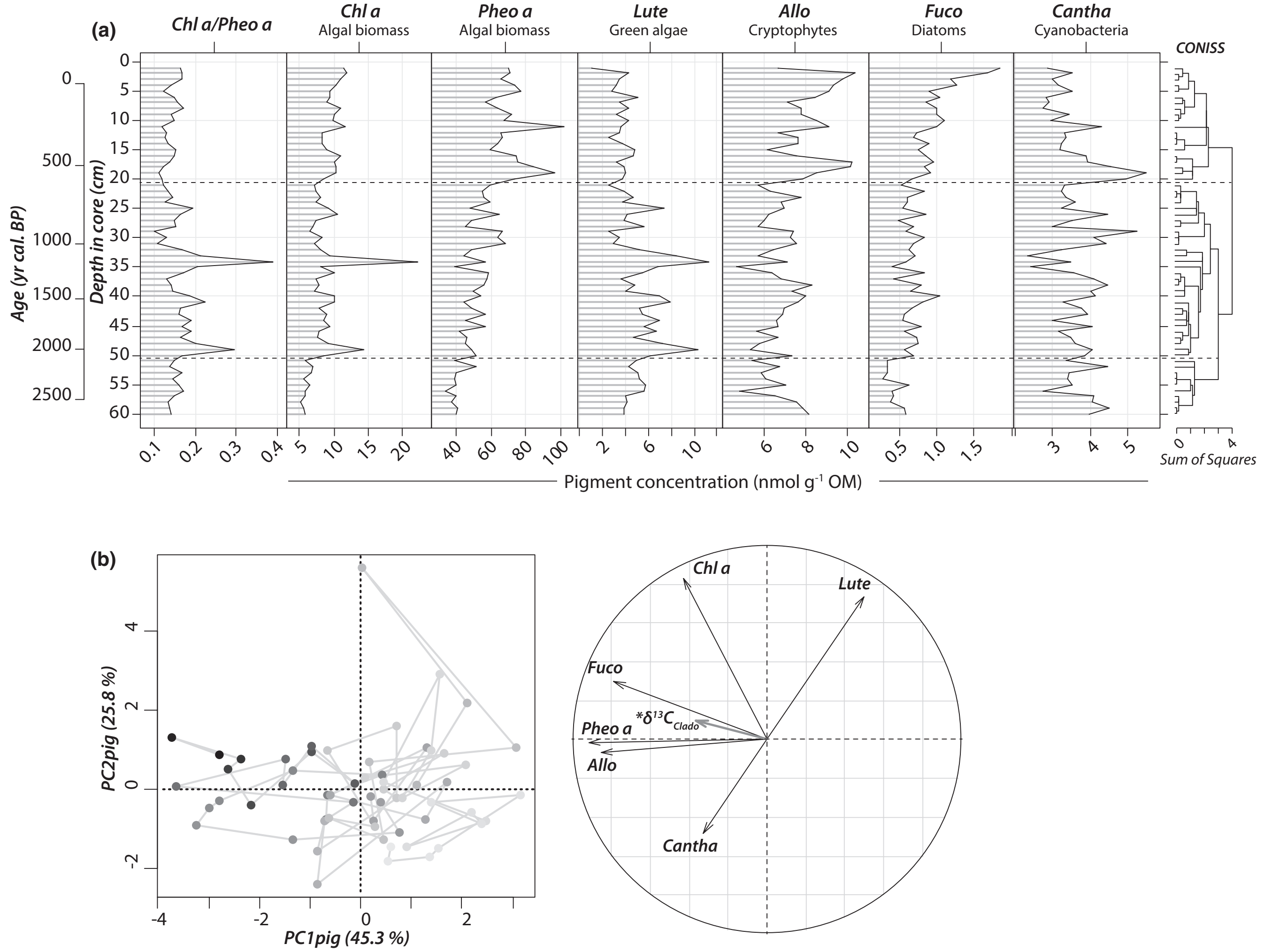

FIGURE 3 (a) The stratigraphic diagram shows temporal trends of investigated sedimentary pigments. Individual pigments are expressed in terms of nmol/g of organic matter (OM). Pigment names are abbreviated as follows (from left to right): chlorophyll *a*: Chl *a*, pheophytin *a*: Pheo *a*; lutein: Lute, alloxanthin: Allo, fucoxanthin: Fuco, canthaxanthin: Cantha. Age and depth scales are both given on y-axes. Dendrogram is based on the pigment data and constructed by hierarchical clustering analysis (Bray–Curtis distance, CONISS linkage method). Horizontal dashed lines indicate significant zones defined by major patterns in sedimentary pigment concentrations. (b) Factorial map of principal component analyses ($PC1_{pig}$ vs. $PC2_{pig}$) performed on sedimentary pigment data. A grey-scale was used to identify the sample age ranging from light-grey colours for the oldest samples, to black symbols for the youngest samples. The $\delta^{13}C_{Clado}$ values have been added to correlation circles as a passive variable (grey arrow). Correlation circle representing variable contributions to the first two PC-axes

$\delta^{13}C_{OM}$ and $\delta^{15}N_{OM}$ values probably reflected the gradual, major changes in the catchment that have occurred over this time period and associated changes in the contribution of organic matter of aquatic versus terrestrial origin to lake sediments (Gu et al., 1996; Meyers & Ishiwatari, 1993). For example, these results showed that autochthonous/aquatic organic matter was relatively more important during warm periods (i.e. from *c*. 2,000 to 600 cal. BP, and from *c*. 1850 AD–present; Figure 2a), suggesting drastic changes in the algal community and an increase in primary productivity. Furthermore, the integrated analyses of sedimentary pigments throughout a late-Holocene sequence allowed us to: (1) identify variables associated with of algal biomass; and (2) detect changes in algal community structure and their associated variables. Overall, the observed temporal changes in algal biomass were closely correlated to those of sedimentological proxies, suggesting potential influences of landscape processes (e.g. nutrient and organic matter run-off) in the catchment area on algal community composition. These observations showed relatively good agreement with known climate trends during the late Holocene in central Sweden (Linderholm & Gunnarson, 2019), and our study therefore suggests an overriding climatic control of the dynamics of sedimentary organic matter and algal communities in lakes.

The highest taxon-specific pigment concentrations were found for cryptophytes (i.e. alloxanthin; Lami et al., 2000), suggesting the predominance of this algal group during the late Holocene (the last 2,600 k years in this study). Then, the onset of the Little Ice Age (*c*. 600 cal. BP) induced declining abundances of almost all other dominant algal groups (i.e. lutein and canthaxanthin as markers for Chlorophyceae and cyanobacteria, respectively), and were not compensated by increases in other algae/pigments (such as diatoms with fucoxanthin marker pigment). This pattern is mainly explained by differences in temperature tolerance/optima of diatoms and cyanobacteria, because diatoms are more cold-adapted (Randsalu-Wendrup et al., 2012) than cyanobacteria that grow well under higher temperatures (Kosten et al., 2012; Paerl & Huisman, 2008). Interestingly, planktonic cryptophytes (alloxanthin), a group adapted to a relatively wide temperature spectrum (see also Padisák, 2009), showed a marked increase (25% on average) during the Little Ice Age, and formed one of the predominant algal groups. As concurrent increases in sediment organic matter of allochthonous/terrestrial origin (as shown by higher C/N ratio and $\delta^{13}C_{OM}$) also were observed, we conjecture that associated terrestrial inputs may have favored planktonic cryptophytes (alloxanthin). Indeed, cryptophytes are known to be mixotrophs that use organic carbon sources, characteristics that give them a competitive advantage under such conditions (Lepistö & Rosenström, 1998). Hence, our results support the view that in boreal lakes, algal production is governed by a delicate balance between direct (i.e. set by temperature optimum) and indirect effects (i.e. effects of terrestrial organic matter on light availability and inputs of nutrients and ions from the catchment) effects of climate change in regulating algal composition in boreal lakes (Havens & Paerl, 2015; Stivrins et al., 2015; Tõnno et al., 2019).

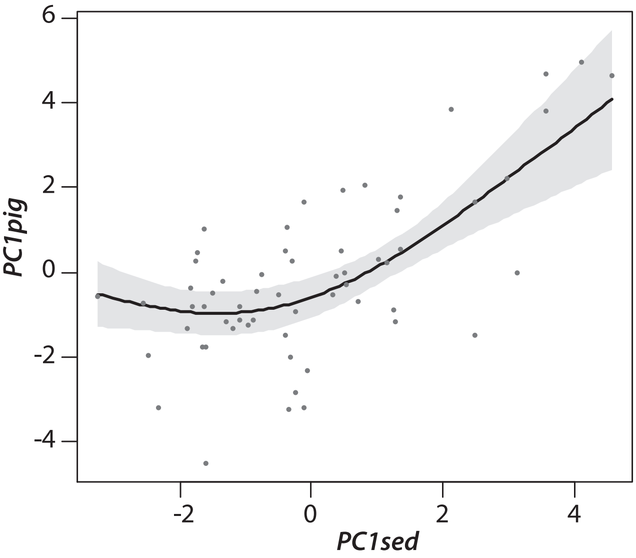

FIGURE 4 Fitted generalised additive model results showing the relationship between first axis scores of the principal component analyses performed on sedimentary pigment ($PC1_{pig}$) and on sedimentological data ($PC1_{sed}$). Grey surface indicates 95% confidence intervals

4.2 | Trends and fluctuations in climate, algal community, and carbon resources for zooplankton

Tracing the origin of organic matter that sustains food webs is an ongoing challenge in aquatic ecology (Tanentzap et al., 2017). Despite the high abundance of terrestrial organic matter in boreal environments, aquatic organic matter (i.e. algae) often is preferentially assimilated by aquatic consumers (Karlsson et al., 2012; Lau et al., 2014), while terrestrial organic matter may contribute very little to the growth of consumers due to its lower nutritive value (Guo et al., 2016; Karlsson et al., 2012; Tanentzap et al., 2017). Recently, novel paleolimnological approaches have provided complementary insights into long-term resource partitioning in aquatic consumers (Belle et al., 2017) and have shown that zooplankton consumers in subarctic lakes are mainly fuelled by aquatic resources (Belle et al., 2019; Rantala et al., 2015). In the present study, $\delta^{13}C$ values of cladoceran resting eggs ($\delta^{13}C_{Clado}$) ranged from −35.2‰ to −30.9‰, also indicating the preferential assimilation of ^{13}C-depleted aquatic basal resources by primary consumers.

Temperature has little effect on trophic fractionation (defined as the difference between a resource and its consumer) in aquatic consumers (Belle et al., 2020; Masclaux & Richoux, 2017). Temporal changes in $\delta^{13}C_{Clado}$ values can therefore mainly be interpreted as an immediate response of changes in basal resources incorporated in zooplankton biomass. Our model linking $\delta^{13}C_{Clado}$ to sediment composition and algal groups was highly significant, emphasing that zooplankton diet is affected by both climate-induced changes in algal biomass ($\delta^{13}C_{OM}$ as a proxy of proportion of algal biomass in sediments) and community composition ($PC1_{pig}$). These results confirm previous findings that the zooplankton diet and basal resources are closely linked, and that climate change is responsible for those changes (Belle et al., 2019; Rantala et al., 2015).

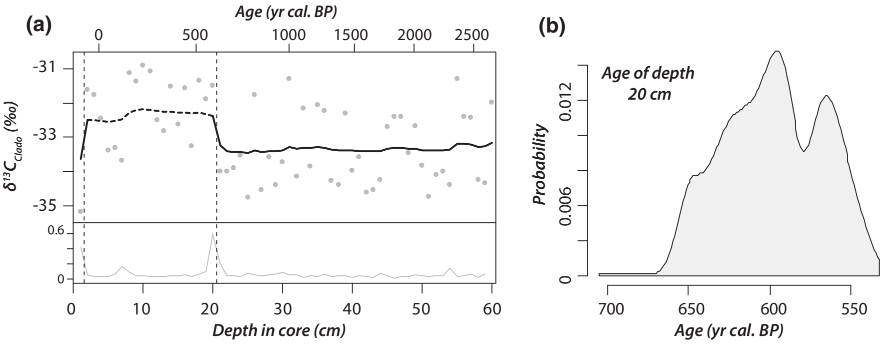

FIGURE 5 (a) Trends in carbon stable isotope composition of cladoceran remains in sediment core STBJ_17_C1 from Lake Stor-Björsjön ($\delta^{13}C_{Clado}$; ‰), and results of change point analysis (considering mean and variance) applied on $\delta^{13}C_{Clado}$ values revealing significant shift occurring at 20 and 1 cm depth in core (vertical dashed lines). In the bottom plot, the black line represents the posterior probabilities of changes. (b) Probability distribution frequencies of age of change observed in $\delta^{13}C_{Clado}$ data

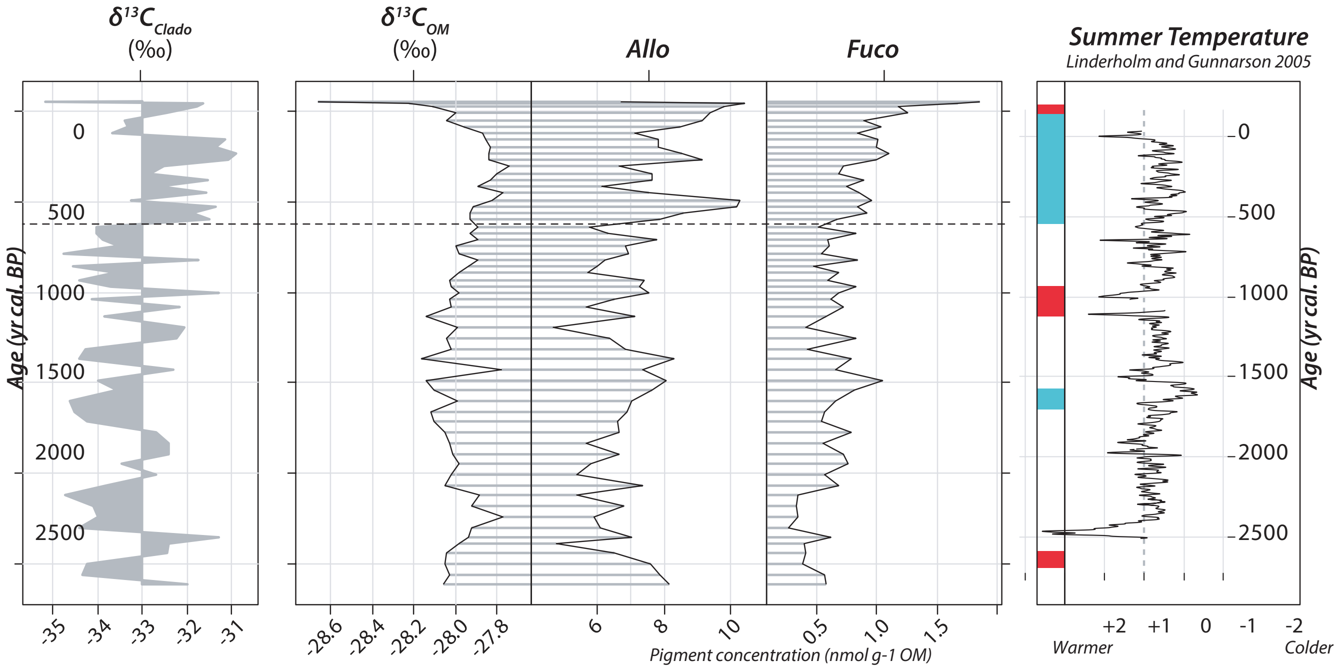

FIGURE 6 Trends in carbon stable isotopic composition of cladoceran remains ($\delta^{13}C_{Clado}$) and associated variables ($\delta^{13}C_{OM}$, alloxanthin: Allo and fucoxanthin: Fuco) identified based on correlations from principal component analyses performed on sediment and pigment data, and reconstructed summer (June–August) temperatures from Jämtland presented as anomalies from the 1961–1990 period (e.g. positive anomalies refers to warm summers periods; Linderholm & Gunnarson, 2005). Horizontal dashed line indicates the most drastic changes in sediment, pigment and Cladocera data

TABLE 2 Summary of statistics for the generalised additive models fitted with a Gaussian distribution to the time-series of $\delta^{13}{}_{Clado}$ values (‰) of cladoceran remains in Lake Stor-Björsjön

Lake Stor-Björsjön	Intercept	*t*-value	*p*	*r*²
$\delta^{13}C_{Clado} \sim s(PC1_{pig}) + s(\delta^{13}C_{OM})$	−33	−258.6	<0.001	0.35
Terms	***edf***	***F***	***p***	
$s(PC1_{pig})$	2.43	5.6	<0.001	
$s(\delta^{13}C_{OM})$	1.16	10.81	<0.001	

Abbreviation: *edf*, effective degrees of freedom.

Our study revealed the influence of both climate trends and fluctuations on algae–zooplankton interactions in Lake Stor-Björsjön. Firstly, major changes in $\delta^{13}C_{Clado}$ patterns matched well with main climate periods during the last 2,600 years, specifically the colder period known as the Little Ice Age. During the Little Ice Age, colder climate impacted (through cooling and changes in terrestrial inputs) algal community structure and biomass by favoring the development of cryptophytes and disadvantaging algal groups better adapted to warmer temperatures, ultimately inducing a large shift in the basal sources contributed to zooplankton. These results therefore suggest the link between past climate change and energy flows to both benthic and pelagic consumers in the long term (Belle et al., 2017, 2018, 2020). Large temporal variability in $\delta^{13}C_{Clado}$ values was also observed during these *homogenous* climatic periods when several groups of successive samples showed similar $\delta^{13}C_{Clado}$ values followed by a marked change in $\delta^{13}C_{Clado}$ values for consecutive samples (with differences up to 4‰). As algae and most zooplankton species have a fast life cycle, short-term climate fluctuations could also be strongly influential on shifts in basal resources for zooplankton. Furthermore, one of the most recent significant changes in $\delta^{13}C_{Clado}$ occurred in the topmost sediment layers, and similar drastic changes can be observed for other sedimentary proxies. However, pigment and sedimentary markers can also be strongly affected by early diagenesis of organic matter (see also Gälman et al., 2009), limiting the reliability of ecological inferences. Nevertheless, several studies have shown that diagenesis might only slightly impact subfossil chitinous remains in lakes (see also Wooller et al., 2004), and $\delta^{13}C_{Clado}$ should thus show only negligible changes over time due to diagenetic alteration. As this period is also the warmest throughout the period covered by the study (Linderholm & Gunnarson, 2019), this result therefore suggests a strong influence of ongoing warming and possible unprecedented ecological change that needs to be confirmed in the future.

5 | CONCLUSION

Our study revealed major effects of both climate trends and fluctuations over the last 2,600 years on algae–zooplankton interactions in a boreal lake. We find that major climate trends, in particular the Little Ice Age, probably induced algal biomass and community composition changes and drastic changes in the origin of organic carbon and carbon assimilation by zooplankton. Interestingly, we also found that temperature fluctuations could contribute to regulate algae–zooplankton interactions. Specifically, our finding that drastic changes in both sedimentary markers and stable isotope composition of zooplankton remains occurred during the most recent period suggests a strong influence of ongoing climate change on algae–zooplankton interactions. The combined use of paleolimnological approaches, long-term monitoring and/or space-for-time-substitution will help reveal changes over large temporal scales, quantify ongoing change, and make predictions for future trajectories (Randsalu-Wendrup et al., 2014).

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DATA AVAILABILITY STATEMENT

Data will be available upon request.

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